

Does spatial arrangement of 3D plants affect light transmission and extinction coefficient within maize crops?

J.-L. Drouet ^{a,*}, J.R. Kiniry ^b

^a INRA/AgroParisTech Environnement et Grandes Cultures, BP 01, F-78850 Thiverval-Grignon, France

^b USDA-ARS Grassland Soil and Water Research Laboratory, 808 E. Blackland Road, Temple, TX 76502, USA

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Abstract

Row spacing effects on light interception and extinction coefficient have been inconsistent for maize (*Zea mays* L.) when calculated with field measurements. To avoid inconsistencies due to variable light conditions and variable leaf canopies, we used a model to describe three-dimensional (3D) shoot structures combined with a model of 3D light transfer. The MODICA model mimics 3D shoot structures of maize plants from digitizations in the field and makes it possible to simulate associated hypothetical canopies by re-arranging plants into different row spacings. All row spacings examined with the model had 10 plants m⁻². By using the light model RIRI, simulations showed the relative importance of development stage and time integration on fraction of light transmitted and on the extinction coefficient. Narrow row spacings consistently had less transmitted light and greater values of extinction coefficient. This modelling tool shows promise to effectively evaluate row spacing to optimize light interception.

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1. Introduction

Altered planting patterns, especially reduced row spacing, have been used to suppress weeds and reduce soil evaporation through increased light interception. Often, intercepted photosynthetically active radiation (IPAR) increases with reduced row spacing when planting density is held constant (Yao and Shaw, 1964; Scarsbrook and Doss, 1973; Sharratt and McWilliams, 2005). This causes the increased light extinction coefficient k of Beer's law reported by Flénet et al. (1996). In contrast, other researchers have reported that row spacing had an inconsistent effect or negligible, nonsignificant effect on light interception (Ottman and Welch, 1989; Westgate et al., 1997; Steglich et al., 2000). Recently, Maddonni et al. (2006) demonstrated that much of these discrepancies probably related to the leaf area index (LAI) attained, which was strongly dependent on planting density. In their study, at high planting densities of 9–12 plants m⁻², the greater LAI greatly reduced the advantage of narrow row spacing for increased intercepted PAR as compared to 3–4.5 plants m⁻².

While taking field measurements of LAI and IPAR (or TPAR, transmitted photosynthetically active radiation) is the most direct method of calculating k , shoot three-dimensional (3D) models such as MODICA (Drouet, 2003) combined with light models offer a method of efficiently determining IPAR with different planting arrangements, different LAI values, and different times of day. The objectives of the present study were to investigate the effect of maize row spacing on TPAR and k using MODICA and the light model RIRI (Sinoquet and Bonhomme, 1992), and to investigate development stage and time integration effects. This provided a more controlled, structured, and definable analysis of TPAR and k than field measurements with much random variation due to clouds, errors in measurements, and variations due to uneven plant stands and uneven leaf distributions.

2. Materials and methods

2.1. Field experiment design

A field experiment was carried out at Grignon (France, 48°N, 2°E), using the maize hybrid Déa. Maize was sown within a field of 100 m × 80 m in early May 1996 at a

* Corresponding author. Tel.: +33 1 30 81 55 68; fax: +33 1 30 81 55 63.
E-mail address: Jean-Louis.Drouet@grignon.inra.fr (J.L. Drouet).

10 plants m^{-2} density (row spacing = 0.8 m; distance between plants within the rows = 0.125 m). Mineral nitrogen was applied at sowing, plants were kept free of water stress by liberal drip irrigation and weeds were removed by hand.

2.2. Description of 3D shoot structure

The 3D geometric structure of the plants was measured using a magnetic FASTRAK 3D-digitizer (Polhemus, 1993; see Sinoquet and Rivet, 1997; Drouet, 2003 for more details). For each plant, the co-ordinates along the axis of the stem and the midrib of each lamina were recorded. The number of points per axis varied from 10 to 30 according to the length and the curvature of the organ. Data were obtained at three stages of development: beginning of stem elongation (days after sowing, DAS = 60 i.e., 60 days after sowing), end of stem elongation (DAS = 74) and end of silking (DAS = 90). At each stage of development, measurements were carried out on one canopy of 20 plants (4 successive rows with 5 successive plants per row). The location of each canopy was randomly chosen within the field at 10 m at least away from field borders. For each stage of development, the canopy characteristics are shown in Table 1. Measurements were taken in the morning to minimize possible wind and water stress effects.

2.3. Reconstruction of 3D shoot structure

The 3D shoot structure of plants was reconstructed using the MODICA model (Drouet, 2003). The curvature of the axes of each plant (stem and leaf midribs) was obtained through digitizing. The shape of the organs was then reproduced after plant dissection. To reduce noise on the 3D structure, digitized coordinates were smoothed according to a cubic spline procedure (Farin, 1997). To describe the shape and the area of the lamina, allometric relationships were established between lamina length and maximal width using a quadratic polynomial (Bonhomme and Varlet-Grancher, 1978). The stem was reconstructed by measuring internode length and diameter. Each plant was geometrically represented by a set of about 1000 triangles and was visualized using the Freeware program *Geomview* (<http://www.geomview.org/>, Fig. 1a, d and g). The

reconstruction was indirectly validated by comparing the length of each measured lamina to the reconstructed one, and by comparing the reconstructed plants to photographs (Drouet, 2003).

2.4. Modelling associated hypothetical canopies

To evaluate the effect of plant arrangement on transmitted PAR and PAR extinction coefficient, we generated two groups of associated hypothetical canopies at each date of measurements from the actual ones. The plant density remained the same (10 plants m^{-2}) whatever the canopy (Table 1). Since no clear effect of plant spatial arrangement was observed on lamina characteristics (i.e., length, width, shape) for a given lamina rank (e.g., Sonohat-Popa, 1997, using hybrid Déa), lamina characteristics were assumed to be the same for a given lamina rank whatever the canopy. In the first group of canopies, the relative spatial plant position (RP) was kept unchanged. In the second group, plants were randomly re-arranged within the canopy, without changing the plant orientation. Within each group, the distance between rows (i.e., row spacing, RS), and consequently the distance between plants within the rows (i.e., plant spacing, PS), was changed from RS = 0.32 m to RS = 1.0 m. Fig. 1 shows two examples of spatial plant re-arrangement: (i) the distance between rows was half that of actual canopies (RS = 0.40 m), so that the distance within the rows was twice that of actual canopies (PS = 0.26 m; Fig. 1b, e and h), (ii) the distance between rows was equal to that within the rows (RS = PS = 0.32 m, square plant re-arrangement; Fig. 1c, f and i). By combining three dates of measurements to eight row spacings per date, we therefore obtained 2 groups of 24 canopies each (Table 1).

2.5. Simulation of transmitted PAR and PAR extinction coefficient (k)

A 3D volume-based version of the light transfer model RIRI (Radiation Interception in Row Intercropping; Sinoquet and Bonhomme, 1992) was used to calculate irradiance distribution inside the canopies. It had previously been validated using radiation measurements for several crops, including maize

Table 1
Dates of measurements (days after sowing) and characteristics of spatial plant arrangement of the actual and associated hypothetical canopies

Date (DAS)	Inter-row distance (m)	Intra-row distance (m)	Spatial plant arrangement	Relative plant position
60, 74, 90	0.32	0.32	A _{32,a} –A _{32,r}	Actual–random
60, 74, 90	0.40	0.26	A _{40,a} –A _{40,r}	Actual–random
60, 74, 90	0.50	0.21	A _{50,a} –A _{50,r}	Actual–random
60, 74, 90	0.60	0.17	A _{60,a} –A _{60,r}	Actual–random
60, 74, 90	0.70	0.15	A _{70,a} –A _{70,r}	Actual–random
60, 74, 90	0.80	0.13	A _{80,a} (actual)	Actual
60, 74, 90	0.80	0.13	A _{80,r}	Random
60, 74, 90	0.90	0.12	A _{90,a} –A _{90,r}	Actual–random
60, 74, 90	1.00	0.10	A _{100,a} –A _{100,r}	Actual–random

DAS = 60 corresponded to an average of 6 ligulated leaves, 13 visible leaves and beginning of stem elongation. DAS = 74 corresponded to an average of 14 ligulated leaves, all visible leaves and end of stem elongation. DAS = 90 corresponded to end of silking. The date of 50% silking was DAS = 84. For each spatial arrangement, estimated vegetation area index (sum of lamina, sheath and stem area indices) were 2.8 at DAS = 60, 4.6 at DAS = 74 and 5.7 at DAS = 90. Likewise, for each spatial arrangement, lamina area index were 2.6 at DAS = 60, 3.5 at DAS = 74 and 4.1 at DAS = 90.

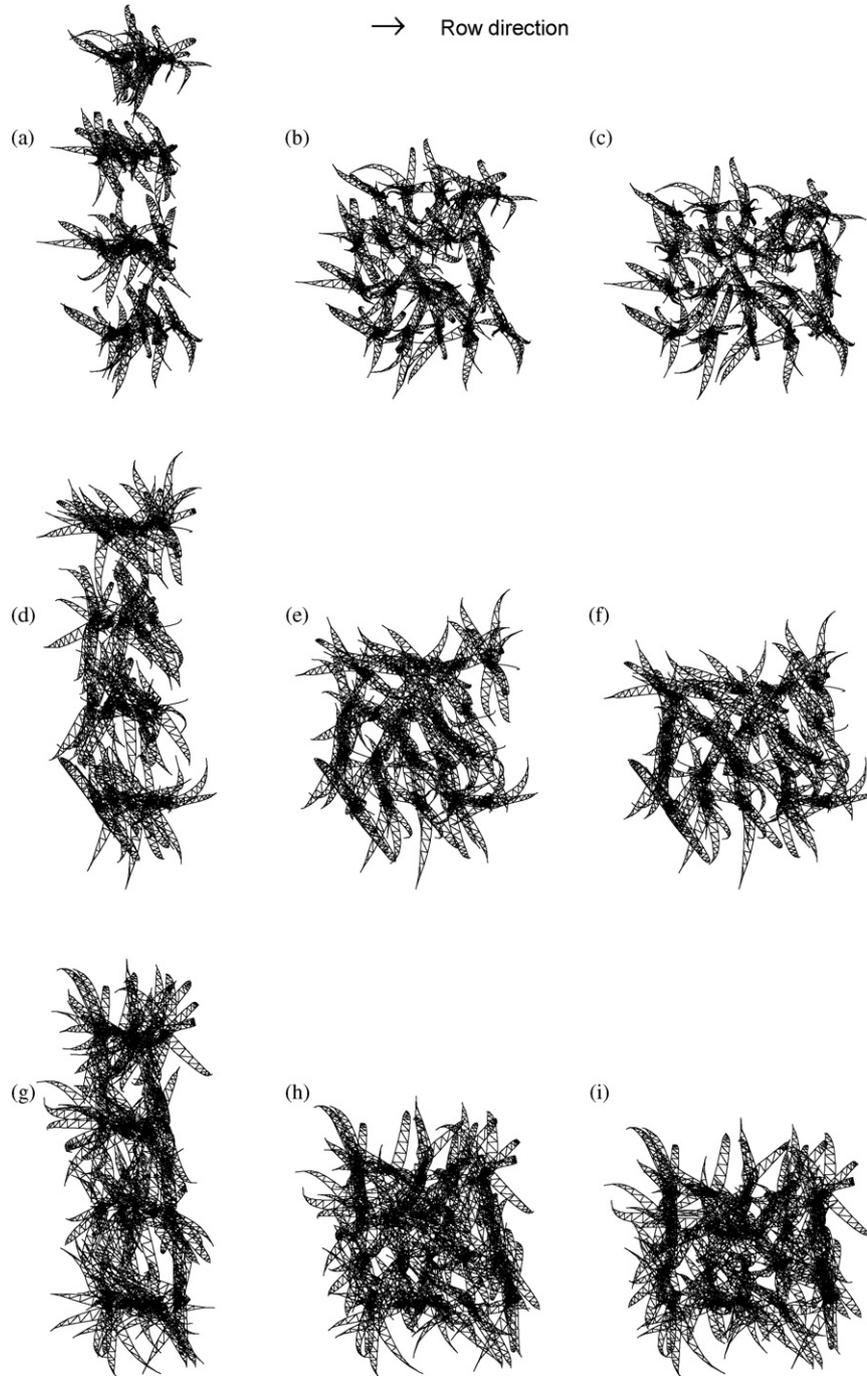


Fig. 1. Vertical views of the three-dimensional (3D) shoot structure of maize canopies at three development stages (days after sowing, DAS): DAS = 60 (a, b and c), DAS = 74 (d, e and f) and DAS = 90 (g, h and i). Shown canopies were reconstructed for three spatial plant arrangements according to the distance between rows (row spacing, RS) and between plants within the rows (plant spacing, PS): RS = 0.80 m and PS = 0.13 m (a, d and g), RS = 0.40 m and PS = 0.26 m (b, e and h), RS = 0.32 m and PS = 0.32 m (square plant re-arrangement; c, f and i). The plant density (10 plants m^{-2}), as well as the relative spatial position of plants, were kept unchanged.

(Sinoquet and Bonhomme, 1989, 1992). This model is based on the turbid-medium analogy. In this way, the canopy structure is abstracted by an array of 3D cells (0.1 m wide) which may contain foliage or be empty. For each canopy cell, the lamina area density and the lamina angle distribution are calculated from the area and the orientation of the triangles (Fig. 1) using a program developed by Andrieu (INRA, Thiverval-Grignon, France, pers. comm.). The model deals with direct and diffuse

incident radiation and scattered radiation, which makes it possible to obtain, within each cell of the canopy, the instantaneous lamina irradiance for sunlit and shaded lamina area, as well as the instantaneous transmitted irradiance to each square (0.1 m wide) of soil (for more details, see Sinoquet and Bonhomme, 1992). Foliage reflectance and transmittance were set equal to 0.07 and land soil reflectance to 0.10 (Drouet, 1998).

For each canopy, simulations were performed in the photosynthetically active radiation waveband (PAR, 400–700 nm) from six values of daily global radiation (Table 2). Instantaneous values of direct radiation and diffuse radiation were simulated for each time step (0.1 h) from the daily ratio between diffuse radiation and global radiation (Table 2; Spitters et al., 1986) and sinusoidal curves (Perrin de Brichambault and Vauge, 1982). A shift was assumed at each time step between a fully clear sky and a fully overcast sky (i.e., only diffuse radiation) according to the daily ratio between diffuse radiation

Table 2

Characteristics of the daily incident radiation simulated for the six values of daily global radiation used in computations of light transmission

Daily global radiation (MJ m ⁻²)	Daily ratio diffuse radiation/global radiation
5	1.00
10	0.89
15	0.79
20	0.61
25	0.43
30	0.25

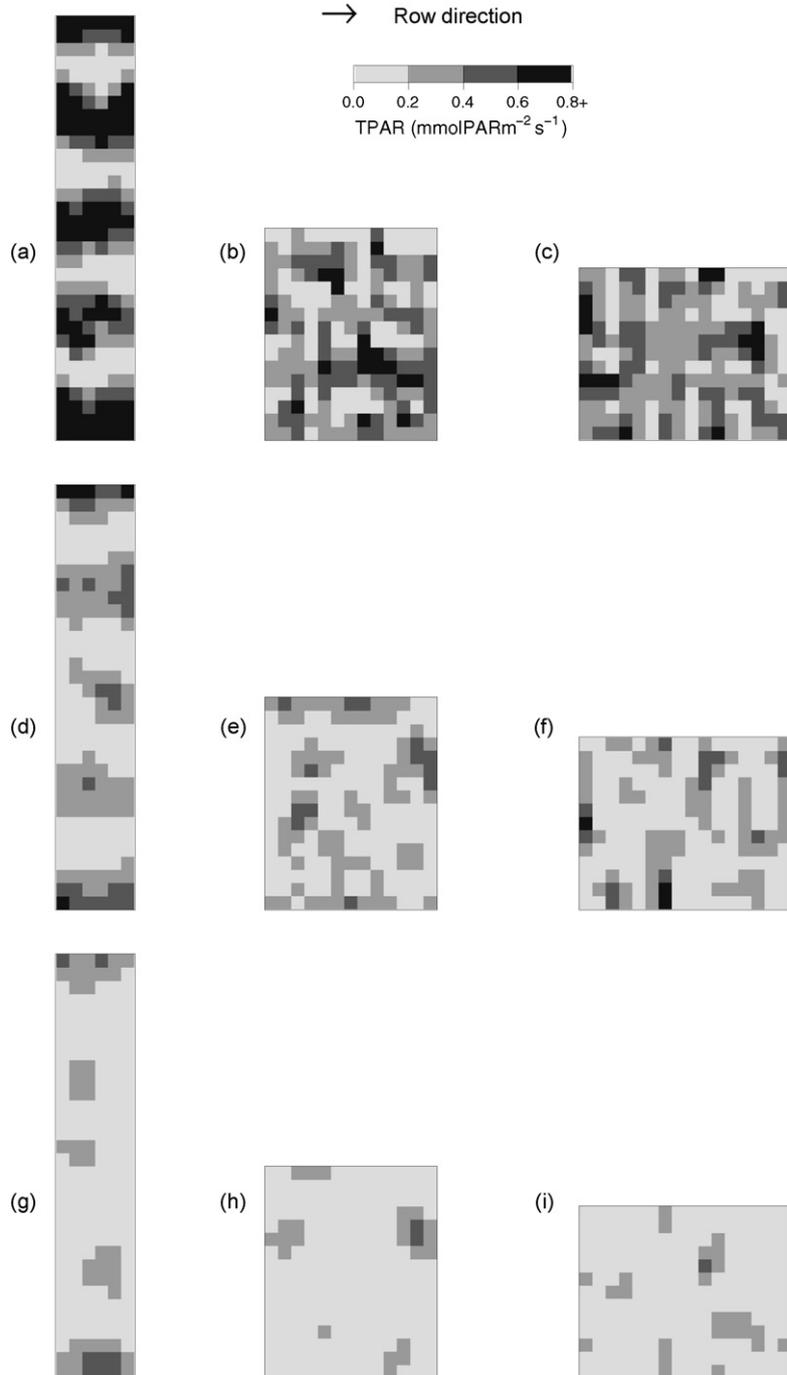


Fig. 2. Daily average transmitted photosynthetically active radiation (TPAR) by the nine canopies presented Fig. 1, simulated for a sunny day (25 MJ m⁻²) and by soil squares of 0.10 × 0.10 m².

and global radiation (Allirand, INRA, Thiverval-Grignon, France, pers. comm.; see Drouet, 1998 for more details). The PAR extinction coefficient k was calculated from transmitted (TPAR) and incoming (PAR) values by

$$\frac{\text{TPAR}}{\text{PAR}} = \exp(-k \times \text{LAI})$$

which is equivalent to

$$k = (-1/\text{LAI}) \times \ln (\text{TPAR}/\text{PAR})$$

For each canopy, TPAR was integrated from the instantaneous values: (i) daily time integration (Fig. 2) and (ii) time integration of 2 h around solar noon (i.e., between 1100 h and 1300 h).

2.6. Data analysis

Data were analyzed with regression tests, mean comparisons using the Student's test, graphs using the S-PLUS computer package (S-PLUS, 1996).

3. Results and discussion

3.1. Effect of development stage and row spacing on daily TPAR fraction and extinction coefficient (k)

According to development stage (DAS) and row spacing (RS), means of daily TPAR fraction varied between 0.09 and 0.53 (Fig. 3a and Table 3). Values simulated for RS = 0.8 m at DAS = 60 were consistent with data measured by Varlet-Grancher et al. (1989). Whatever the spatial plant arrangement, daily TPAR fraction decreased 40–50% from DAS = 60 to

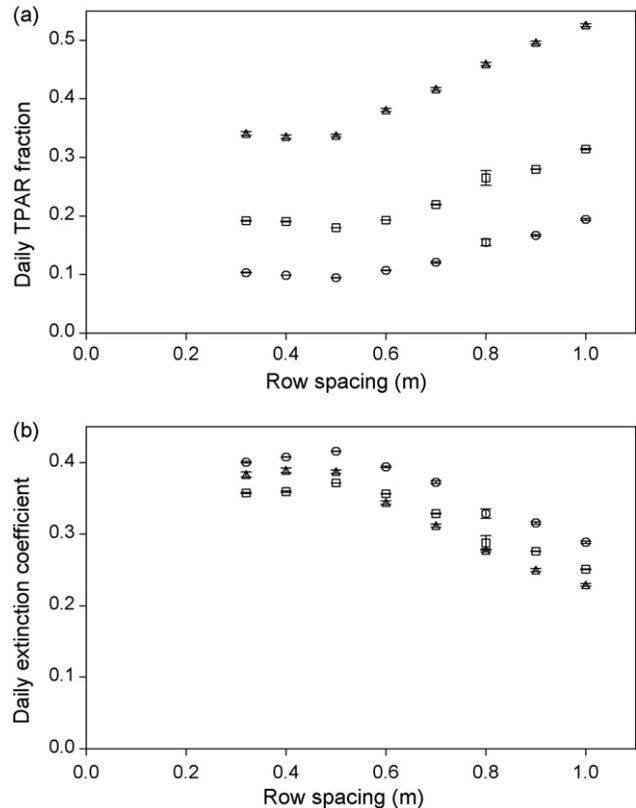


Fig. 3. Daily transmitted photosynthetically active radiation (TPAR) fraction (a) and daily extinction coefficient (b) values simulated for the actual and the associated hypothetical canopies obtained without changing the actual relative spatial position of plants (see Table 1). Simulation results are shown for three development stages (days after sowing): DAS = 60 (Δ), DAS = 74 (\square) and DAS = 90 (\circ). Mean and standard deviation were calculated for the six daily incident radiation characteristics shown in Table 2.

Table 3
Mean and standard deviation of daily TPAR fraction and daily extinction coefficient (k) calculated from six daily incident radiation characteristics (see Table 2) at each development stage (days after sowing) and for each spatial plant arrangement (see Table 1)

Spatial plant arrangement	Daily TPAR fraction			Daily extinction coefficient (k)		
	60 ^a	74 ^a	90 ^a	60 ^a	74 ^a	90 ^a
A _{32,a}	0.341 ± 0.003 α ,F,a	0.192 ± 0.001 β ,DE,a	0.103 ± 0.001 γ ,F,b	0.383 ± 0.003 β ,A,a	0.357 ± 0.001 γ ,BC,b	0.400 ± 0.001 α ,C,a
A _{32,r}	0.344 ± 0.003 a	0.173 ± 0.001 b	0.111 ± 0.001 a	0.381 ± 0.003 a	0.381 ± 0.001 a	0.387 ± 0.002 b
A _{40,a}	0.336 ± 0.003 α ,F,a	0.190 ± 0.001 β ,E,a	0.099 ± 0.000 γ ,F,a	0.389 ± 0.003 β ,A,a	0.359 ± 0.001 γ ,B,b	0.408 ± 0.000 α ,B,b
A _{40,r}	0.339 ± 0.003 a	0.171 ± 0.000 b	0.095 ± 0.000 b	0.385 ± 0.003 a	0.383 ± 0.001 a	0.415 ± 0.001 a
A _{50,a}	0.337 ± 0.002 α ,F,b	0.180 ± 0.000 β ,F,b	0.094 ± 0.000 γ ,G,a	0.387 ± 0.002 β ,A,a	0.371 ± 0.000 γ ,A,a	0.416 ± 0.000 α ,A,b
A _{50,r}	0.349 ± 0.003 a	0.182 ± 0.000 a	0.091 ± 0.001 b	0.375 ± 0.003 b	0.369 ± 0.001 b	0.422 ± 0.002 a
A _{60,a}	0.381 ± 0.003 α ,E,b	0.193 ± 0.000 β ,D,b	0.107 ± 0.001 γ ,E,a	0.344 ± 0.002 γ ,B,a	0.356 ± 0.000 β ,C,a	0.394 ± 0.001 α ,D,b
A _{60,r}	0.390 ± 0.003 a	0.211 ± 0.001 a	0.097 ± 0.001 b	0.336 ± 0.003 b	0.337 ± 0.001 b	0.411 ± 0.001 a
A _{70,a}	0.417 ± 0.003 α ,D,a	0.219 ± 0.000 β ,C,a	0.121 ± 0.001 γ ,D,b	0.312 ± 0.002 γ ,C,a	0.329 ± 0.000 β ,D,a	0.372 ± 0.002 α ,E,a
A _{70,r}	0.414 ± 0.002 a	0.220 ± 0.002 a	0.125 ± 0.001 a	0.315 ± 0.002 a	0.328 ± 0.002 a	0.366 ± 0.001 b
A _{80,a} (actual)	0.459 ± 0.003 α ,C,a	0.265 ± 0.013 β ,B,a	0.155 ± 0.006 γ ,C,a	0.277 ± 0.002 β ,D,a	0.288 ± 0.010 β ,E,a	0.329 ± 0.006 α ,F,a
A _{80,r}	0.455 ± 0.002 a	0.265 ± 0.016 a	0.147 ± 0.007 a	0.281 ± 0.002 a	0.288 ± 0.013 a	0.338 ± 0.008 a
A _{90,a}	0.496 ± 0.003 α ,B,a	0.280 ± 0.000 β ,B,a	0.167 ± 0.001 γ ,B,a	0.250 ± 0.002 γ ,E,b	0.276 ± 0.000 β ,E,a	0.316 ± 0.002 α ,G,b
A _{90,r}	0.484 ± 0.002 b	0.279 ± 0.001 a	0.150 ± 0.000 b	0.258 ± 0.002 a	0.276 ± 0.001 a	0.334 ± 0.000 a
A _{100,a}	0.526 ± 0.003 α ,A,a	0.314 ± 0.001 β ,A,b	0.194 ± 0.002 γ ,A,a	0.229 ± 0.002 γ ,F,a	0.251 ± 0.001 β ,F,a	0.289 ± 0.001 α ,H,b
A _{100,r}	0.529 ± 0.002 a	0.323 ± 0.001 a	0.182 ± 0.000 b	0.227 ± 0.002 a	0.245 ± 0.001 b	0.300 ± 0.000 a

For each line and for each variable (daily TPAR fraction and daily k), means with the same symbol (α , β and γ) were not significantly different at a p -value < 0.001 (mean comparisons between development stages). For each column, means with the same upper-case letter (A, B, C, D, E, F, G and H) were not significantly different at a p -value < 0.001 (mean comparisons between row spacings at a given relative plant position: actual or random). For each column too, means with the same lower-case letter (a and b) were not significantly different at a p -value < 0.001 (mean comparisons between relative spatial plant positions at a given row spacing).

^a Date (DAS).

DAS = 74 and decreased 70% from DAS = 60 to DAS = 90. Standard deviations simulated from a large range of daily incident radiation (Table 2) remained low whatever the development stage and the spatial plant arrangement.

For a given development stage and for any actual relative spatial plant position, daily TPAR fraction slightly decreased when RS increased from 0.32 m (square plant re-arrangement) to 0.5 m. It significantly (p -value < 0.001) increased when RS increased from 0.5 m to 1.0 m whatever the development stage (Fig. 3a and Table 3). That result was consistent with those from several authors (e.g., Yao and Shaw, 1964; Scarsbrook and Doss, 1973; Sharratt and McWilliams, 2005) who found that IPAR increased with reduced row spacing when planting density was held constant. But our results differed from those reported by Maddonni et al. (2001) who found no large difference between values of daily intercepted PAR simulated for maize at RS = 0.35 m and RS = 0.7 m. They also contrasted with results from other researchers who reported that row spacing had an inconsistent or negligible effect on light interception (e.g., Ottman and Welch, 1989; Westgate et al., 1997; Steglich et al., 2000).

According to development stage and row spacing, means of simulated daily k values varied between 0.23 and 0.42 (Fig. 3b and Table 3). Whatever the spatial plant arrangement, simulated daily k values were significantly higher (p -value < 0.001) at DAS = 90 than at DAS = 60 and DAS = 74. They were not so clearly different between the two previous stages (DAS = 60 and DAS = 74). Simulated daily k values were smaller than several values found in the literature (e.g., Flénet et al., 1996; Maddonni et al., 2001; Sinclair, 2006). Part of the difference may be explained by whether TPAR is simulated from the actual area of laminae or the projected area of laminae. In the latter case which corresponds to our case, k values can be much smaller. Another explanation may be the difference of lamina angle between literature results and ours. In our experiment, lamina insertion angle was around 64° in average for lamina ranks between 6 and 13, especially 66° in average for larger leaves i.e., lamina ranks between 10 and 12 (unpublished results). Such erected laminae can provide smaller k values than more horizontal laminae, i.e., angle around 30 – 40° (Varlet-Grancher et al., 1989; Sinclair, 2006). Effects of latitude (i.e., sun angle) may add to the previous factors of variations.

For a given development stage and for any actual relative spatial plant position, daily k slightly increased when RS increased from 0.32 m (square plant re-arrangement) to 0.5 m. It significantly (p -value < 0.001) decreased when RS increased from 0.5 m to 1.0 m whatever the development stage (Fig. 3b and Table 3). That result is consistent with that reported by Flénet et al. (1996).

3.2. Effect of relative spatial plant position (actual or random) on daily TPAR fraction and extinction coefficient (k)

At each development stage and for each row spacing, daily TPAR fraction (Fig. 4a) did not differ between the relative spatial plant positions (actual or random). Among the 24

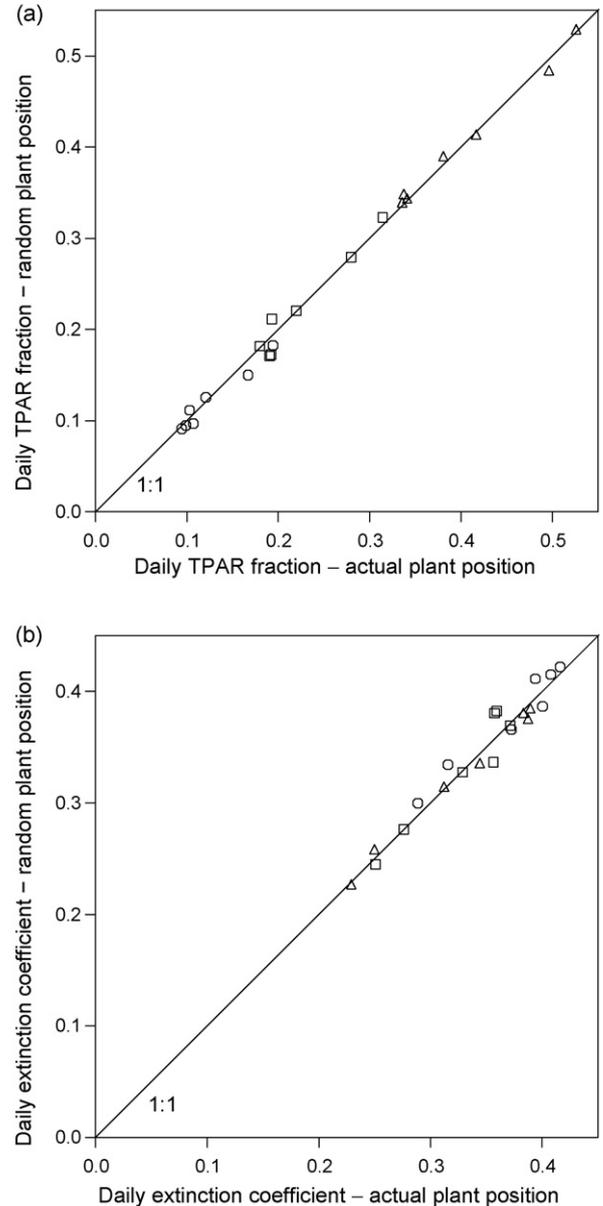


Fig. 4. Daily transmitted photosynthetically active radiation (TPAR) fraction (a) and daily extinction coefficient (b) values simulated for canopies obtained without changing the relative spatial position of plants compared to values simulated for the associated hypothetical canopies obtained by randomly re-arranging the relative spatial position of plants (see Table 1). Simulation results are shown for three development stages (days after sowing): DAS = 60 (Δ), DAS = 74 (\square) and DAS = 90 (\circ). In order to clarify the figure, only mean values calculated for the six daily incident radiation characteristics shown in Table 2 are represented. Standard deviations for values simulated for the associated hypothetical canopies obtained without changing the relative spatial position of plants are presented in Fig. 3. Linear regression for TPAR fraction (a) $y = 1.012 \pm 0.006x - 0.005 \pm 0.002$ ($R^2 = 0.99$, p -value < 0.001) and for extinction coefficient (b): $y = 0.988 \pm 0.017x + 0.006 \pm 0.006$ ($R^2 = 0.96$, p -value < 0.001).

studied cases (3 development stages \times 8 row spacings), means were not significantly different (p -value < 0.001) between the actual and random relative spatial plant positions in nine cases (Table 3). They were significantly higher (resp. lower) for the actual positions in eight (resp. seven) cases (Table 3).

Simulations also showed no effect of relative spatial plant positions on daily k (Fig. 4b). Means of daily k were not significantly different (p -value < 0.001) between the actual and random relative spatial plant positions in nine cases. They were significantly higher (resp. lower) for the actual positions in seven (resp. eight) cases (Table 3).

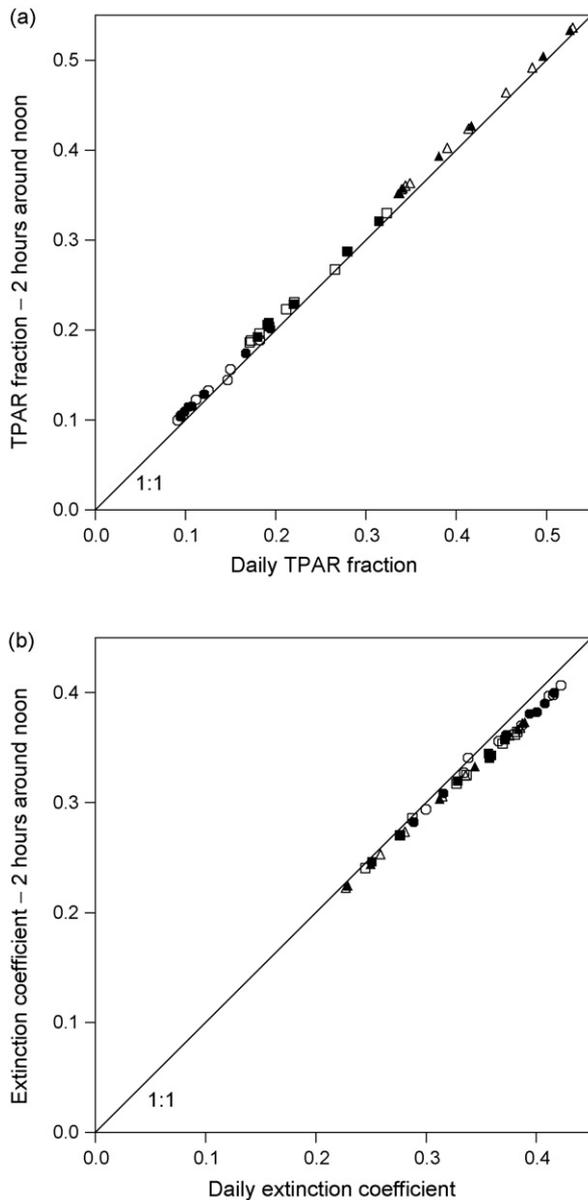


Fig. 5. Transmitted photosynthetically active radiation (TPAR) fraction (a) and extinction coefficient (b) values simulated for a daily time integration compared to values simulated for a time integration of 2 h around solar noon. Simulation results are shown for canopies obtained without changing the actual relative spatial position of plants (empty symbols) and for the associated canopies obtained by randomly re-arranging the relative spatial position of plants (full symbols). Simulation results are shown for three development stages (days after sowing): DAS = 60 (\triangle , \blacktriangle), DAS = 74 (\square , \blacksquare) and DAS = 90 (\circ , \bullet). In order to clarify the figure, only mean values calculated for the six daily incident radiation characteristics shown in Table 2 are represented. Standard deviations for daily simulations are presented in Fig. 3. Linear regression for TPAR fraction (a) $y = 1.003 \pm 0.006x + 0.009 \pm 0.002$ ($R^2 = 0.99$, p -value < 0.001) and for extinction coefficient (b): $y = 0.915 \pm 0.010x + 0.018 \pm 0.004$ ($R^2 = 0.99$, p -value < 0.001).

For a given development stage and a given row spacing, each plant can be assumed to play a similar role on daily TPAR fraction and k (Fig. 3a and b). This was in accordance with results from Drouet et al. (1999) who showed from light simulations that leaf azimuthal distribution, including actual and random ones, had no significant effect on light absorbed daily by maize canopies.

3.3. Effect of time integration on TPAR fraction and extinction coefficient (k)

Simulations indicated that the time integration (daily or 2 h around solar noon) had no effect on integrated values of TPAR fraction (Fig. 5a). That result was consistent with experimental observations made on maize (Tollenaar and Bruuselman, 1988; Daughtry et al., 1992), simulations on forest canopies (Ter-Mikaelian et al., 1997), and theoretical calculations (Goward and Huemmrich, 1992). But the time integration had a larger effect on integrated values of k : they were 8% higher when integrated daily than when integrated on 2 h around solar noon (Fig. 5b). This was smaller than the values reported in the literature: 3.5-fold smaller than that of Flénet et al. (1996) and threefold smaller than that of Sinclair (2006). This discrepancy may be explained by the difference of time integration between our study (2 h around noon) and that of those literature studies (measurements at noon). Moreover, measurements may greatly vary according to sky cloudiness, especially in the case of instantaneous measurements (e.g., at solar noon). Canopy structure (LAI, angular leaf distribution, canopy heterogeneity) may also involve discrepancies between daily and 2-h integrated values of k .

4. Conclusion

This study described a new approach to investigating effects of planting patterns on the proportion of light intercepted. Simulations showed that crop development stage and row spacing, especially when row spacing increased from 0.5 m to 1.0 m, had a strong effect on daily TPAR fraction and a weak effect on daily extinction coefficient k . The relative spatial position of plants (actual or random) within the canopy had no clear effect on daily TPAR fraction and daily k . The time integration for simulations affected the integrated values of k .

This technique, associating a 3D model of shoot geometry with 3D light model, helps overcome some of the difficulties of field studies, with variable light conditions, uneven plant stands, and errors in measurement. Results of this study illustrated the complexities of relating both light interception and light extinction coefficient to planting pattern. This technique promises to be a valuable tool for future work on other planting arrangements and with other crops, helping optimize both planting density and row spacing for the most efficient light interception.

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