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Response of canopy structure, light interception and grain yield to plant density in maize

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Abstract

Good canopy structure is essential for optimal maize (*Zea mays* L.) production. However, creating appropriate maize canopy structure can be difficult, because the characteristics of individual plants are altered by changes in plant age, density and interactions with neighbouring plants. The objective of the current study was to find a reliable method for building good maize canopy structure by analysing changes in canopy structure, light distribution and grain yield (GY). A modern maize cultivar (ZhengDan958) was planted at 12 densities ranging from 1.5 to 18 plants/m^2 at two field locations in Xinjiang, China. At the silking stage (R1), plant and ear height increased with plant density as well as leaf area index (LAI), whereas leaf area per plant decreased logarithmically. The fraction of light intercepted by the plant (F) increased with increasing plant density, but the light extinction coefficient (K) decreased linearly from 0.61 to 0.39. Taking the optimum value of F (95%) as an example, and using measured values of K for each plant density at R1 and the equation from Beer's law, the corresponding (theoretical) LAI for each plant density was calculated and optimum plant density (9.72 plants/m^2) obtained by calculating the difference between theoretical LAIs and actual observations. Further analysis showed that plant density ranging from 10.64 to 11.55 plants/m^2 yielded a stable GY range. Therefore, taking into account the persistence time for maximum LAI, the plant density required to obtain an ideal GY maize canopy structure should be increased by 10–18% from 9.72 plants/m^2.

Introduction

Plant canopy structure is the spatial arrangement of the above-ground organs of plants in a plant community, and consists of three major features: plant geometry, plant quantity and spatial distribution of leaves (Tharakan *et al*., 2008; Li *et al*., 2017). The main variables that characterize crop canopy structure are plant height (PH), ear height (EH), leaf area index (LAI), leaf angle and leaf orientation (Bolaños and Edmeades, 1993; Stewart *et al*., 2003). Those variables are affected by different agricultural practices. For example, hybrids with different PH, leaf number, individual leaf area, leaf angle and leaf area density distribution along the main stem vary in their canopy structure (Maddonni *et al*., 2006; Torres *et al*., 2017). PH and EH increase significantly with an increase in plant density (Li *et al*., 2015*a*). The amount of leaf area expansion is reduced when plants are defoliated (e.g. by frost, hail or insects) or subjected to water or nutrient stress during the vegetative stage (Barbieri *et al*., 2000; Zhang *et al*., 2015; Turc *et al*., 2016).

Changes in canopy structure are related directly to the fraction of incident photosynthetically active radiation (PAR) intercepted by the crop (F). Toler *et al*. (1999) analysed the effect of leaf azimuth distribution on light interception for the hybrid DK689 and found that the greatest light interception values were measured in canopies with leaves perpendicular to rows. Ottman and Welch (1989) demonstrated that narrow rows (1.52 m twin rows with 0.13 m spacing) intercepted 10% more incident radiation with the lower than upper leaves compared with other planting patterns (0.38 m single rows, 0.76 m twin rows, 0.76 m single rows, 1.14 m twin rows) in an erect leaf hybrid grown at high plant density. The effect of changes in LAI on F by a plant has also been reported in previous studies. For light interception <95%, F increased consistently with LAI (Watiki *et al*., 1993; Maddonni *et al*., 2001*b*). In fact, F was found to be the most important factor affecting maize crop growth and grain production (Andrade *et al*., 1992; Edwards *et al*., 2005). Westgate *et al*. (1997) showed that early canopy closure maximizes F and increases grain yield (GY) and dry matter (DM) per unit area. Major *et al*. (1991) reported an increase in whole-plant DM and F with plant density for ten hybrids grown in Alberta, Canada. Andrade *et al*. (2002) showed that decreasing row spacing increased

F and biomass production. Flenet *et al.* (1996) observed that when the value of *F* was <95%, GY and biomass production increased consistently with an increase in the light interception. That is because a higher *F* increases plant-to-plant competition for available water and nutrients and reduces biomass production (Tollenaar and Bruulsema, 1988). Therefore, optimization of the population canopy structure and light interception (building an optimal structure) to ensure light is distributed evenly throughout the canopy and that all leaves are exposed to intermediate nearly saturating quantum flux densities is essential for maximizing crop yield (Maddonni *et al.*, 2001*a*; Li *et al.*, 2015*b*).

The effect of canopy architecture on light interception has generally been simplified in crop growth simulations, with light intercepted by the crop often related exclusively to LAI by means of exponential functions that express Beer's law (Jones *et al.*, 1986; Maddonni *et al.*, 2001*a*). As a consequence, the extinction coefficient (*K*) was found to be an appropriate summary parameter for characterizing light interception. Variations in *K* for crops grown under different cultivation conditions (e.g. plant density and row spacing) have been studied. Hikosaka and Hirose (1997) demonstrated that *K* tended to decrease as leaf angle increased, while Flenet *et al.* (1996) concluded that low *K* values in the mid- and upper canopy regions result in a more gradual attenuation and deeper penetration of light, especially if LAI is high (e.g. in high-density populations). Westgate *et al.* (1997) pointed out that altering the space between plant rows had little effect on *K* and suggested that this could be due to leaf azimuth distribution being adjusted to accommodate the planting pattern. Although previous studies have described changes in canopy structure and light interception based on different values of *K* within the plant canopy, the relationship between them and the configuration required to build an optimal canopy structure based on changes in *K* within the plant canopy remain unclear. Previous studies have reported that canopy light interception increased consistently with increasing LAI and that there was a close relationship between the two variables for values of LAI below the critical LAI value required to intercept 95% of incident irradiance (Pearce *et al.*, 1965; Papadopoulos and Pararajasingham, 1997). This implies that the value for optimal light interception is 95%. If plant density achieves optimal light interception and *K* is determined for the plant density, then according to Beer's law, the optimal plant density for building an ideal canopy can be determined.

In China, the highest yielding maize farms are located in the north-west spring maize region between 40°00′N and 45°00′N (Li and Wang, 2010; Chen *et al.*, 2012) where the highest GY in the country has increased from 17.0 t/ha in 2006 to the current value of 22.71 t/ha. During the same period, plant density has increased from 7.5 to 12.5 plants/m^2 (Wang *et al.*, 2012). However, mean plant density in the region has been reported as only 9.77 plant/m^2 (Li *et al.*, 2015*a*). Clearly, increasing plant density is an important tool for maximizing GY in this major spring maize region. However, when the plant density of maize hybrids exceeds a certain limit, GY per area decreases due to its competitive effect both on canopy structure and light distribution at the individual plant and canopy levels (Tollenaar and Lee, 2002; Widdicombe and Thelen, 2002; Borrás *et al.*, 2003; Tokatlidis and Koutroubas, 2004; Liu *et al.*, 2011). The objectives of the current study were to investigate the variability in canopy structure characteristics with changing plant density and the changes in light distribution with changing plant density, and to assess a new effective method for building an ideal canopy structure. Therefore, a field density experiment was carried out over a period of 3 years with 12 densities ranging from 1.5 to 18 plants/m^2.

Materials and methods

Field experiments were conducted during the growing season (April to October) in 2010, 2011 and 2012 using a randomized complete block design with four replications at two high-yield sites, 71 Group (43°30′N, 83°13′E, 851 m a.s.l.) and Qitai Farm (43°50′N, 89°46′E, 1020 m a.s.l.), located in the Xinjiang region of Uygur, China. The meteorological data of 2010, 2011 and 2012 and the long-term average for the 10 years from 2003 to 2012 are listed in Table 1. From 2003 to 2012, the mean daily maximum temperature ($T_{\max}$), minimum temperature ($T_{\min}$), diurnal temperature variation (T_{d}), solar radiation and precipitation (Pre) from Qitai Farm were lower than that from 71 Group during the maize life cycle, as well as over the whole year. The $T_{\max}$, $T_{\min}$, T_{d}, solar radiation and precipitation in 2010, 2011 and 2012 were similar to the 10-year average value at Qitai Farm, and the same result was found at 71 Group. The maize hybrid ZhengDan958 was selected for the current study and was grown at 12 stand densities, i.e. 1.5, 3.0, 4.5, 6.0, 7.5, 9.0, 10.5, 12.0, 13.5, 15.0, 16.5 and 18.0 plants/m^2 denoted by the labels D1 to D12, respectively. Maize hybrid ZhengDan958, with a growth period of approximately 140 days within the north-western spring maize region, was developed in 2000 by the National Crops Variety Examination and Approval Committee, China. It was also the most widely cultivated hybrid in China at the time of the current study (Li and Wang, 2010). At each experimental site, plots containing alternating narrow (0.5 m) and wide (0.7 m) rows (i.e. 1.2 m twin rows, alternately 0.5 and 0.7 m apart, with two rows as a unit), which was the main cultivation pattern used locally, were set up (Fig. 1). The intended planting density was changed by adjusting the plant spacing and each plot consisted of ten rows with an east-west orientation and a length of 10 m. At all sites, the seeds were planted in mid-April and harvested in mid-October. Three seeds were planted by hand in each hole and then thinned to one plant per hole at the third-leaf stage (V3 according to Ritchie *et al.*, 1986), and tillers were removed during the growing season so that the surviving plants reached the intended planting densities. In order to keep the crops free from drought and nutrient stress, irrigation and nitrogen were applied by drip irrigation as practised by local farmers during the growing stage. The drip irrigation system included single wing labyrinth drip tape placed in the middle of each narrow row. The dripper spacing was 0.3 m and flow rate was 3.2 l/h at an operating pressure of 0.1 MPa (Tianye Inc., China). Discharge and pressure were stable due to careful design and management. Each plot was connected to a high precision water meter (LXS-25F, Ningbo, China) and control valve. Application time and level were determined based on the local super-high-yield field quota (Table 2). Irrigation was applied 8–10 times using drip irrigation during the growing stage. The first irrigation was 60 days after sowing, with subsequent irrigations every 7–10 days, and the amount of water applied during each irrigation was 600–650 m^3/ha. Base fertilizers were supplied at 75 kg/ha urea, 150 kg/ha super phosphate and 75 kg/ha potassium sulphate prior to sowing, with an additional 800–850 kg/ha urea applied four or five times during the growing stage via drip irrigation. The first nitrogen application was 60 days after sowing, with subsequent applications every 14–20 days (double the irrigation interval), applying 150–200 kg/ha urea each time. Additionally,

Table 1. Mean daily maximum temperature, minimum temperature, diurnal temperature variation, solar radiation and precipitation during the maize growing season at Qitai Farm and 71 Group in 2010, 2011, 2012 and the long-term average for 2002–2012

		Growing season					Annual				
Site	Year	T_{max}[a] (°C)	T_{min}[b] (°C)	T_d[c] (°C)	Solar radiation (MJ m^2/d)	Pre[d] (mm)	T_{max} (°C)	T_{min} (°C)	T_d (°C)	Solar radiation (MJ m^2/d)	Pre (mm)
Qitai	2002–2012	25.31	9.54	17.60	19.85	158.7	13.69	−1.09	6.10	14.36	265.2
	2010	25.37	9.52	17.45	19.01	149.2	13.97	−1.96	5.51	14.45	235.1
	2011	25.69	9.68	17.68	19.48	150.6	13.19	−1.89	5.65	14.66	268.7
	2012	25.17	9.57	17.37	19.56	160.6	14.61	−1.30	6.15	14.88	303.1
71 Group	2002–2012	27.03	11.66	19.40	20.37	195.4	17.28	3.58	10.43	15.14	401.6
	2010	26.88	11.77	19.32	20.03	183.8	16.76	3.59	10.18	14.97	409.5
	2011	27.39	11.99	19.69	20.49	158.1	16.63	2.92	9.78	15.23	385.9
	2012	27.13	11.82	19.48	19.98	167.2	18.44	4.22	11.33	15.22	*394.8*

[a] Mean daily maximum temperature.
[b] Minimum temperature.
[c] Diurnal temperature variation.
[d] Precipitation.

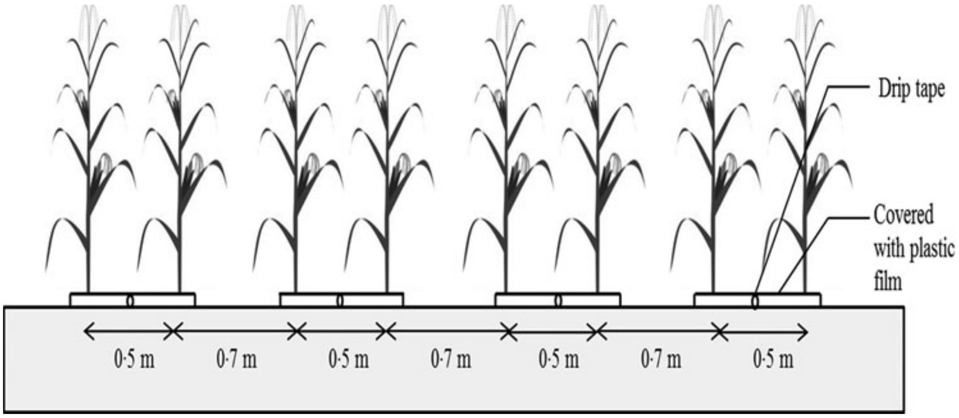

Fig. 1. Schematic diagram showing the planting patterns (0.5 + 0.7) used in the current study.

Table 2. Summary of the irrigation and fertilization events during the maize growing season at Qitai Farm and 71 Group in 2010, 2011 and 2012

Application time	1	2	3	4	5	6	7	8	9	10
Growth stage[a] (d)	60	70	80	90	100	110	120	130	140	150
Irrigation rate (m^3/ha)	60	60	60	60	60	60	60	60	60	60
Fertilizer rate (kg/ha)	200	–[b]	150	–	150	–	150	–	150	–

[a] The data are expressed as day after sowing.
[b] Indicates no application.

crops were kept free from pests, weeds and diseases at each site using conventional approved pesticides.

At V3, five successive plants were tagged in the central row of each plot. Tags were placed between leaves 3 and 4, which allowed the identification of individual leaves. The tags were moved upward (between leaves 9 and 10) at V10, and at the silking stage (R1), tags were placed at the green leaf adjacent to the ear. The green leaf area per plant at the full expansion stage of each leaf was measured in tagged plants using a non-destructive method based on lamina length and maximum lamina width (Montgomery, 1911). A leaf was considered to have senesced when half or more of its area had yellowed. The green leaf area and LAI are given by the following equations:

$$\text{Green leaf area per plant} = \Sigma\ \text{lamina length} \times \text{maximum width} \times 0{\cdot}75 \quad (1)$$

$$\text{LAI} = \text{leaf area per plant} \times \frac{\text{plant population density}}{\text{land area occupied by the plants}} \quad (2)$$

Table 3. Changes in plant and ear height with plant density for ZhengDan958 maize hybrid at 12 stand densities in 2010, 2011 and 2012

Plant density (plants/m^2)	1.5	3.0	4.5	6.0	7.5	9.0	10.5	12.0	13.5	15.0	16.5	18.0
Plant height (m)												
Mean[a]	2.67	2.68	2.71	2.75	2.78	2.82	2.86	2.89	2.92	2.96	3.00	3.04
S.E.[b]	0.021	0.032	0.022	0.024	0.019	0.016	0.028	0.026	0.031	0.039	0.027	0.026
Ear height (m)												
Mean	1.16	1.17	1.18	1.20	1.22	1.24	1.26	1.28	1.30	1.32	1.34	1.38
S.E.	0.019	0.012	0.018	0.014	0.012	0.014	0.027	0.018	0.016	0.019	0.023	0.024

[a] The data are expressed as the mean values during the three study years.
[b] Standard error.

Table 4. Analysis of variance of canopy structure, *k* and grain yield for ZhengDan958 at 12 stand densities in 2010, 2011 and 2012

	Plant height		Ear height		LAI at silking stage		LAI at mature stage		*K* at silking stage		Grain yield	
Source	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Year (*Y*)	3.503	0.051	0.063	0.939	10.354	0.061	0.871	0.427	2.15	0.131	0.901	0.415
Plant density (*D*)	84.11	<0.001	46.44	<0.001	1013.38	<0.001	1243.83	<0.001	290.43	<0.001	159.68	<0.001
Y × *D*	0.275	0.965	0.139	0.918	1.114	0.378	0.814	0.69	0.948	0.543	0.783	0.724
S.E.[a]	11.09		6.71		0.15		0.03		0.01		1.03	

[a] standard error.

The fraction of light intercepted by the plant was measured in completely developed leaves at the V6, V9, V12, V15, V18 and V21 stages, and at 15-day intervals between R1 and physiologically mature stage (R6) using a 1.0 m line LI-191SA quantum-sensor (LI-COR, Lincoln, NE, USA). All measurements were taken at the bottom (above the senescing leaves) and top (above the tassel) of the canopy. In each plot, 15 independent records were taken within each level between 11:00 and 14:00 h on clear days. The incident PAR for each level was obtained as the average of 15 measurements: five with the sensor bar placed at equidistant positions across the narrow-row space and perpendicular to the row, five with the sensor bar placed at the centre of the narrow-row space and parallel with the row and five with the sensor bar placed at the centre of the wide-row space and parallel with the row. Based on Beer's law, *F* and *K* were calculated as follows (Flenet *et al.*, 1996; Maddonni *et al.*, 2001*a*).

$$F = \left(1 - \frac{\mathrm{PAR_B}}{\mathrm{PAR_A}}\right) \times 100 \qquad (3)$$

$$K = \frac{-\mathrm{Ln}((\mathrm{PAR_B})/(\mathrm{PAR_A}))}{\mathrm{LAI}}$$

where $\mathrm{PAR_B}$ was the PAR measured at the bottom of the canopy (above the senescing leaves) and $\mathrm{PAR_A}$ was the incident PAR at the top of the canopy. The LAI (green areas) was measured from the bottom to the top of the canopy.

To calculate PH (the distance from the soil surface to the uppermost tassel), EH (the distance from the soil surface to the uppermost ear), number of rows per ear and number of seeds per row, 20 plants from the two central rows in each plot were harvested randomly at R6 and the mean values recorded. To calculate total DM, the total number of plants, number of ears per plant and grain weight, 8 m of the two central rows (considering the border effect) was harvested in each plot. After separating the different plant parts, including (stem + leaf + tassel), cob, husk and grain, the samples from each part were dried to a constant weight at 80 °C for approximately 3 days and their weight recorded. GY was calculated at 14% moisture content as determined using a PM-8188 portable moisture meter (Kett Electric Lab., Tokyo, Japan) and the harvest index (HI) determined.

Data sets collected over the 3 years were pooled and various relationships and correlations among variables were tested. Associations among variables were investigated using linear and non-linear models. Analysis was performed using the SAS statistical software (version 9.0, SAS Institute Inc., Cary, NC, USA).

Results

Plant and ear height

Plant density affected plant agronomic parameters significantly (Table 3). As plant density increased, PH and EH increased from 2.67 to 3.04 m and from 1.16 to 1.38 m, respectively, and the increases observed in PH and EH in response to plant density were approximately linear ($P < 0.01$). Analysis of the changes in PH and EH in the three growing seasons showed that only plant density influenced PH and EH significantly ($P < 0.01$) (Table 4).

Leaf area

Leaf area per plant varied with time after plant emergence (VE) and measurements were divided into two stages (before R1 and after R1) for each plant density (Fig. 2). Before R1, leaf area per

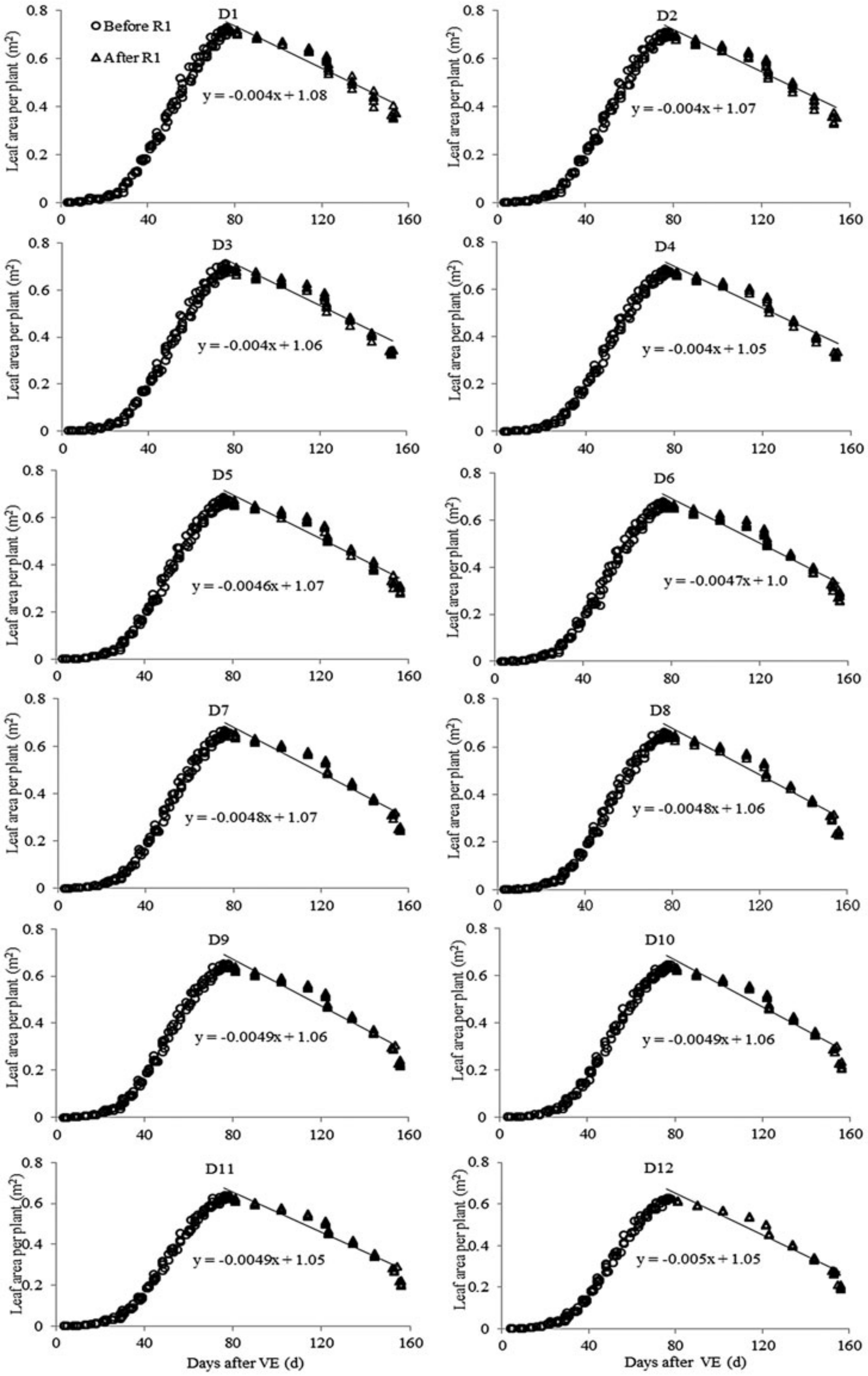

Fig. 2. Variability in leaf area per plant with number of days after plant emergence (VE) for ZhengDan958 maize hybrid cultivated at 12 stand densities in 2010, 2011 and 2012.

plant increased with the number of days after VE. The maximum leaf areas per plant were measured at R1 and these decreased logarithmically from 0.72 to 0.63 m^2 with plant densities of 1.5–18 plants/m^2, respectively (Fig. 3(*a*)). After R1, the leaf area per plant decreased significantly in proportion to the number of days after VE, and those relationships were linear ($P < 0.01$). The minimum leaf areas per plant were measured at R6 and these decreased logarithmically from 0.37 to 0.2 m^2 with increasing plant density from 1.5 to 18 plants/m^2, respectively (Fig. 3(*a*)).

At R1, LAI increased from 1.08 to 10.18 when the plant density increased from 1.5 to 18 plants/m^2, respectively, and a linear equation fitted that relationship ($P < 0.01$) (Fig. 3(*b*)). At R6, the response of LAI to changes in plant density followed a similar trend to that at R1 (Fig. 3(*b*)), but the relationship between the two was described by a logarithmic equation ($P < 0.01$). Analysis of the changes in LAI at R1 and R6 in three growing seasons showed that only plant density exhibited a significant influence on LAI ($P < 0.01$) (Table 4).

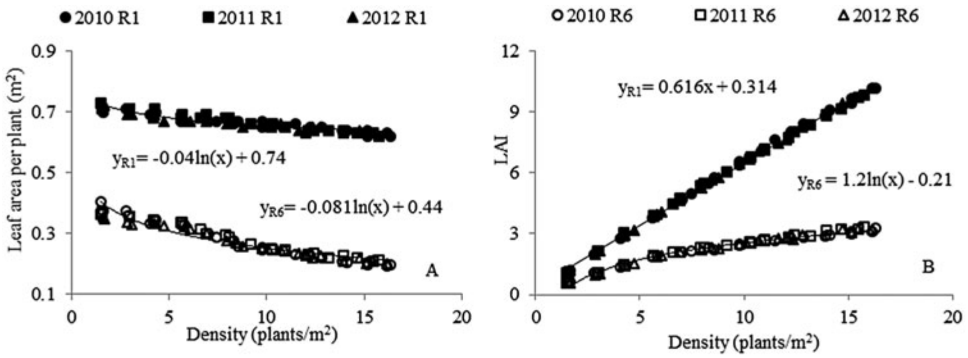

Fig. 3. Relationships between leaf area per plant and plant density (*a*), and leaf area index (LAI) and plant density (*b*) at the silking (R1) and mature stages (R6) for ZhengDan958 maize hybrid cultivated at 12 stand densities in 2010, 2011 and 2012.

Light interception

The relationship between F and number of days after VE followed a trend similar to that of leaf area per plant for each plant density (Fig. 4). Before R1, F increased with number of days after VE. Maximum F values were obtained at R1 and increased from 40.74 to 99.04% (mean values for 3 years) with increasing plant density from 1.5 to 18 plants/m^2. However, after R1, F showed a significant linear decrease with increasing number of days after VE ($P < 0.01$).

Extinction coefficient

The extinction coefficient for each plant density at R1 was calculated: the relationship between K and plant density demonstrates that plant density affects K significantly at R1 ($P < 0.01$) (Fig. 5). As plant density increased from 1.5 to 18 plants/m^2, K decreased from 0.61 to 0.39. The relationship between K and plant density was described by linear regression ($P < 0.01$) and further analysis demonstrated that K decreased by 0.02 with each 1 plant/m^2 density increase. Analysis of the changes in K in three growing seasons showed that only plant density exhibited a significant influence on K ($P < 0.01$) (Table 4).

Theoretical optimum density at the silking stage for building an ideal canopy structure

The results from the current study demonstrate that LAI exhibits a significant positive correlation with plant density at R1 ($P < 0.01$), and the relationship between the two can be described by a linear equation (Fig. 3(*b*)). The line was labelled line 1 (line AOB), as shown in Fig. 6.

The K represents the efficiency of light interception, and it decreased linearly with plant density at R1 (Fig. 5). Previous studies confirmed that 95% was the optimal value for light interception in maize. Therefore, taking the optimal light interception value (95%) as an example and using the measured values of K for each plant density at R1, the corresponding LAI for each plant density was calculated and the relationship between the theoretical LAI values and plant density described by a linear equation. This was labelled line 2 (line A′OB′), as shown in Fig. 6.

Since the values of K for calculated LAIs were obtained from experimental data, the computed LAI values did not match their corresponding plant densities, with one exception. This point represents the best combination between observed data and theoretical prediction and was located at the intersection of line 1 and line 2 (named point O), as shown in Fig. 6.

Based on the two regression equations (line 1 and line 2), the coordinates of O were determined to be LAI = 6.3 and plant density = 9.72 plants/m^2. Therefore, under field conditions, optimal F value might be achieved with maize plants at a density of 9.72 plants/m^2, with LAI maintained at a value of 6.3. For plant densities <9.72 plants/m^2 (AOA′ in Fig. 6), the plant density and LAI values were too low for the maize canopy to reach 95% intercepted light, whereas for plant densities >9.72 plants/m^2 (BOB′ in Fig. 6), the maize plant density and LAI values were too high. Therefore, point O represents optimal F value for a maize canopy at R1, and the corresponding plant density could be regarded as optimal for building an ideal canopy.

Optimum plant density for building an ideal canopy structure

All data used to calculate the optimum plant density were collected at R1 of maize. However, because light leakage occurs during canopy formation before R1 and senescence occurs after R1, the optimal plant density for building an ideal canopy should be higher than estimated at point O.

To find that point, variations in DM per unit area at the mature stage, GY per unit area and HI at different plant densities were taken into account ($P < 0.01$). The DM per unit area varies by a logarithmic curve in response to changes in plant density (Fig. 7(*a*)). Using multiple comparisons between DM per unit area at each plant density, it was found that the response of DM per unit area to plant density could be divided into two ranges: the change range ($\leqslant$10.42 plants/m^2) and the stable range (>10.42 plants/m^2). Plant density at the turning point (10.42 plants/m^2) was 6.72% higher than that at point O (9.72 plants/m^2). It indicated that to build a maize canopy structure with a high DM yield, plant density should be 6.72% higher than that at point O.

The GY per unit area increased from 8.5 to 19.45 t/ha, then decreased from 19.45 to 15.95 t/ha; a quadratic equation fitted the relationship between plant density and GY (Fig. 7(*b*)). Analysis of the changes in GY per unit area over three growing seasons showed that only plant density exhibited a significant influence on GY per unit area ($P < 0.01$) (Table 4). The highest GY (19.59 t/ha) was obtained at a plant density of 11.09 plants/m^2, which was 14.09% higher than that at point O (9.72 plants/m^2). In fact, a GY higher than 95% of the maximum GY could be considered the stable GY range, and it corresponded to a plant density ranging from 10.64 to 11.55 plants/m^2 (denoted as points O′ and O″, respectively), which was 9.47 and 18.83% higher, respectively, than at

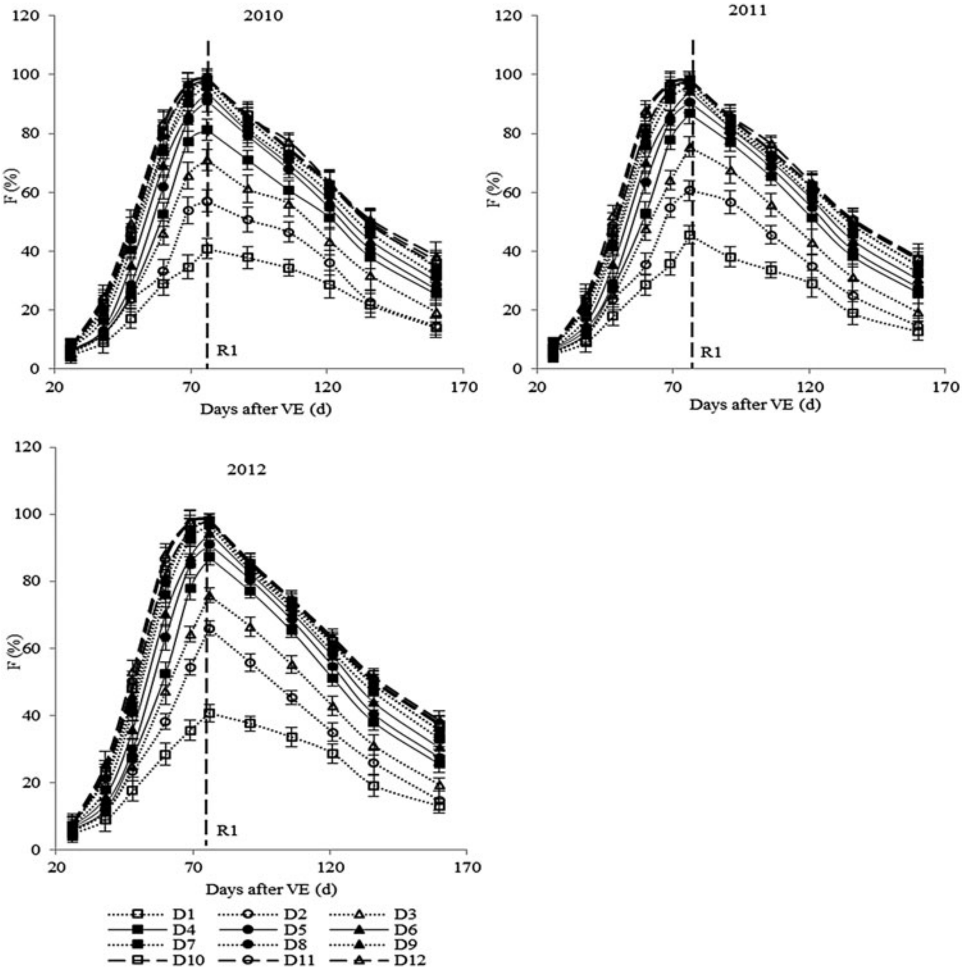

Fig. 4. Variability in the fraction of light intercepted by the plant (*F*) with number of days after plant emergence (VE) for ZhengDan958 maize hybrid cultivated at 12 stand densities in 2010, 2011 and 2012.

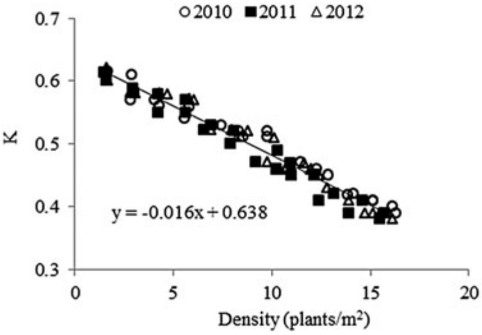

Fig. 5. Relationship between light extinction coefficient (*K*) at the silking stage (R1) and plant density for ZhengDan958 maize hybrid cultivated at 12 stand densities in 2010, 2011, and 2012.

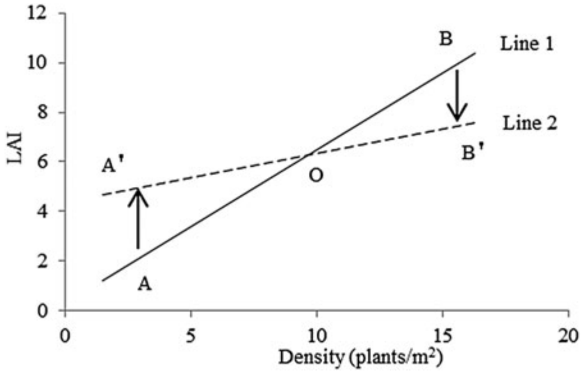

Fig. 6. Relationship between leaf area index (LAI) and plant density at the silking stage (R1): line 1, LAIs are from experimental values; line 2, LAIs are from theoretical values.

point O. Therefore, taking the stable GY range into account, the plant density for building a high-yield maize canopy structure should not exceed 18.83% of that at point O.

The HI decreased from 0.64 to 0.4 with increased plant density. The relationship between the two variables is described by a cubic-curve equation (Fig. 7(*c*)), with a turning point in the HI (0.52) at a plant density of 8.33 plants/m^2. According to the relationship between HI and plant density, HI values >95% of the maximum HI and <105% of the maximum HI could be considered as the stable HI range, corresponding to a plant density of 5.73–11.64 plant/m^2 (which was 19.75% higher than at point O). Therefore, given a stable HI range, the plant density for building a high-yield maize canopy structure should not exceed 19.75% of that at point O.

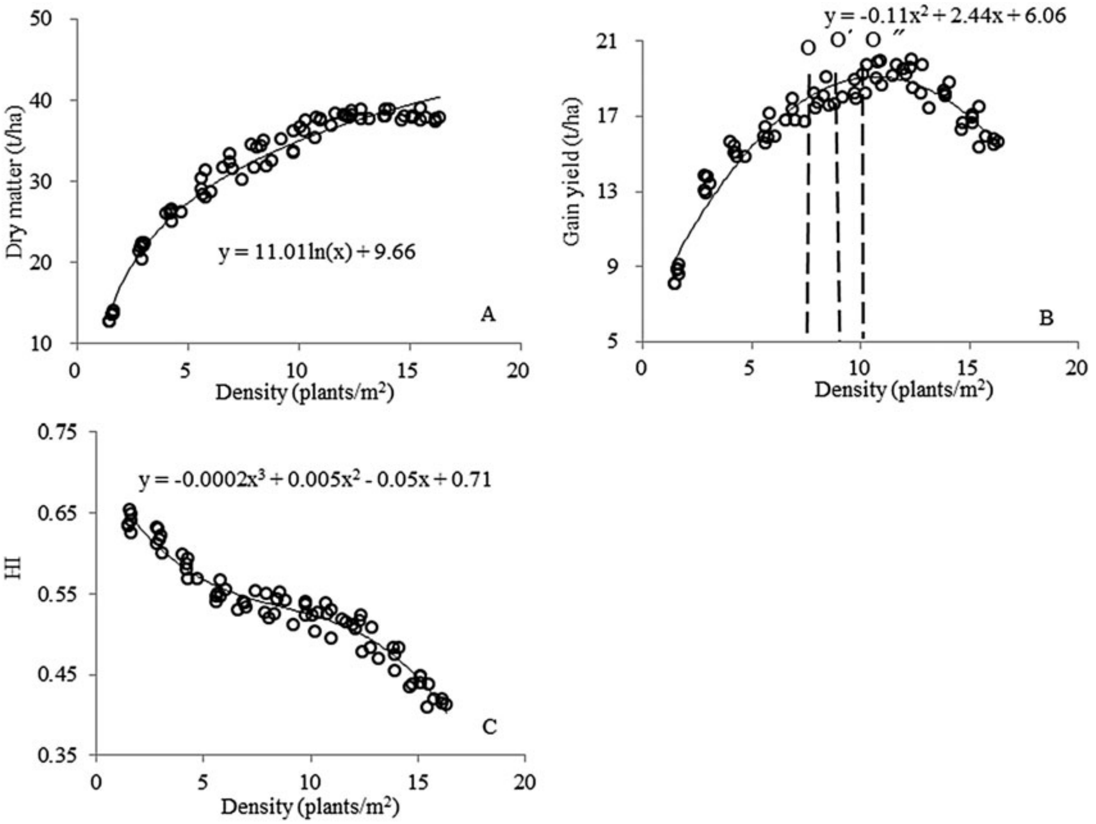

Fig. 7. Relationships between dry matter per unit area (*a*), grain yield (*b*) and HI (*c*), and plant density for ZhengDan958 maize hybrid cultivated at 12 stand densities in 2010, 2011 and 2012.

Thus, taking the stable DM, GY and HI ranges into account, the plant density for building a high-yield maize canopy structure should be 10–18% higher than at point O (9.72 plants/m^2).

Discussion

Changes in plant density can produce significant changes in canopy architecture. Li *et al.* (2015*a*) showed that an increase in plant density from 6.0 to 15.96 plants/m^2 resulted in increases in PH and EH values of 2.66–3.36 m and 0.93–1.55 m, respectively, and significant positive linear relationships between both PH and EH and plant density were detected. Westgate *et al.* (1997) reported that when maize crops were grown at row widths of 0.76 and 0.5 m, the plant population modified the maximum LAI. Tollenaar *et al.* (1994) planted maize at three plant densities (4, 7 and 10 plants/m^2) and showed that LAI increased from 4 to 10 plants/m^2 at R1, but leaf area per plant decreased from 0.56 to 0.42 plant/m^2; similar results were obtained by Cox (1996) and Pepper *et al.* (1977). The current results demonstrated that variations observed in canopy characteristics were consistent with previous studies; however, with an increase in plant density from 1.5 to 18 plants/m^2, leaf area per plant decreased logarithmically at the silking and mature stages, while LAI increased linearly at R1 and logarithmically at R6, which differed from previous studies (Maddonni *et al.*, 2006; Torres *et al.*, 2017). The differences between the current results and those of previous studies are possibly associated with the larger plant density range and smaller density gradients, which allowed calculation of a more accurate regression equation.

Modifying the canopy architecture affects the distribution of light within the maize canopy. The current results showed that the variability in *F* followed a trend similar to that of LAI for each plant density, increasing then decreasing with number of days after VE; the maximum values were obtained at R1, which was consistent with previous studies (Watiki *et al.*, 1993; Westgate *et al.*, 1997; Maddonni *et al.*, 2001*a*). From those results, it can be inferred that light interception increased rapidly with increasing maize LAI, particularly in the high-density plots. Canopy light interception increased with increasing LAI and there was a close relationship between the two variables for values of LAI up to the critical LAI, i.e., that which is required to intercept 95% of incident radiation (Pearce *et al.*, 1965; Papadopoulos and Pararajasingham, 1997). This implies that 95% was the maximum value for the optimal *F* in a maize canopy. Additionally, previous studies showed that the relationship between *F* and LAI can be described by Beer's law (Jones *et al.*, 1986; Maddonni *et al.*, 2001*a*). Therefore, in the current study, it was assumed that if each plant density at R1 can achieve optimal *F*, and that *K* for each plant density can be determined based on a density experiment, then according to Beer's law, LAIs (theoretical values) can be calculated for each plant density at the optimal light interception. As a result, the optimal plant density and LAI values for the canopy were determined based on two regression equations using experimentally observed and theoretically calculated LAI values. Accordingly, the current results suggest that a maize canopy should reach optimal *F* when maize plants are at a density of 9.72 plants/m^2 and the LAI is maintained at 6.3.

In fact, plant morphological structures, such as PH, EH, LAI, leaf angle and leaf orientation, have not developed completely before R1 and they change constantly with day after VE (Bolaños and Edmeades, 1993; Stewart *et al*., 2003). Thus, the response of canopy structure (LAI) and the *F* to plant density before R1 did not reflect the maize hybrid's density tolerance in the current study. After R1, although the plant morphological structures have developed completely, the LAIs and *F* are constantly declining due to leaf senescence (Barbieri *et al*., 2000; Zhang *et al*., 2015). Again, the responses of canopy structure and *F* to plant density after R1 in the current study did not reflect the density tolerance of the maize hybrid. Therefore, all values used in the current calculations were collected at R1: because the plant morphological structures have developed completely, the LAIs and *F* are maximal and stable over a short period of time at this stage (Bolaños and Edmeades, 1993; Stewart *et al*., 2003). But taking into account the persistence time for maximum LAI and *F* at R1, the plant density required to obtain an ideal high GY maize canopy structure should be increased (Tollenaar and Bruulsema, 1988; Watiki *et al*., 1993; Girardin and Tollenaar, 1994; Borrás *et al*., 2003). Therefore, to build an ideal high GY maize canopy structure, GY per unit area, DM accumulation and HI should be considered. The results from the current study suggest that under field conditions, if the plant density for a maize canopy capable of reaching the optimal *F* was known, then an ideal canopy structure may be built by increasing the current plant density by 10–18% from 9.72 plants/m^2.

In the current study, all data were obtained under optimal growth and development conditions (appropriate climate and abundant provision of water and nutrients) and the maize hybrid ZhengDan958 was used, which is widely grown in China. Therefore, studies on the effects of plant density on maize canopy structure and light distribution are essential for determining optimal canopy structure and maximizing the northwest spring maize yield of China. Additionally, the current research represents a study of the relationships between canopy structure and light distribution within the plant canopy that is generally applicable to maize. However, changes in light distribution and GY under different plant densities also exist in DM partitioning and light use efficiency and more research is required in those areas.

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Ethical standards. Not applicable.

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