Maize photosynthesis and microclimate within the canopies at grain-filling stage in response to narrow-wide row planting patterns

T.D. LIU[*,**] and F.B. SONG[*,**,+]

Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Jinlin, Changchun 130012, China[*]
Graduate University of Chinese Academy of Sciences, Beijing 100049, China[**]

Abstract

In China, narrow-wide row planting pattern has been advocated for maize (*Zea mays* L.) production. However, no previous study has clearly elucidated the complexity of factors affecting maize canopy such as the microclimatic factors, and the effect of photosynthesis in narrow-wide row planting pattern. The current study was undertaken to identify the planting patterns that influence microclimatic conditions and photosynthesis of two maize cultivars (Beiyu288 and Xianyu335) grown 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 (*3*) uniform row of 65 cm (CK, conventional row as control, 6.4 plants m^{-2}). Light interception, temperature, relative humidity (RH), CO_2 concentration, and leaf photosynthesis within the canopy were measured in each planting treatment at the grain-filling stage. The net photosynthetic rate (P_N), intercellular CO_2 concentration (C_i), stomatal conductance (g_s), transpiration rate (E), and temperature of the narrow-wide row exceeded that of the conventional row. The CO_2 concentration and RH of the narrow-wide row were lower than CK by 50 cm strata. The narrow-wide row had a more uniform light intercepted at the whole canopy profile. The results of the current study suggest that narrow-wide row-planting pattern has a positive effect on canopy microclimate factors and promotes photosynthesis.

Additional key word: maize; microclimate; photosynthesis; planting pattern.

Introduction

The planting pattern for crops indicates management relations of space and time in crop cultivation. Planting pattern can lead to changes in the microclimate environment within crop canopy, mainly in the light transmission rate of crop groups (Maddonni *et al.* 2001b, Awal *et al.* 2006), sunshine hours, temperature, and evapotranspiration (Gardiol *et al.* 2003). Other natural properties such as leaf area index (Wang *et al.* 2008), CO_2 fixation (Arkebauer *et al.* 2009), and even the final production (Vidovič 1974, Shuting *et al.* 1993) are also affected. Therefore, to take full advantage of land, energy, and climate resources, the appropriate choice of cropping patterns is essential.

Maize is a heliophilous plant. When solar radiation reaches the top of maize canopy, more than 50% of photosynthetically active radiation (PAR) was absorbed by the canopy, part of the solar radiation was reflected back to the sky, and the other part reaches the bottom after the transmission in the canopy. Within the plant canopy, microclimatic factors can affect the surrounding microenvironment of leaves, thus, affecting the net photosynthetic rate (P_N). The change in atmospheric CO_2 concentration on photosynthetic rate and other properties (Watling *et al.* 2000, Cousins and Bloom 2003, Kim *et al.* 2006) can be significant factors affecting the photosynthesis process. However, the direct effect of CO_2 on photosynthesis was not clear (Fan *et al.* 2011). Temperature during photosynthesis influences the enzyme activity of leaf photosynthesis and leaf respiration rate, and ultimately affects the crop yield (Stewart *et al.* 1998). Temperature also affects the evapotranspiration of plant canopy, producing moisture difference between the inside

Received 29 June 2011, *accepted* 28 December 2011.
[+]Corresponding author; tel: +86 431 8554 2226; e-mail: liutd121@yahoo.com.cn
Abbreviations: C_i – intercellular CO_2 concentration; CK – control; E – transpiration rate; F – fraction of photosynthetically active radiation; g_s – stomatal conductance; IPAR – incident photosynthetically active radiation; LAI – leaf area index; LSD – least significant difference; PAR – photosynthetically active radiation; P_N – net photosynthetic rate; RH – relative humidity; RUE – radiation-use efficiency; SD – standard deviation.
Acknowledgement: This study was supported by the Knowledge Innovation Program of the Chinese Academy of Sciences, Grant No. KSCX2-YW-N-077.

and outside of the leaf, which blocks the transport of nutrients, and decrease the photosynthesis (Kimball and Bernacchi 2006, Ben-Asher *et al.* 2008). In actual production, relative humidity (RH) depends on temperature. Temperature should change clearly and quickly while interacting with RH. The effect of RH in the photosynthetic process of leaf at canopy in the microlevel can alter plant stomatal conductance, thereby affecting plant transpiration and P_N (Sciutti and Morini 1995). The effect of RH in the photosynthetic process can affect also surface evaporation and crop root uptake of soil moisture, thus, affecting the nutrients of crop needed for growth (Swan and Volum 1986).

Although the range in foliage physiological capacities is impressive, P_N still varies, and is less than the theoretically required one to maximize canopy photosynthesis for a given total leaf nitrogen of foliar biomass. The discrepancies between the actual and theoretical canopy photosynthetic profiles are still poorly understood (Anten 2005). There are other important interactions between the environmental factors within the canopies. Both temperature and water vapor pressure deficit scale positively with canopy light availability. Simultaneous acclimation to multiple environment factors can significantly modify the profiles of P_N within the canopy (Baldocchi *et al.* 2002, Niinemets and Valladares 2004). With the decrease of space between plant, the lower parts of the transmission group will reduce the amount of diurnal irradiation (Maddonni *et al.* 2001b) all day to reach a very weak light, resulting in leaf yellowing and shedding at lower level. This explains why the lower part, which accounted for more than quarter of LAI, contributed only less than 20% of the canopy assimilation rate (Pattey *et al.* 1991). The planting of maize in close distances with each other in the group results in an almost dark condition in the lower strata of canopy. The respiration is increased while solar energy utilization efficiency within the crop canopy is reduced (Heichel 1970). Thus, the growth rate of material production lowered during this time.

The current research aims to determine the impact of canopy on the microclimate in the narrow-wide row planting patterns, and to analyze the effect of different micrometeorological environment on leaf photosynthesis at different leaf strata.

Materials and methods

Field design: The current study was carried out from May to October in 2009 and 2010 (growing season) at the Experimental Station (44°12′ N, 125°33′ E), Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences in Dehui County, Jilin Province, China. 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 rotation 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 cultivars of maize, Beiyu288 (maximum height 275.6 cm) and Xianyu335 (maximum height 304.6 cm), planted in black soil clay were induced for comparison. The sowing period was early May and the harvest period was end of September. Two healthy seeds were planted in one hole, and the ratio of fertilization was 2:1:1 (N, P, K). The experimental design was a big plot contrast (single plot area ≥ 667 m^2) in 2009 and a randomly complete block contrast with four replicates (single block area 10 m× 10 m) in 2010. The crops were free from pest, weeds, and disease.

Light interception: The incoming photosynthetically active radiation (PAR) was measured at the following upground heights: 0, 50, 100, and 150 cm. Ten independent measurements were made at each canopy layer within each plot between 10:30 h and 12:00 h on a clear day. The fraction of PAR was calculated using the following equation:

$$F = \left(1 - \frac{I_0}{I_t}\right) \times 100\%$$

where F is the fractional amount of intercepted radiation, I_o is the measured incident PAR (IPAR) on the ground surface, and I_t is the radiant flux density on top of the canopy, read by quantum sensor *LI-190* (*LI-COR Inc.,* Lincoln, NE, USA). The I_o value was measured at a vertical height level using a line quantum sensor *191-SB* (*LI-COR Inc.,* Lincoln, NE, USA). The measurement followed the procedure of Gallo and Daughtry (1986) with slight modification because the 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 h to 14:00 h on a clear day.

Concentration of CO_2, relative humidity, and temperatures: The completely developed leaf at a given height (50, 100, and 150 cm) at grain-filling stage was measured from 11:00 h to 12:00 h using a portable photosynthesis system (*LI-6400, LI-COR Inc.*, Lincoln, NE, USA). The leaves at each height were determined with three replicates in each block. The RH, concentration of CO_2, and temperature of the environment was recorded.

P_N, g_s, C_i, and E were measured using a *Li-6400* portable photosynthesis system (*LI-COR Inc.*, Lincoln, NE, USA) equipped with a LED leaf chamber. Prior P_N, g_s, C_i, and E measurements, the CO_2 concentration in the leaf

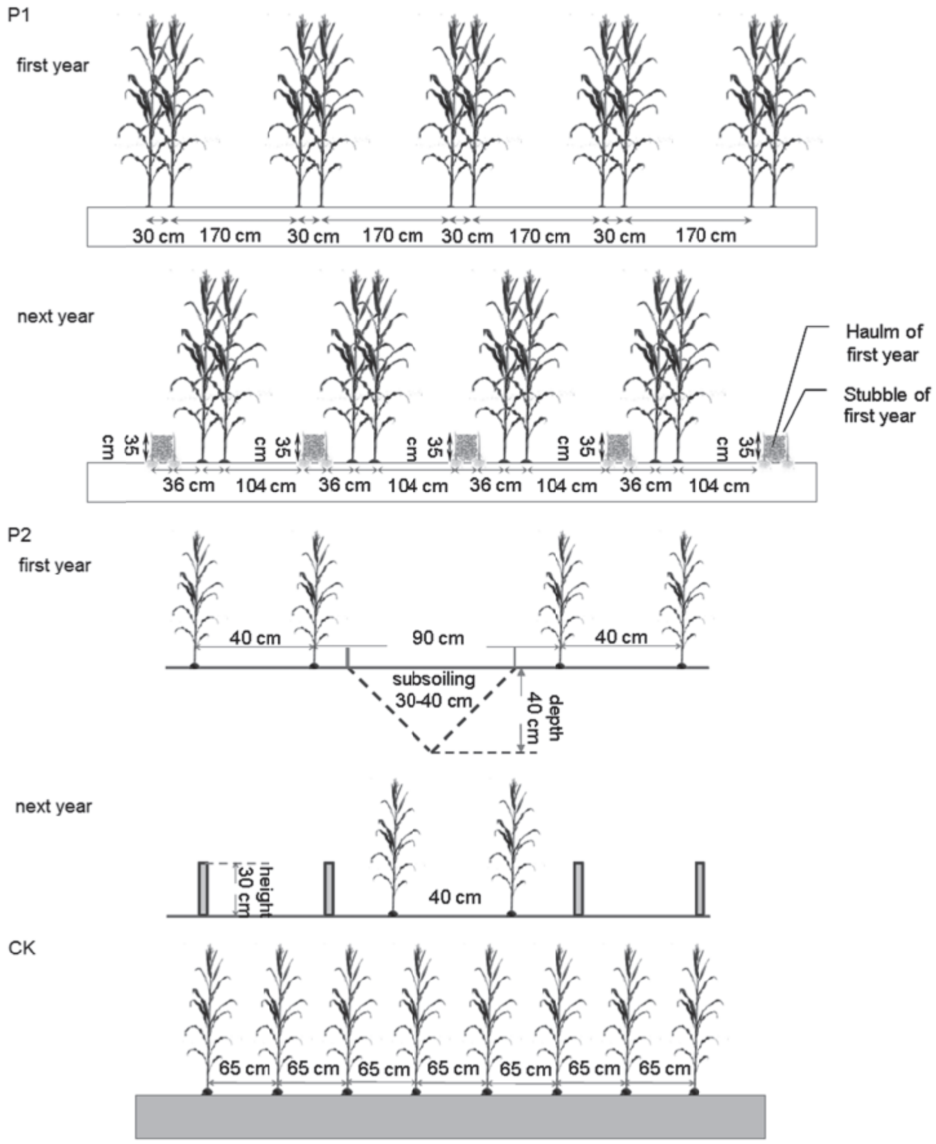

Fig. 1. A schematic diagram showing P1“30+170”, P2“40+90” and CK“65” planting patterns at density 6.4 plants m^{-2}.

chamber (airflow was 500 μmol s^{-1}), the leaf chamber temperature, and the humidity were set as the environmental date. The date was read when the photosynthetic photon flux density was 2,000 μmol m^{-2} s^{-1}. Every point where the rate of photosynthesis became stable was identified, which occurred after gas exchange stabilized (from 10:00 h to 12:00 h).

Statistical analysis: *ANOVA* was used to analyze the significant differences between the measured data compared with the means of these data. 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 light interception at different leaf strata: For the cultivar Beiyu288, in P1, a reduced F was found at the different leaf strata (Fig. 2). Maximum light captured by the canopies at grain-filling stage were equal in P2 and CK, which is lower in P1. For P1, 70.9% of the total IPAR was intercepted by the upper 150 cm stratum, and 14.5%, 10.5%, and 4.1% were intercepted by the 100 cm to 150 cm, 50 cm to 100 cm, and 0 cm to 50 cm stratum, respectively. In P2, the top level of the canopy intercepted 68.2% of the total IPAR whereas the other strata intercepted 10.6%, 8.9%, and 2.7% IPAR, respectively, by turns. In CK, 78.1% of incoming radiation was intercepted at the upper 150 cm canopy, whereas 14.5%, 4.9%, and 1.8% were intercepted

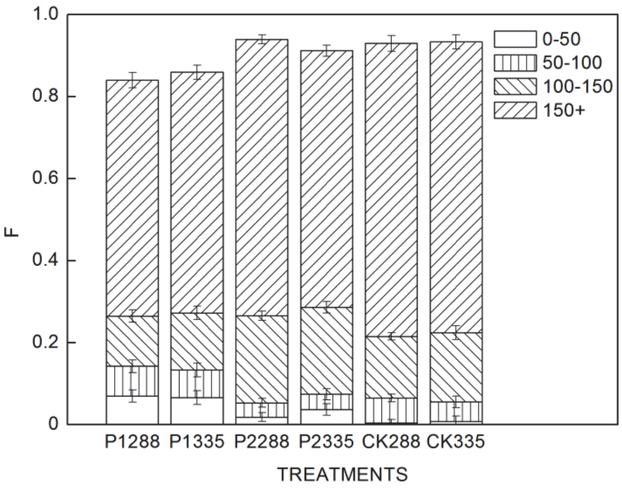

Fig. 2. Vertical distributions of F at 0–50, 50–100, 100–150 and 150+ cm heights in canopy during silking stage of two maize cultivars Beiyu288 and Xianyu335 in P1"30+170", P2"40+90" and CK"65" planting patterns. Means ± SD, (n = 12).

at the other three strata. Similar result was detected for the cultivar Xianyu335. A significant effect of planting pattern on F was found throughout the whole canopy (p<0.05). However, at the upper 150 cm level, the F of P1 was significantly lower than P2 and CK. At 100 cm to 150 cm heights, a higher (p<0.05) F in P2 was recorded compared with the other planting patterns. In contrast, the highest F was recorded in P1 at 50 cm to 100 cm and 0 cm to 50 cm levels (p<0.05).

Effect of planting patterns on temperature, RH, and concentration of CO_2 at different leaf strata: Fig. 3 shows the trend of temperature of two-cultivar maize in three planting patterns at 50, 100, and 150 cm height. In cultivar Beiyu288, the temperature in different treatment at height 50 cm were equal to the temperature at 100 cm, but significantly lower than at 150 cm (LSD, p<0.05), and the trend of temperature in the three planting patterns exhibit P1>P2>CK. With cultivar Xianyu335, the temperature at 100 cm was lowest whereas the temperature at 150 cm was highest in CK. For the other two narrow-wide planting patterns, the temperature increased with increasing height. Nevertheless, the significant effect (LSD, p<0.05) was detected by narrow-wide planting pattern on temperature compared with CK.

The RH of canopy was a single-peak curve, the value of Beiyu288 in P1 was similar to the value in P2 at the height of 50 cm, whereas the RH in CK was significantly lower than P1 and P2 (Fig. 4). With respect to the height of 100 cm, the significant difference among three planting patterns was measured (LSD, p<0.05). No significant effect (LSD, p<0.05) was found at the height of 150 cm. For the cultivar Xianyu335, there were significant differences among the treatment. The value of RH was CK>P2>P1.

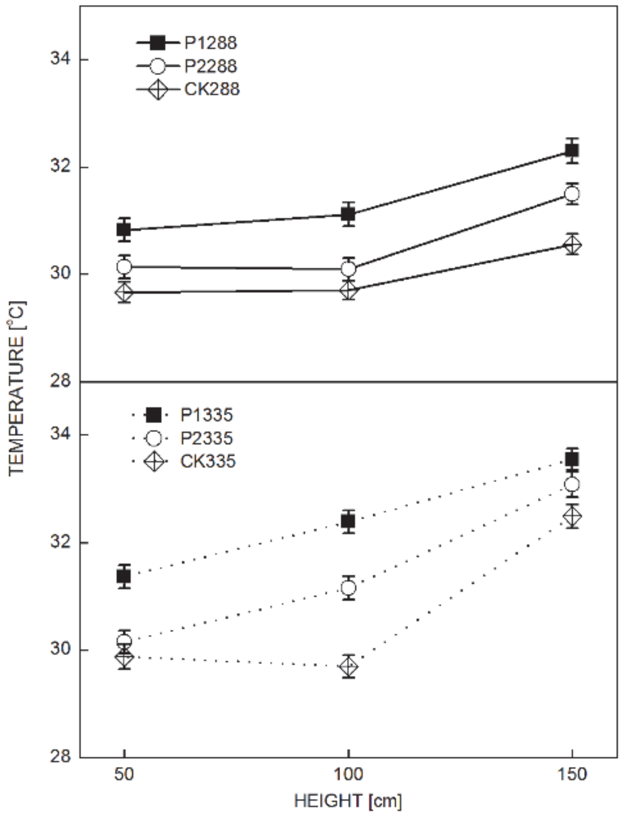

Fig. 3. The temperature of circumstance at 50, 100, and 150 cm heights of two maize cultivars Beiyu288 and Xianyu335 in P1"30+170", P2"40+90" and CK"65" planting patterns. Means ± SD, (n = 12).

The narrow-wide row planting pattern affected the CO_2 concentration within the canopy of two maize cultivars (Fig. 4). In the three planting patterns of Beiyu288, the CO_2 concentration at 50 cm displayed a trend of P1<CK<P2; at the 100-cm height, the value in P1 was lowest, and there was no significant difference (LSD, p<0.05) between P2 and CK; at 150 cm, (LSD, p<0.05) the significant effect of planting pattern was displayed as P1<P2<CK. Similar effect of planting patterns was also found in Xianyu335.

Effect of planting patterns on P_N, C_i, g_s, and E at different leaf strata: Table 1 shows that the variation patterns of P_N are highly similar at different planting patterns, as characterized by a rise at low level and subsequently decline at high level. Beiyu288 reached a maximum of approximately 32.6 μmol(CO_2) m^{-2} s^{-1} at the height of 150 cm, and a significant difference was detected at these strata. The P_N in P1 is also significantly higher than CK at the heights of 100 cm and 50 cm (p<0.05). No significant difference was found between P2 and CK. Whereas for Xianyu 335, the maximum P_N was 26.68 μmol(CO_2) m^{-2} s^{-1} at the height of 150 cm in P1. There were significant differences among the three planting patterns (LSD, p<0.05).

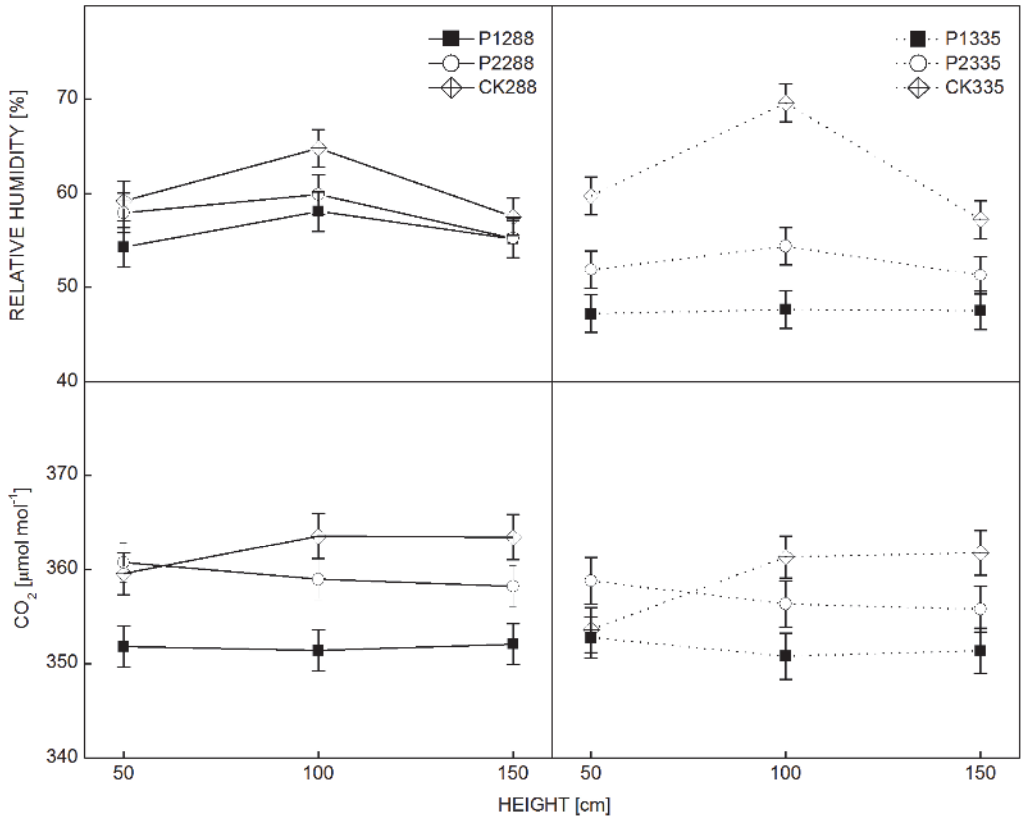

Fig. 4. The relative humidity and CO_2 concentration of circumstance at 50, 100, and 150 cm heights of two maize cultivars Beiyu288 and Xianyu335 in P1"30+170", P2"40+90" and CK"65" planting patterns. Means ± SD, (n = 12).

Table 1. Responses of net photosynthetic rate (P_N), intercellular CO_2 concentration (C_i), stomatal conductance (g_s), and transpiration rate (E) of two maize cultivars Beiyu288 and Xianyu335 leaves at 50, 100, 150 cm height in P1"30+170", P2"40+90" and CK"65" planting patterns. Means ± SD, (n = 12).

Height [cm]	Treatments	P_N [μmol(CO_2) m^{-2} s^{-1}]	g_s [mol(H_2O) m^{-2} s^{-1}]	C_i [μmol(CO_2) mol^{-1}]	E [mmol(H_2O) m^{-2} s^{-1}]
150	P1-Beiyu288	26.7 ± 2.1^a	0.1559 ± 0.0082^a	117.2 ± 9.6^a	2.71 ± 0.25^a
	P2-Beiyu288	24.3 ± 2.3^a	0.1460 ± 0.0048^{ab}	91.7 ± 1.7^b	3.37 ± 0.23^a
	CK-Beiyu288	23.0 ± 1.8^a	0.1254 ± 0.0110^b	107.6 ± 6.4^{ab}	3.21 ± 0.32^a
100	P1-Beiyu288	25.1 ± 2.0^a	0.0984 ± 0.0060^a	154.1 ± 14.6^a	1.57 ± 0.09^{ab}
	P2-Beiyu288	24.2 ± 1.6^a	0.0845 ± 0.0110^a	88.9 ± 16.3^b	1.76 ± 0.15^a
	CK-Beiyu288	22.9 ± 1.6^a	0.0754 ± 0.0118^a	105.5 ± 11.6^b	1.34 ± 0.15^b
50	P1-Beiyu288	24.0 ± 0.9^a	0.0684 ± 0.0027^a	88.9 ± 3.6^b	1.15 ± 0.04^{ab}
	P2-Beiyu288	21.3 ± 1.1^a	0.0563 ± 0.0044^a	112.1 ± 5.4^a	1.40 ± 0.07^a
	CK-Beiyu288	17.1 ± 1.3^b	0.0443 ± 0.0060^b	104.3 ± 3.7^a	0.95 ± 0.29^c
150	P1-Xianyu335	32.6 ± 2.2^a	0.2301 ± 0.0245^a	111.6 ± 6.1^a	3.59 ± 0.33^{ab}
	P2-Xianyu335	28.4 ± 2.5^a	0.1763 ± 0.0158^b	103.4 ± 5.1^a	4.04 ± 0.37^a
	CK-Xianyu335	23.6 ± 2.3^b	0.1274 ± 0.0925^c	107.6 ± 6.0^a	2.46 ± 0.18^b
100	P1-Xianyu335	31.9 ± 2.9^a	0.2245 ± 0.0160^a	137.1 ± 11.2^a	2.93 ± 0.16^a
	P2-Xianyu335	23.5 ± 1.5^b	0.1560 ± 0.0079^b	101.4 ± 10.3^b	3.26 ± 0.17^a
	CK-Xianyu335	22.0 ± 1.7^b	0.1781 ± 0.0103^b	116.1 ± 8.8^{ab}	2.34 ± 0.16^b
50	P1-Xianyu335	23.3 ± 1.6^a	0.1219 ± 0.0114^a	125.0 ± 12.3^a	2.13 ± 0.13^b
	P2-Xianyu335	22.8 ± 1.1^{ab}	0.1277 ± 0.0163^a	99.2 ± 6.5^a	2.77 ± 0.29^a
	CK-Xianyu335	19.8 ± 1.3^b	0.1427 ± 0.0079^a	110.3 ± 6.7^a	1.36 ± 0.12^c

In the case of cv. Beiyu288, an increased g_s and C_i were detected in P1 (Table 1). At 150 cm, g_s and C_i in P1 were significantly (LSD, $p<0.05$) higher than those in P2 and CK, respectively. A similar result was observed at the 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 g_s and C_i in each level was detected in cv. Xianyu355. Narrow-wide row spacing had no effect on leaf E in both cultivars at the 150 cm level in contrast to CK. However, the E of two cultivars (Beiyu288 and Xianyu335) was increased at the 100-cm and 50-cm heights, a significant (LSD, $p<0.05$) planting pattern effect on E was recorded in both cultivars (Table 1).

Discussion

Light availability typically varies within the canopies of closed vegetation stand, and significant variation in light occurs even within the crown of a free-standing plant (Valladares 2003). Traditionally, canopy structure was strongly related to the amount of radiation intercepted (Maddonni *et al.* 2001a). In field condition, an adjustment to fluctuating environmental factors critically affect plant resource-using efficiency and competitive potential in heterogeneous environments (Schurr *et al.* 2006). The heterogeneous light distribution was sustained during the whole growing season, even within daytime.

Light interception was associated with intracanopy light distribution and maximum light interception capacity. In the current study, total fraction of light interception of the whole canopy of maize differed significantly ($p<0.05$) between P1 and CK in two cultivars, especially at low levels of intracanopy. Higher light interception capacity is more important for maximizing RUE (Leuning *et al.* 1991) rather than intra-canopy light distribution. Light distribution through the canopy was probably heterogeneous as shown in Fig. 2 since most of the incoming PAR was intercepted at the canopy region of the upper 150 cm. Intercepted radiation by the whole canopy (84%) indicated that light validation was concentrated on the upper level of the canopy. The comparison of F between P1 and CK showed the detection of the enhancement of light interception at each level and is lower than 150 cm, especially at the height of 0 cm to 100 cm. This is based on the assumption of the function of leaf blade in maize (Zhao 1986). Leaf between a height of 0 cm to 100 cm mainly produces photosynthate for root growth metabolism and more distribution of light in these level is attributed to better root development. As for the enhancement of light interception at the height of 100 cm to 150 cm at the critical period silking stage, leaf provide nutrition to maize ear growth and more available light aid in the forming function of leaf blade. With respect to P2, the fraction of total and upper 100 cm light interception has no significant difference with CK, the leaf at the height of 0 cm to 100 cm in P2 intercept more PAR than CK, which is advantageous for root development and mineral nutrient assimilation.

The concentration of CO_2 in the atmosphere greatly affects photosynthesis and dry matter production (Morison 1985, Drake *et al.* 1997, Ward and Strain 1999, Loewe *et al.* 2000). However, the effect of CO_2 concentration was affected by other environmental factors (Curtis *et al.* 2000, Nowak *et al.* 2004). Low concentration of CO_2 in the air was continually the limiting factor of photosynthesis. High-density cultivation of crops, fertilizer, and sufficient water facilitates the absorption of more CO_2 in plants, especially during midday. Hence, CO_2 has become one of the limiting factors of production. Accounting for the four dual-acid cycle of carbon, carbon dioxide played the role of the pump to double the bundle sheath cells off carbon dioxide for C_4 plant. Therefore, the normal concentration of carbon dioxide in air conditions can make photosynthesis reach saturation. Plants using CO_2 and light intensity is related to the case in low irradiation and can only use lower concentrations of CO_2 and lower photosynthesis. However, the photosynthesis response to concentration of CO_2 was a reflection of the CO_2 effects on plant nutrient conditions rather than a direct effect of CO_2 on photosynthesis (Saxe *et al.* 1998). With the increase in irradiation, plants can absorb higher concentration of CO_2 during photosynthesis (Ihnken *et al.* 2011), and this may be due to the reduction of CO_2 concentration around the narrow-wide row maize canopy.

In natural canopies, both temperature and water vapor pressure deficit generally increased with increasing light availability from the bottom to the top of the canopy (Baldocchi *et al.* 2002, Niinemets and Valladares 2004). This covariation of environmental drivers suggests that plants in the upper canopy are often exposed to greater heat stress and may suffer greater water stress. There is evidence of lower leaf water potentials and a greater degree of midday and drought-dependent stomata closure in the upper canopy leaves in a temperate forest. Further, there is an evidence that foliage heats up to higher temperatures in the upper than in the lower canopy (Singsaas and Sharkey 2000), collectively suggesting that leaves are exposed to interacting stresses in the upper canopy. The dark reaction of photosynthesis is the chemical reaction catalyzed by enzymes. Temperature directly affects the enzyme activity (Kalttorres *et al.* 1987), and an increase in canopy temperature likely causes shifts in the optimum geographic climate areas for growth of crops and other species (Kimball and Bernacchi 2006). In the narrow-wide row-planting pattern, the canopy temperature inside each height was significantly higher than the control, which is related with extended row spacing, increased of absorbed solar radiation at surface of soil, and increase in temperature. The temperature is higher when the canopy is closer to the surface. As for the RH of canopy, the canopy in narrow-wide row planting patterns was significantly lower than that of the control, which probably results from the combined effects of temperature, intercepted PAR, and ventilation.

Photosynthesis is affected by many external conditions such as light, CO_2, and temperature. In a certain range, the photosynthetic rate is faster and the impact of these factors on photosynthesis is interrelated. Foliage photosynthetic capacity (P_N) increases two to four fold from the bottom to the top of the canopy (Meir *et al.* 2002, Niinemets *et al.* 2006). The individual plant photosynthesis and population photosynthesis of maize are always contradicting. Maize canopy change in the microenvironment plays a critical role on maize yield, especially in the light distribution characteristic of CO_2. These factors are the driving force of energy and material sources. Planting patterns on environmental factors, manifested light available radiation, temperature, and concentration of CO_2 in each level within the canopy. However, existing research shows that, in the field condition, light interception is the most important factor influencing photosynthesis (Kim *et al.* 2006, 2007; Maddonni *et al.* 2006, Agele *et al.* 2007).

Experimental results show that, under narrow-wide row planting patterns, according to the light surrounding microclimate, the photosynthesis of leaves increased significantly at different heights. The same conclusion is also proven in different cultivars of maize. The current paper argues that the narrow-wide row-planting pattern will help improve the microenvironment of crops canopy to promote photosynthesis in maize at grain-filling stage.

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