Canopy structure, light interception, and photosynthetic characteristics under different narrow-wide planting patterns in maize at silking stage

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Abstract

Planting pattern affects canopy structure of crops and influences other physiological characteristics such as light interception and radiation use efficiency. In the current paper, the effects of planting patterns on the canopy structure, light interception, and photosynthetic characteristics at silking stage of two maize (*Zea mays* L.) cultivars (Beiyu288 and Xianyu 335) were examined in three planting patterns narrow–wide rows of (1) 30 cm + 170 cm (P1, 6.4 plants m^{-2}), and (2) 40 cm+90 cm (P2, 6.4 plants m^{-2}), and uniform row of 65 cm (control, *i.e.* CK, 6.4 plants m^{-2}). The ratio of leaves perpendicular to rows was highest in P1 and the leaf orientation value in P1 was constant and slightly lower in P2 compared with that in CK. Although a decrease in the total intercepted photosynthetically active radiation (IPAR) of P1 was found in the two cultivars, more incoming PAR was detected at the middle-low canopy strata of P1. The apparent quantum yield and the net photosynthesis rate (P_N) in P1 and P2 were significantly higher than those in CK. The P_N and stomatal conductance (g_s) values in P1 were significantly higher than those in CK, and the intercellular CO_2 concentration decreased with an increase in P_N. These results indicated that narrow-wide row planting patterns improved the canopy structure, allowed more IPAR to reach the middle–low strata of the canopy, and enhanced the leaf photosynthetic characteristics of maize crops at silking stage compared with CK.

Additional key words: intercellular CO_2 concentration; net photosynthesis rate; stomatal conductance; *Zea mays* L.

Resumen

Estructura de la cubierta vegetal, intercepción de luz y características fotosintéticas en el cultivo de maíz en floración bajo diferentes patrones espaciales de las plantas

El patrón espacial de las plantas puede afectar a la estructura de la cubierta vegetal de los cultivos y a diversas características fisiológicas. En este trabajo se analizó el efecto del patrón espacial sobre la estructura del cultivo, la intercepción de luz, y la capacidad fotosintética en dos híbridos de maíz (Beiyu288 y Xianyu335). Estos se sembraron siguiendo tres patrones espaciales: en hileras estrechas y anchas de 30 cm+170 cm (P1), 40 cm+90 cm (P2) y en hileras a 65 cm (CK), con una densidad de siembra de 6,4 plantas m^{-2}. El patrón espacial de las plantas no afectó al índice del área foliar, pero si afectó a su distribución espacial: en P1 se registró la mayor proporción de hojas perpendiculares a la hilera de siembra y las hojas presentaron una angulación uniforme con respecto al tallo; en P2 presentaron menor ángulo que en CK. La captura de luz resultó menor en P1, y una mayor cantidad de luz alcanzó a los estratos inferiores de la cubierta vegetal. Con todos los patrones espaciales, al incrementar la P_N se redujeron tanto la tasa de fotosíntesis neta (P_N) como la conductancia estomática (g_s) y la concentración de CO_2 intracelular (C_i). Sin embargo, la P_N y la g_s fueron mayores en P1 que en CK. Los resultados indican que en el momento de plena cobertura del maíz (cercano a floración femenina), el patrón espacial en hileras anchas-estrechas mejora la estructura de la cubierta, favoreciendo la entrada de luz hacia la parte media e inferior de la cubierta, lo que incrementa la capacidad fotosintética de dichos estratos.

Palabras clave adicionales: concentración de CO_2 intracelular; conductancia estomática; tasa de fotosíntesis neta; *Zea mays* L.

Abbreviations used: AQY (apparent quantum yield); Ci (intercellular CO_2 concentration); F (the fraction of incident photosynthetically active radiation intercepted by crops); g_s (stomatal conductance); IPAR (intercepted photosynthetically active radiation); K (extinction coefficient); LA (leaf angle); LAI (leaf area index); LOV (leaf orientation value); PAR (photosynthetically active radiation); P_N (net photosynthesis rate).

Introduction

A detailed analysis of crop canopy structure was first introduced by Monsi and Saeki (1953) and thereafter became the focus of agronomists. It refers to the amount and spatial distribution of plant organs above the ground, and involves three major features: plant geometry, quantity, and spatial distribution of leaves. The leaf area index (LAI), leaf angle (LA), leaf orientation, and extinction coefficient (K) are the main parameters that characterize the crop canopy structure. These parameters are affected by factors such as cultivar, row spacing, and planting density (Andrade *et al.*, 2002; Elmore *et al.*, 2005). Both plant density and row spacing determine the planting pattern of crops. When crops are cultivared under a more square planting pattern, improved canopy structure, light availability, and proper ventilation, may benefit crop growth (Maddonni, 2001a).

The fraction of incident photosynthetically active radiation intercepted by crops (F) is affected by the canopy structure, which in turn depends on the LAI and crop geometry. F changes continuously from the emergence to harvesting of crops, these changes in F depend on K, which is a constant that that describes light attenuation in the canopy as a function of LAI (Flenet *et al.*, 1996). A number of papers have reported the effect of row spacing (Flenet *et al.*, 1996; Widdicombe and Thelen, 2002), LAI (Kiniry *et al.*, 2004), and plant density (Watiki *et al.*, 1993) on light interception. However, less attention has been paid to planting pattern.

Photosynthesis is the basis of crop growth and grain production. An improvement in photosynthetic performance is important in increasing maize yield. Light distribution in the canopy is the most important factor that affects maize photosynthesis. Photosynthesis varies with the light intensity (Xu *et al.*, 1997). In the range of low irradiances, net photosynthesis rate (P_N) increases with increasing irradiances. When both photosynthesis rate and irradiance are represented in the same units (mol m^{-2} s^{-1}), the slope of the photosynthesis-light response at low irradiances is the apparent quantum yield (AQY) of photosynthesis. These linear responses occur at the leaf expansion stage when canopy LAI and mutual plant shading are reduced (Trouwborst *et al.*, 2010). Irradiance decreases exponentially with canopy depth and the leaves gradually acclimate to this response

but there is a decline in photosynthetic capability with canopy depth (Xu *et al.*, 1997; Boonman *et al.*, 2006).Hence, the response of photosynthetic capacity of maize leaves to the different light environments of the contrasting planting patterns could add valuable information to understand changes of radiation use efficiency (Maddonni *et al.*, 2006).

In the present study, three planting patterns were used to establish different canopy structures. The objective of this work were to (i) determine changes of canopy spatial structure, (ii) analyze the light interception at different heights within fully developed canopies, and (iii) identify changes of the photosynthetic characters of maize leaf response to light.

Material and methods

Field design

The study was conducted at the Experimental Station (44°12′ N, 125°33′ E), of the Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences in Dehui County, Jilin Province, China, during the growing season from May to October in both 2009 and 2010. The three planting patterns (Fig. 1) were (1) P1, "30+170" narrow-wide row planting (*i.e.,* the narrow row was 30 cm, the wide row was 170 cm, 6.4 plants m^{-2}, with rotation in the wide row region in the next year); (2) P2, "40+90"narrow-wide row planting (*i.e.,* the narrow row was 40 cm, the wide row was 90 cm, 6.4 plants m^{-2}, a subsoiling district is created in the wider row region, with cultivate in the subsoiling district in the next year); and (3) CK single line with a row spacing of 0.65 m (6.4 plants m^{-2}). Two maize cultivars: Beiyu 288 (maximum height 275.6 cm) and Xianyu 335 (maximum height 304.6 cm), were sown at early May in a black clay soil. Crops were harvested at the end of September. Two seeds per hole were planted and thinned after seedling emergence. Total 900 kg h^{-2} (500 kg ha^{-1} when planting; 400 kg ha^{-1} at jointing stage) fertilization (N, P, K) was applied. The experimental design was a big plot contrast (single plot area ≥667 m^2) in 2009 and a randomly complete block design with four replicates (single block area 10 m×10 m = 100 m^2) in 2010. The crops were conducted free from pest, weeds, and diseases.
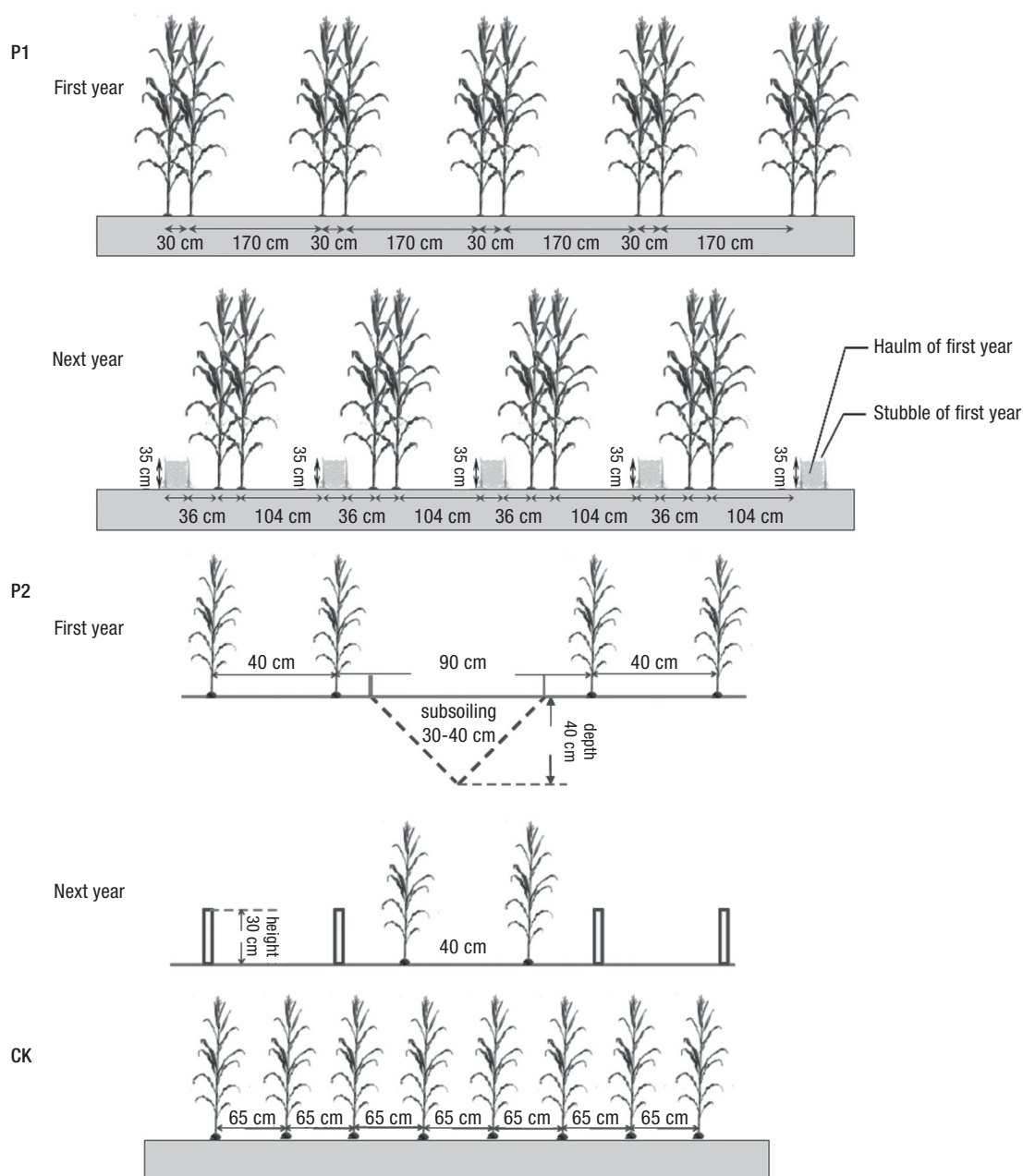
Figure 1. A schematic diagram showing P1, P2 and CK (30+170, 40+90 and 65, respectively) planting patterns at a density of 6.4 plants m^{-2}.

Measurement and computation

Leaf azimuth distribution

After silking, the azimuths of five successive plants were measured using Maddonni's method (Maddonni *et al.*, 2001b) with a plastic circular plate divided evenly into 16 sectors (22°30′ per sector). The 0°-180° line diameter was always oriented on the row direction with the 0° axis toward the east; the projection of the leaves within a sector was recorded. When the leaf projection was located between 67°30′ and 112°30′ or 247°30′ and 292°30′, the leaf was considered perpendicular to the row orientation. In contrast, it was assumed parallel to the rows when the value was within the 337°30′-22°30′ or 157°30′-202°30′.

Calculation of LAI and LOV

LAI was calculated using the following equations:

LAI= *leaf area per plant × plant population density* [1]

where *leaf area per plant* = Σ *leaf area* and *leaf area* = *lamina length × maximum width × 0.75* (Montgomery, 1911).

The leaf orientation value (LOV) was calculated using the following equation (Pepper and Pearce, 1977):

$$LOV = \sum_{i=1}^{n} [\theta(l_1 / l)]i / n \qquad [2]$$

where θ is the leaf angle determined by the leaf and the horizontal plate, n is the number of the leaf, l_l is the length between the collar and the flagging point of the leaf, and l is the leaf length.

Photosynthesis

At silking stage (84 and 92 after planting), photosynthesis was measured in completely developed leaves from 09:00 to 14:00 h using a Li-6400 portable photosynthesis system (Licor Inc., Lincoln, NE, USA). The leaves at each height were measured with three replicas in each block. The span of photosynthetic photon flux density (PPFD) values was set as 2000, 1850, 1500, 1200, 1000, 850, 700, 500, 300, 200, 100, 50, 25, and 0 $\mu mol\ m^{-2}\ s^{-1}$. The relative humidity was maintained at 65%, the leaf temperature was 25 °C, and the ambient CO_2 concentration was 500 $\mu mol\ m^{-2}\ s^{-1}$. The light response curves of P_N with changing irradiance in each treatment were simulated according to the index model of the light response of maize (Guo *et al.*, 2005):

$$P_N = P_{max} \left(1 - e^{\frac{AQY\ PAR}{P_{max}}}\right) - |R_D| \qquad [3]$$

where P_N represents the net leaf photosynthesis rate under a different PAR, P_{max} is the maximum photosynthesis rate, AQY is the apparent quantum yield, PAR is the photosynthetically active radiation, and R_D is the dark respiration. Net photosynthesis was measured using the portable photosynthesis system Li-6400, and the measured leaves were at the following heights when the canopy was closed: 50, 100, and 150 cm. All values were read under saturated light 2000PPFD, and all treatments were replicated five times.

Light interception

The incoming PAR was measured at the following heights: 0, 50, 100, and 150 cm from ground level. Ten independent measurements were made at each canopy layer within each plot between 10:30 and 12:00 h on a clear day. The fraction of PAR was calculated using the following equation:

$$F = \left(1 - \frac{I_o}{I_t}\right) \times 100\% \qquad [4]$$

where F is the fraction of incident solar radiation intercepted by a canopy layer, I_o is the measured incident PAR below a canopy layer, and I_t is the radiant flux density on the top of the canopy, read by LI-190 (Licor, Lincoln, NE, USA). The I_o value was measured at vertical height level using a line quantum sensor 191-SB (Li-cor). The measurement followed the procedure of Gallo and Daughtry (1986) with slight modification because row spacings of P1 and P2 were not uniform (100 cm length of 191-SB ×2 in width 30+170 for P1, and 100 cm × 2 × cos 49.46° in width 40+90 for P2). All measurements were carried out between 10:00 to 14:00 h on a clear day.

Data analysis

ANOVA was used to analyze significant differences in the measured variables. The significance level was 0.05(α). Multiple comparisons were used to determine the least significant difference (LSD) at 0.05(α).

Results

Effect of planting patterns on the canopy structure

The interaction between planting patterns and cultivars generated changes in the spatial distribution of leaf organs, such as the azimuthal leaf orientation (Fig. 2) and LOV. The mean vertical angle of the lamina at a height of 150 cm in the stalk for P1 was significantly higher than that for CK in the cv. Beiyu288 (Table 1). For P1 at 150 cm, the ratio of leaves perpendicular to rows was 22.8%. The ratio was the same (10%) at the 100 and 50 cm heights. In contrast, LOV values at 150, 100, and 50 cm were 14.4%, 2.8%, and 7.2% respectively higher in P2 than in P1; and 11.8%, 8.7%, 6.6%
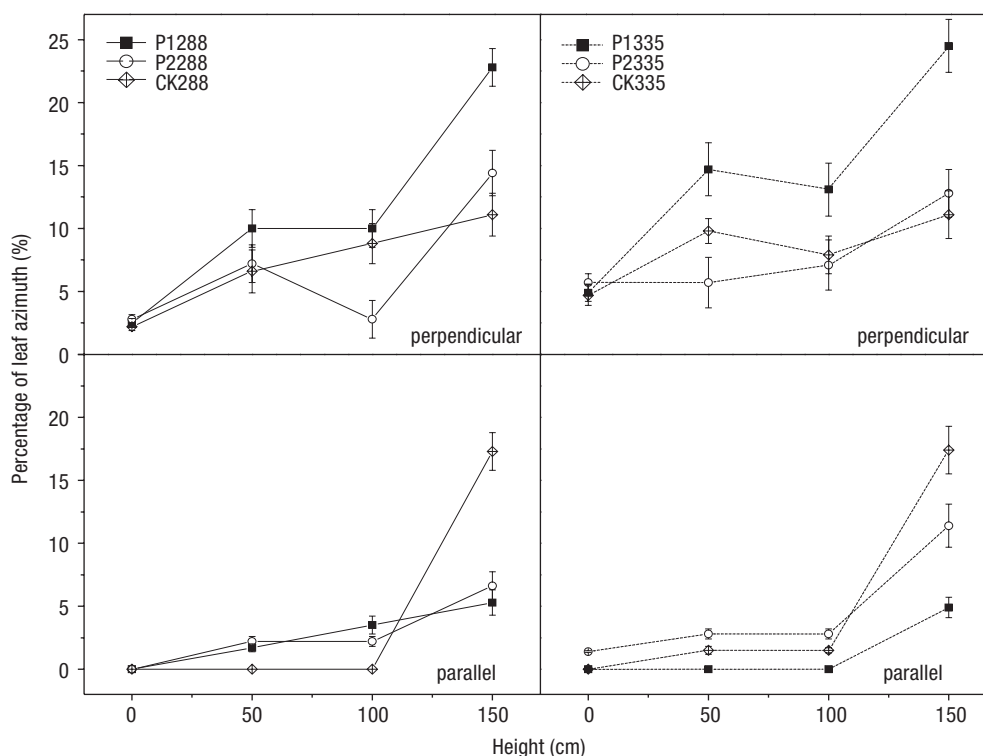
Figure 2. Percentage of distribution of leaf azimuth perpendicular (above) and parallel (below) to row orientation at 0, 50, 100, 150 cm height of two maize cultivars Beiyu288 (left) and Xianyu335 (right) in three planting patterns. Means ± SD (n=5).

respectively higher in CK than in P1. For cv. Xianyu335, the ratios of leaves perpendicular to rows for P1 were 13%, 5%, and 6% higher than those for CK at the 150, 100, and 50 cm heights, respectively, whereas

the ratio at each height in P2 were similar than those in CK.

For cv. Beiyu288, the leaf LOV above 150 cm was lower than that at 100-150 cm; the LOV at 50-100 cm

Table 1. Responses of leaf angle (LA) and leaf oriented value (LOV) of leaves of two maize cultivars, Beiyu288 and Xianyu335, at 50, 100 and 150 cm height in three planting patterns. Significant differences among means at $p<0.05$

Height (cm)	Patterns	Beiyu288		Xianyu335	
		LA	LOV	LA	LOV
0-50	P1	19.60 ± 3.04a	47.24 ± 3.60b	34.33 ± 1.39a	35.75 ± 2.30c
	P2	19.80 ± 2.20a	55.84 ± 2.36a	26.80 ± 2.35b	56.11 ± 1.75b
	CK	17.16 ± 2.15a	58.93 ± 5.03a	20.33 ± 0.66c	60.03 ± 1.37a
50-100	P1	21.20 ± 1.52a	51.76 ± 2.24b	30.93 ± 1.38a	49.39 ± 1.89b
	P2	15.33 ± 0.71b	59.69 ± 1.61a	23.73 ± 1.93b	53.84 ± 3.05ab
	CK	15.27 ± 1.68b	60.99 ± 3.10a	21.46 ± 1.20b	59.11 ± 2.33a
100-150	P1	17.80 ± 1.18a	48.89 ± 1.77b	26.60 ± 2.03a	49.39 ± 1.89a
	P2	15.46 ± 1.42a	60.87 ± 2.36a	28.13 ± 3.54a	48.25 ± 3.84a
	CK	17.91 ± 3.37a	54.44 ± 3.86b	28.53 ± 3.60a	50.47 ± 2.10a
>150	P1	21.90 ± 1.26ab	39.27 ± 2.00b	34.68 ± 2.08a	43.41 ± 3.31b
	P2	19.78 ± 1.35b	45.76 ± 2.44a	32.50 ± 2.01a	45.14 ± 3.05ab
	CK	26.35 ± 1.96a	45.49 ± 2.99a	29.68 ± 2.15a	49.69 ± 2.70a

was the highest in all levels, whereas that at 50 cm was the lowest in all three planting patterns (Table 1). A significant increase was found at every P1 level. The Beiyu288 and Xianyu335 leaf angle (LA) at 0-50 cm and 50-100 cm in P1 were significantly higher than those in P2 and CK. A genotype difference was observed, and the average of the LA range in Xianyu335 was higher than that in Beiyu288.

Effect of planting patterns on light interception at different leaf strata

Planting patterns caused a significant decrease in F in both cultivars (Fig. 3). For cv. Beiyu288, in P1 a reduced F was found at the different leaf strata. Maximum light captured by the canopies at silking stage were equal in P2 and CK, which is lower in P1. For P1, 68.5% of the total IPAR was intercepted by the upper 150 cm stratum, and 14.5%, 8.6%, and 8.4% were intercepted by the 100-150 cm, 50-100 cm, and 0-50 cm stratum, respectively. In P2, the top level of the canopy intercepted 71.8% of the total IPAR; the other strata intercepted 22.5%, 3.8%, and 1.9% IPAR, respectively, by turns. In CK, 76.8% of incoming radiation was intercepted at the upper 150 cm canopy, whereas 16.2%, 6.5%, and 0.3% were intercepted at the other three strata. As for the cultivar Xianyu335, similar result was detected. A significant effect of planting

pattern on F was found throughout the whole canopy ($p<0.05$). However, at the upper 150 cm level, F of P1 was significantly lower than those in P2 and in CK. At 100-150 cm heights, a higher ($p<0.05$) F in P2 was recorded in comparison with those of the other planting patterns. In contrast, in P1 the highest F were recorded at 50-100 cm and 0-50 cm levels ($p<0.05$).

Effect of planting patterns on the photosynthesis of leaves at different strata

The effective quantum yield showed a different response to light availability among the different planting patterns (Table 2). In the case of cv. Beiyu288, an increased AQY was detected in P1. At 150 cm, the AQY in P1 was 27% and 11% higher than that in P2 and CK, respectively. A similar result was observed at 100 and 50 cm heights, and there were significant differences among the three planting patterns (LSD, $p<0.05$). A similar positive effect of narrow-wide rows (P1 and P2) on AQY in level was detected in cv. Xianyu355. In comparison with CK the increase of P_{max} was 40% and 9.6% in P1, and 12% and 5.8% in P2 at the 50 and 100 cm heights, respectively; the planting patterns also significantly affected P_{max} at the 150 cm height. For cv. Xianyu335, crops in narrow-wider rows also exhibited higher P_{max} (30% and 14% in P1, and 30% and 8% in P2 at 50 and 100 cm
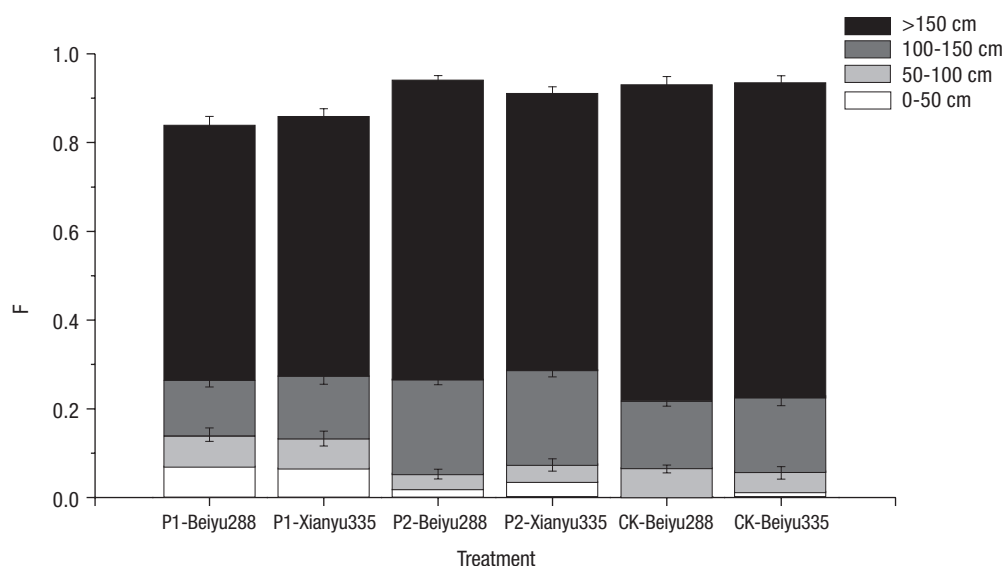

Figure 3. Vertical distributions of the fraction of incident photosynthetically active radiation intercepted by crops (F) at 0, 50, 100, 150 cm height in canopy during silking stage of two maize cultivars, Beiyu288 and Xianyu335, in three planting patterns. Means ± SD, n=4.

Table 2. Responses of apparent quantum yield (AQY), maximum net photosynthetic rate (P_{max}) and dark respiration rate (R_D) of leaves of two maize cultivars, Beiyu288 and Xianyu335, at 50, 100 and 150 cm height in three planting patterns. Significant differences among means at $p < 0.05$

Height (cm)	Patterns	Beiyu288			Xianyu335		
		AQY [mol(CO_2)mol^{-1}]	P_{max} [μmol(CO_2)m^{-2}s^{-1}]	R_D [μmol(CO_2)m^{-2}s^{-1}]	AQY [mol(CO_2)mol^{-1}]	P_{max} [μmol(CO_2)m^{-2}s^{-1}]	R_D [μmol(CO_2)m^{-2}s^{-1}]
50	P1	0.0504 ± 0.006a	23.97 ± 1.79a	1.26 ± 0.01b	0.0449 ± 0.005a	30.30 ± 1.95a	1.37 ± 0.13a
	P2	0.0250 ± 0.003b	19.30 ± 2.38b	1.10 ± 0.21b	0.0374 ± 0.002b	22.80 ± 2.7b	1.02 ± 0.16b
	CK	0.0090 ± 0.001c	17.10 ± 1.33b	2.06 ± 0.11a	0.0296 ± 0.002c	19.80 ± 1.23b	1.08 ± 0.16b
100	P1	0.0406 ± 0.002a	25.08 ± 1.88a	1.52 ± 0.12b	0.0313 ± 0.003a	31.85 ± 2.03a	1.03 ± 0.15b
	P2	0.0389 ± 0.002a	24.20 ± 3.92ab	1.91 ± 0.15a	0.0299 ± 0.001b	23.50 ± 2.06b	1.66 ± 0.12a
	CK	0.0335 ± 0.005b	22.87 ± 2.02b	1.55 ± 0.16b	0.0198 ± 0.001c	21.95 ± 1.50b	1.11 ± 0.09b
150	P1	0.0346 ± 0.003a	26.68 ± 2.14a	1.65 ± 0.12a	0.0351 ± 0.002a	32.60 ± 1.84a	1.21 ± 0.13b
	P2	0.0311 ± 0.001b	24.37 ± 1.20ab	1.08 ± 0.02b	0.0332 ± 0.001a	28.40 ± 2.43b	1.09 ± 0.07b
	CK	0.0272 ± 0.003c	23.03 ± 1.15b	1.15 ± 0.15b	0.0275 ± 0.003b	23.55 ± 2.70c	1.40 ± 0.11a

heights, respectively). At 150 cm, P_{max} increases were 38% and 20% in P1 and P2, respectively. The planting pattern did not significantly affect the R_D of the two cultivars. However, a positive effect of narrow-wide rows on R_D was found.

Diurnal time courses of photosynthesis characteristics

When compared with CK, a significant enhancement in P_N and g_s for Beiyu288 and Xianyu335 in P1 was observed at 150 cm height during the diurnal time courses (Figs. 4-5). The differences in P_N and g_s between P2 and CK were also significant. In P1, P_N and g_s were increased by 20.7% and 44% in Beiyu288, and by 13% and 18% in Xianyu335 over CK, respectively. The peak value of P_N and g_s occurred at 12:00 h and sustained a relatively high value from 10:00 to 14:00 h. Single-peak curves were observed in all treatments. At 100 cm, significant (LSD, $p < 0.05$) enhancements in P_N and g_s still remained in P1, whereas the P_N and g_s values in P2 were at medium level, which were slightly higher than those in CK. A positive effect of P1 on P_N and g_s in both cultivars were found. At 50 cm single-peak curves were also observed in the P_N and g_s of the two cultivars; for Beiyu288, the average values of P_N and g_s in P1 (41% and 22%, respectively) and P2 (26% and 17%, respectively) were still significantly higher (LSD, $p < 0.05$) than those in CK. The P_N and g_s of Xianyu335 cultivar in P1 and P2 were significantly higher than those in CK (LSD, $p < 0.05$).

Narrow-wide row spacing increased leaf C_i in both cultivars at the 150 cm level in contrast to CK. The increase was 28.5% and 17.5% in P1 and P2, respectively, for Beiyu288, and 7.7% and 3.9%, respectively, for Xianyu 335. The C_i of Beiyu288 and Xianyu335 was increased by 71.9% and 26%, respectively, in P1; and 18% and 15%, respectively, in P2 at 100 cm height. At 50 cm, a significant planting pattern effect on C_i was also recorded in both cultivars, where Ci in P1 (25-27%) and P2 (10-18%) was higher than in CK. The diurnal time courses of C_i in cvs. Beiyu288 and Xianyu335 under the three planting patterns displayed single U-curve types at 150, 100, or 50 cm height. The lowest value of C_i occurred at 12:00 h in all treatments (Fig. 6).

Discussion

Leaf canopy structure responses to planting patterns were analyzed by considering the leaf azimuth, LA, and LOV. In cv. Beiyu288, P1 promoted a higher ratio of leaves perpendicular to rows (Fig. 2). Contrarily, the effect of P1 on LOV and leaf angle was significant for both cultivars. These results indicate that adjacent leaves influenced one another. Maddonni *et al.* (2001b) have previously reported genotypic differences in the capacity of maize leaves to fill empty spaces among plants of the canopy. In the quoted work, the vertical angle of leaves increased at high plant population densities, but it did not respond to contrasting row spacings. In the current study, maize crops were planted at
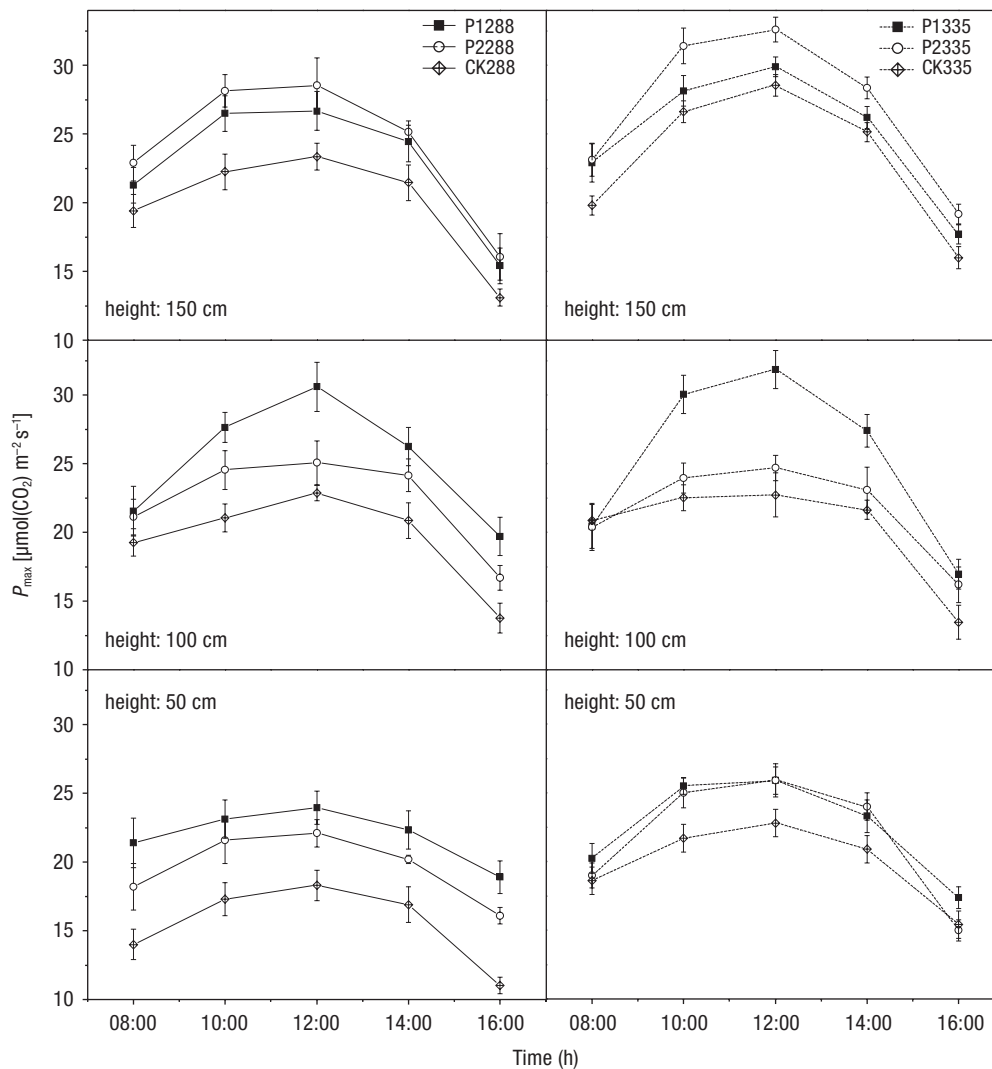
Figure 4. Responses of net photosynthetic rate (P_N) of leaves of two maize cultivars Beiyu288 (left) and Xianyu335 (right) at 50, 100 and 150 cm height in three planting patterns during the diurnal time course. Means ± SD (n=4).

the same plant density, and the planting pattern affected not only the leaf angle but also the leaf azimuth and LOV at silking stage. Similarly to previous works (Westgate *et al.*, 1997; Maddonni *et al.*, 2001b), LAI (5.14, 5.11, 5.0 in P1, P2 and CK for Beiyu 288; 4.61, 4.48, 4.42 in P1, P2 and CK for Xianyu 335) was not affected by the planting pattern, indicating that the plant spatial distribution did not affect leaf expansion. Leaf morphogenesis responses to planting patterns produced changes in space distribution that were critical in the competition for available light (avoiding mutual shading; Maddonni *et al.*, 2002). The adjustments in leaf angle and leaf azimuth were in agreement with the results of Kasperbauer and Karlen (1994), and

fitted the general pattern of phytochrome-mediated shade avoidance reaction of plants (Smith and Whitelam, 1997). The adjustment in leaf azimuth is a morphological mechanism of plants in response to changes in light quality [red-far-red (R:FR) ratio; Maddonni *et al.*, 2002)] by plants responding to the presence of neighbors, such as weeds (Rajcan *et al.*, 2004) or other plants of the same species (Maddonni*et al.*, 2001b). Significant differences were observed in the leaf azimuthal distribution among planting patterns, which agreed with previous results (Girardin and Tollenaar, 1994). In contrast with that mentioned above for leaves perpendicular to rows, the ratios of leaves parallel to the row were smaller in P1 and P2 than in CK (most
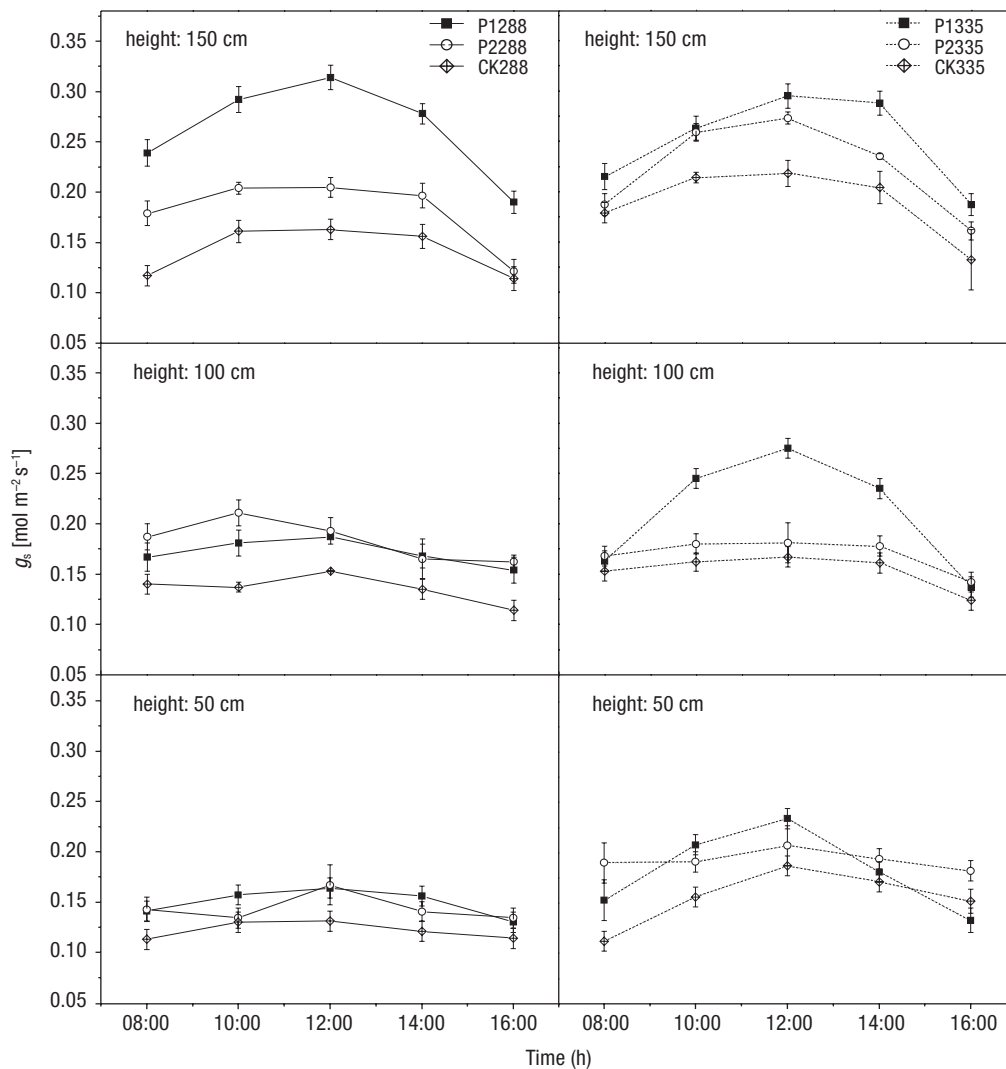
Figure 5. Responses of stomatal conductance (g_s) of leaves of two maize cultivars, Beiyu288 (left) and Xianyu335 (right), at 50, 100 and 150 cm height in three planting patterns during the diurnal time course. Means ± SD (n=4).

plants presented a north-south leaf orientation at a low density). Some researchers (Kasperbauer and Karlen, 1994; Maddonni *et al.*, 2001b) believe that north-south rows receive more far-red radiation reflected from plants in the adjacent rows, which triggers photo-morphogenic responses. A physical contact among leaves of adjacent plants may also reduce the proportion of leaves parallel to rows in the narrow-wide rows planting patterns. Therefore, collectively these results are not in agreement with the hypothesis that leaves in a maize canopy have a random azimuthal distribution (Hodges and Evans, 1990). Moreover, in high-density crop fields, there are steep leaf angles in the uppermost canopy leaves followed by a gradual decrease in leaf

angles along the vertical profile, facilitating gradual light attenuation and better light distribution within the canopy which maximize canopy carbon gain (Ishida *et al.*, 1999). Crops with erect leaves are considered to have a considerable yield advantage over those with horizontal leaves, because the high leaf angles determines a low light attenuation within the canopy (Dickmann *et al.*, 1990). However, in narrow-wide row spacing planting patterns, the number of horizontal leaves tends to increase because of the competition for light and space (Table 1).

Canopy structure was strongly related to the total amount of radiation intercepted (Maddonni *et al.*, 2001a). Light interception is associated with intra-
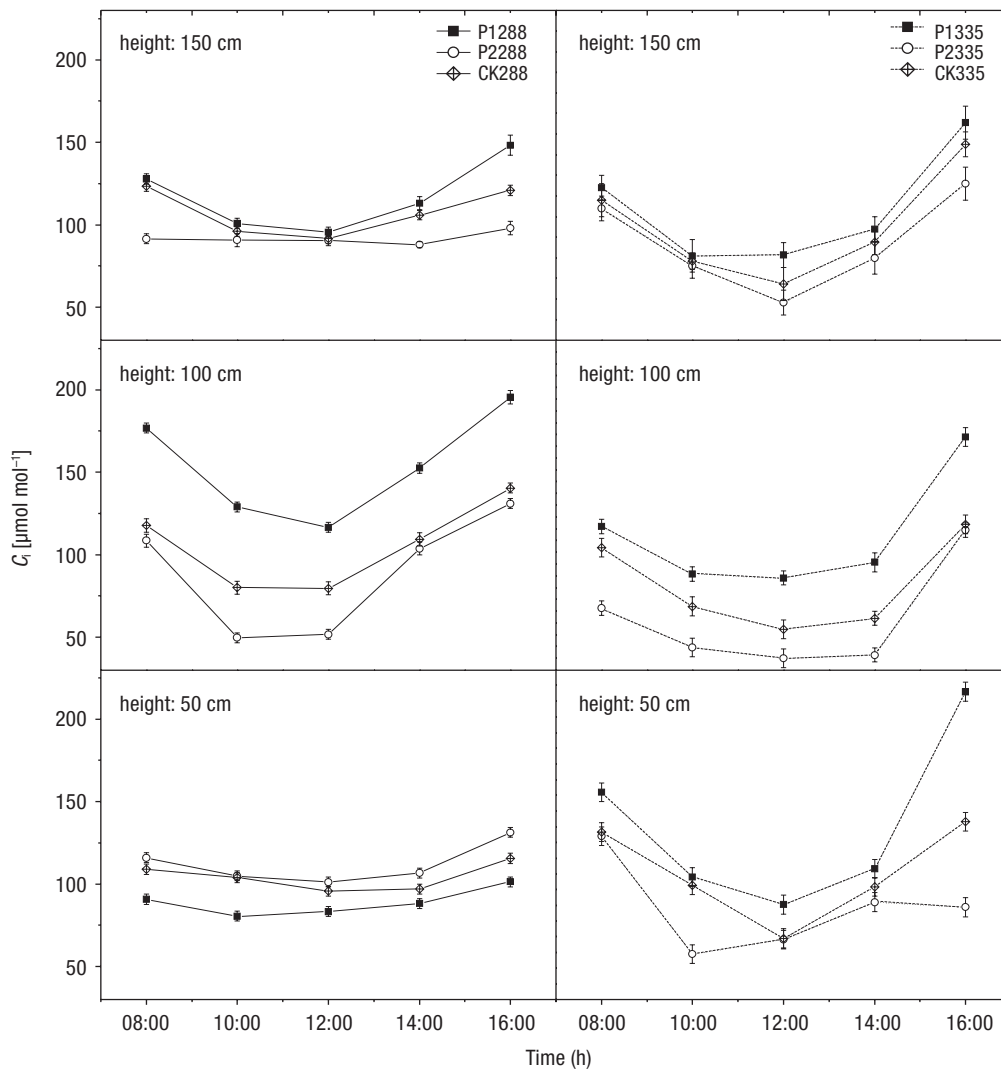
Figure 6. Responses of intercellular CO_2 concentration (C_i) of leaves of two maize cultivars, Beiyu288 (left) and Xianyu335 (right), at 50, 100 and 150 cm height in three planting patterns during the diurnal time course. Means ± SD (n=4).

canopy light distribution and maximum light interception capacity, and the effect of canopy architecture on the mean fractional canopy interception is usually much less analyzed than the LAI (Tharakan *et al.*, 2008). In the current study, a linear relationship between light interception and LAI was not detected. The total fraction of light interception of the whole maize canopy significantly differed ($p<0.05$) between P1 and CK in the two cultivars, whereas a significant difference in LAI was not observed. As light penetrates within a canopy, light interception increases less than LAI, in accordance with Beer's law. In canopies with low LAI, light interception capacity is more important than light distribution within the canopy to maximizing radiation

use efficiency (Leuning *et al.*, 1991). In our work, light penetration within the fully developed canopies, was not homogeneous. As depicted in Fig. 3, most of the incoming PAR was intercepted at the uppermost leaves strata (>150 cm form soil surface). Hence, most intercepted radiation was concentrated on the upper levels of the canopy. A comparison of F between P1 and CK showed that the enhancement of light interception was detected at all levels below 150 cm, especially at 0-100 cm height. Based on the function of maize leaves by the proximity of the sinks (Zhao, 1986), leaves at heights between 0 and 100 cm mainly provide photosynthates for root growth metabolism, and the greater distribution of light at these levels would benefit root

growth. And this effect may be reflected in grain production. Leaves around and above the ear commonly provides assimilates to kernel growth. Thus, the enhancement of light interception at 100-150 cm heights would positively affect grain yield. As was mentioned for P1, for P2 the fraction of incident solar radiation intercepted for the whole canopy and that for the upper 100 cm leaf strata was not different that those of CK, but the leaves at 0-100 cm heights intercepted more PAR than those of CK; probably determining an advantage for root growth and mineral nutrient assimilation.

P_N is an important parameter that determines the photosynthetic capability and status of a photosynthetic organ and AQY reflects the potential photochemical activity of PSII (Zhang and Qiang, 2010). In the current study, both parameters were used to evaluate maize response to the light environment under different planting patterns. At silking stage, weak light stress caused a decline in the fertilization rate and seed-setting rate, consequently leading to a significant reduction in grain yield (Jia *et al.*, 2007). Consequently, final grain yield of crops is decided by the light source assimilation and the transformation capabilities of leaves. Planting pattern establish the micro-environment within the canopy, with factors such as light, temperature, moisture, and CO_2 concentration, which can affect photosynthesis and crop yield. High plant population density combined with narrow row spacing maximizes light capture. By contrast, wide-row spacing may improve the ventilation condition and the photosynthetic capability of leaves at middle-low leaves strata. Therefore, a more uniform light distribution within the canopy, could contribute to a more efficient light use. Planting pattern can affect the parameters of the P_N response to light, such as P_{max} and AQY which affected by moderation of canopy structure. A positive effect of P1 on P_{max} and AQY of both maize cultivars at medium-low leaf strata were detected in the current study (Table 2). In P1 the P_{max} values at middle-lower canopy strata were obviously higher than those of CK and P2 in both maize cultivars, because of the enhancement of light penetration at these leaf layers. The environmental factors that typically affect P_{max} and AQY are light quality, light intensity, temperature, water, air condition, and mineral nutrition (Niinemets, 2007). No obvious effect of light intensity on AQY along a crop cycle was evident. Although the P_{max} of a leaf growing under highly intense light was higher than that of a leaf growing under a low light intensity, their AQY were

similar. The AQY of C_4 plants like maize did not show a co-relationship with O_2 or CO_2 concentration, whereas other factors were quite similar (Leakey and Uribe-larrea, 2006). Therefore, more incoming light increased the P_{max} of the leaves at the middle-low canopy level, and the rise of AQY at these levels may be induced by the increase in the number of factors affecting leaf photosynthetic capability, especially the increase in nitrogen content. R_D is critical for plant growth and carbohydrate accumulation, and some studies have shown that an increase in R_D and a decrease in Rubisco activity result in a decreased average photosynthesis rate (Rey *et al.*, 1990). Other studies suggest that P_N increases with an increase in R_D (Xu, 2002). No effect of the different planting patterns on R_D in both maize cultivars was found; however, different light circumstances are assumed to contribute to changes in leaf properties (such as N concentration and formation of a photosynthesis-related protein, and micro-meteorological circumstance such as CO_2 concentration) (Maroco *et al.*, 1999; Zhang and Qiang, 2010).

P_N and g_s reflect plant's photosynthetic efficiency. The photosynthesis rate is estimated from the CO_2 concentration gradient and the diffusion resistance among internal and external leaves (Zhang and Qiang, 2010). The concentration gradient of CO_2 and the diffusion resistance from outside the leaf surface to the carboxylation tissue affect the P_N value. CO_2 transport from the air environment to the chloroplast encounters a number of resistances, with stomatal resistance as one of the most important limiting factor in photosynthesis. Therefore, P_N, C_i, and g_s were used as indicators of the diurnal time courses of leaf photosynthetic capability at different canopy levels in response to three planting patterns. According to Farquhar and Sharkey (1982), when C_i declines and stomatal restriction increases, the decrease in P_N can account for the decline in g_s. The limiting factor would decrease the photosynthetic activity of the mesophyll cell if the leaf photosynthesis rate decreased with the increase in C_i. Hence, in the current study, the enhancement of P_N cannot result from the increase in g_s and C_i. However, the result suggested that the photosynthetic activity of the mesophyll cells of leaves at individual levels in P1 was stronger than that in CK. This is because the leaf structure and function were not only adjusted by their own genetic factors but were also significantly affected by environmental conditions, especially light (Bjorkman and Holmgren, 1966). The lesser incoming light arriving at the middle-low canopy level is the main reason

for lower P_N in CK. Weak light in the canopy is disadvantageous for the generation of chlorophyll at any given height. Under an open-air environment, the diurnal pattern of maize photosynthetic characters such as P_N and g_s showed single-peak curves at 150 and 100 cm canopy heights. The measured maximum value for P_N and g_s occurred at 12:00 h, and no "noon break" was observed in any treatment. The latter is a consequent inherent rhythm of crops as maize should not be disturbed by planting pattern. And the disturbance in P_N, g_s, and C_i at different times mainly accounted for the change in incoming PAR. Although a significant effect of planting pattern on g_s and C_i was detected, how these two parameters influenced P_N remains to be elucidated. The contributions of other environmental factors such as CO_2 concentration, moisture, and current temperature were also not discussed in the current paper and should be focused on in further research.

In conclusion, the current work reports the canopy structure, light distribution, and photosynthetic properties of the leaves of two maize cultivars at silking stage, at different canopy heights, and in three different planting patterns. The results show that the 30+170 cm planting pattern (P1) had a positive effect on the formation of a better canopy structure; the effect of 40+90 cm planting pattern (P2) on the canopy structure was also significant in some aspects. The total incepted PAR of P1 was lower than that of P2 and CK; but, the light environment at the middle-low canopy stratum was improved in P1 and P2, and the enhancement of photosynthetic characters at individual heights was manifest, especially in P1. However, the effect of planting pattern on micro-environmental factors was not explained in the current discussion. The changing of micro-environmental factors as these affect photosynthetic properties also requires further research.

Acknowledgements

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