

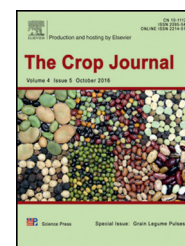
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# Influence of plant architecture on maize physiology and yield in the Heilonggang River valley

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## ABSTRACT

The size and distribution of leaf area determine light interception in a crop canopy and influence overall photosynthesis and yield. Optimized plant architecture renders modern maize hybrids (*Zea mays* L.) more productive, owing to their tolerance of high plant densities. To determine physiological and yield response to maize plant architecture, a field experiment was conducted in 2010 and 2011. With the modern maize hybrid ZD958, three plant architectures, namely triangle, diamond and original plants, were included at two plant densities, 60,000 and 90,000 plants ha<sup>-1</sup>. Triangle and diamond plants were derived from the original plant by spraying the chemical regulator Jindele (active ingredients, ethephon, and cycocel) at different vegetative stages. To assess the effects of plant architecture, a light interception model was developed. Plant height, ear height, leaf size, and leaf orientation of the two regulated plant architectures were significantly reduced or altered compared with those of the original plants. On average across both plant densities and years, the original plants showed higher yield than the triangle and diamond plants, probably because of larger leaf area. The two-year mean grain yield of the original and diamond plants were almost the same at 90,000 plants ha<sup>-1</sup> (8714 vs. 8798 kg ha<sup>-1</sup>). The yield increase (up to 5%) of the diamonds plant at high plant densities was a result of increased kernel number per ear, which was likely a consequence of improved plant architecture in the top and middle canopy layers. The optimized light distribution within the canopy can delay leaf senescence, especially for triangle plants. The fraction of incident radiation simulated by the interception model successfully reflected plant architecture traits. Integration of canopy openness is expected to increase the simulation accuracy of the present model. Maize plant architecture with increased tolerance of high densities is probably dependent on the smaller but flatter leaves around the ear.

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## 1. Introduction

Canopy architecture is an important factor determining yield of many crops as a result of interplant competition for light distribution and absorption, particularly in a dense population [1]. Canopy functions (e.g. photosynthesis) improve as leaf area index (LAI) increases until LAI reaches approximately 4 for many maize (*Zea mays* L.) hybrids, but decrease with further LAI increase [2,3]. Correspondingly, grain yield of maize first increases and then decreases with increasing plant densities. Modern maize hybrids, which have erect leaves above the ear and flat leaves below the ear, can tolerate high plant densities, thus yielding better [4–6]. These cultivars have been widely accepted because of higher yields, but yields are lower than expected in some regions where solar radiation is limited, particularly during critical periods such as the silking or grain-filling periods. Reduced solar radiation can slow elongation of internodes [7], reduce leaf photosynthesis, and result in poor kernel setting in maize [8]. In the Heilonggang River valley (in the northern part of the North China Plain), almost all modern maize hybrids used in the past decade have not produced the expected grain yield under any favorable conditions that researchers or farmers could provide [9]. The suppressed yield in this area is assumed to result from insufficient photosynthetically active radiation (PAR) because of cloudy and drizzly weather conditions during silking and grain filling [10–12]. Canopy architecture could determine how PAR is intercepted and consequently influence canopy photosynthesis and grain yield [13–15]. Thus, optimizing plant architecture could be a method for increasing maize yield in this region.

Photosynthate for maize yield is produced largely by five or six leaves near and above the ear [16–18], but these leaves are largely shaded at high plant densities, resulting in reduced productivity. Liu et al. [18] found that removal of the two uppermost leaves was an effective way to increase maize yield at high densities as a result of increased kernel number per ear and increased ear number per unit area [18]. Kernel setting and kernel growth in maize are associated with light interception during the flowering period [19] and with assimilate production and translocation during the grain filling period (source–sink relationships). Both processes interact with ear position on the plant and are affected by position of leaves relative to the ear [17,20]. With this relationship in mind, it would be possible to achieve a further increase in grain yield for modern maize hybrids if plant architecture could be improved.

As described above, evaluation of plant architecture depends strongly on morphological and physiological parameters such as leaf area, angle and orientation, photosynthesis, and yield formation. It is difficult or impossible to collect robust field measurements of so many parameters, because of the costs of time and labor. Light projection models [21–23] and canopy architectural models [23] have been used in the evaluation of maize plant architecture. However, these models require even more parameters to assure simulation accuracy. It is desirable to develop a simple practice-oriented model that needs fewer parameters, based on a combination of subcomponents of the above models that are related to light interception or light distribution in the crop canopy.

The objectives of this study were accordingly to (i) evaluate physiological and yield responses of summer-planted maize to changes in plant architecture, and to (ii) develop a practice-oriented light interception model for the evaluation of maize plant architecture.

## 2. Materials and methods

### 2.1. Experimental site and design

The field experiment was conducted in 2010 and 2011 at Wuqiao Experimental Station (37°41′02″N, 116°37′23″E) of China Agricultural University, located in the Heilonggang River valley in the east of the North China Plain. In this region, soils are loams with pH of approximately 8.0. Soil at 0–20 cm depth contains 11.5 mg kg<sup>-1</sup> organic matter, 1.1 mg kg<sup>-1</sup> total nitrogen, 45.2 mg kg<sup>-1</sup> available phosphorus, and 187.3 mg kg<sup>-1</sup> available potassium. Mean annual precipitation and temperature are 560 mm and 14.0 °C, respectively. Weather variables during the 2010 and 2011 maize growing seasons are shown in Fig. 1.

The experiment was arranged in a split-plot design with plant density as the main factor and plant architecture as the second factor. Maize hybrid ZD958, which has been widely adopted in the region in the past decade, was used. Two plant densities were applied: 60,000 and 90,000 plants ha<sup>-1</sup>. Regulated plant architectures (triangle and diamond) were obtained by spraying the chemical regulator “Jindele” (with active ingredients ethephon and cycocel; EC). Triangle plants were obtained by spraying 0.15 L ha<sup>-1</sup> EC at the 6- and 8-leaf stages and diamond plants were obtained by spraying 0.225 L ha<sup>-1</sup> EC at the 6-leaf and 0.15 L ha<sup>-1</sup> EC at the 12-leaf stage. The original plants received the same amounts of H<sub>2</sub>O. The plot size was 6 m × 10 m with a row spacing of 0.6 m, and each treatment had three replicates.

### 2.2. Field management

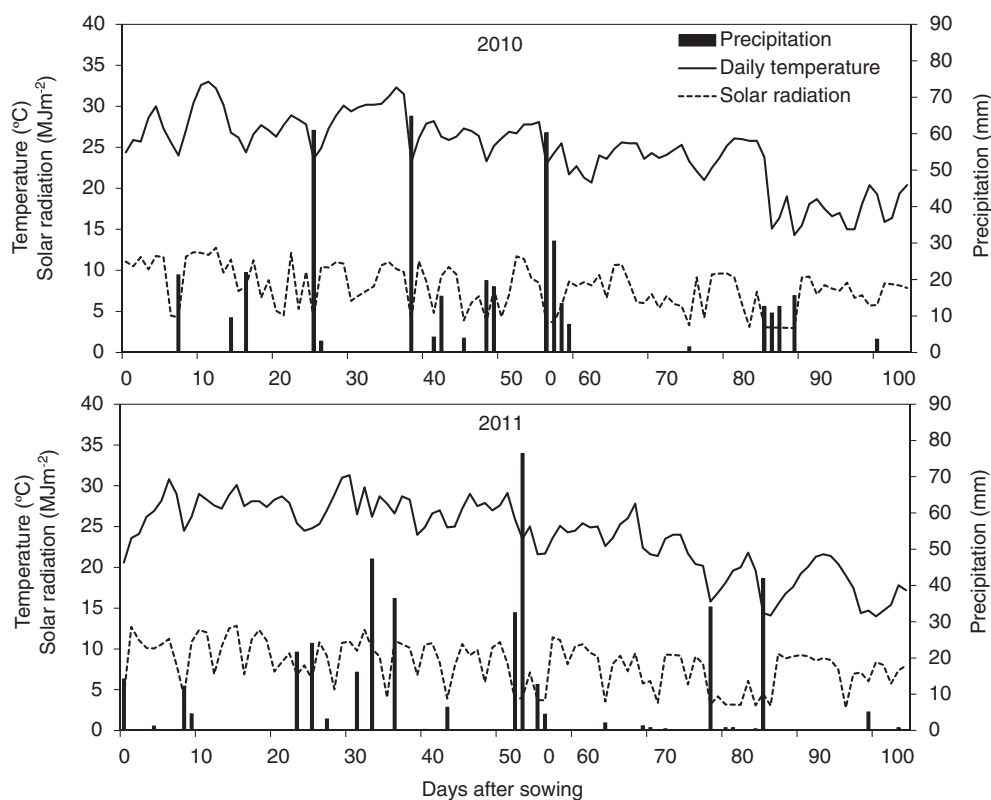
Maize seeds were manually sown into the standing stubble of winter wheat without tillage. The sowing and harvesting dates were June 24 and October 6, respectively, in both years. At sowing, 60 kg N ha<sup>-1</sup>, 105 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup>, 120 kg K<sub>2</sub>O ha<sup>-1</sup>, and 15.0 kg ZnSO<sub>4</sub> ha<sup>-1</sup> were applied, and an additional extra 120 kg N ha<sup>-1</sup> was applied at the 6-leaf stage. Irrigation (approximately 75 mm ha<sup>-1</sup>) was applied immediately after sowing to achieve uniform emergence. Optimal management was used to control weeds, insects and diseases during the entire maize growing period.

### 2.3. Plant sampling and management

#### 2.3.1. Leaf area index and leaf orientation value (LOV)

At silking stage and 25 days after silking in each plot, three plants were selected randomly in each plot to determine green leaf area (GLA). GLA was calculated as  $\Sigma$  (leaf length × maximum leaf width) × 0.75. Leaves with half yellow area were considered as senesced.

Leaf angles (LA) from the vertical of 10 randomly selected plants in each plot were measured with a clinometer at



**Fig. 1 – Mean daily temperature (°C), solar radiation ( $\text{MJ m}^{-2}$ ), and precipitation (mm) during maize growing seasons (104 day; June 24–October 6 in both years) in 2010 and 2011. Weather information is from Wuqiao Experimental Station.**

silking. Leaf length from the collar to the flagging point of each leaf blade was measured to calculate LOV together with LA:

$$\text{LOV} = \sum_{i=1}^n \left[ \alpha \left( \frac{L_f}{L_t} \right) \right] / n.$$

where  $\alpha$  is the measured leaf angle,  $L_f$  the leaf length from collar to flagging point,  $L_t$  the total length of each leaf, and  $n$  the number of measured leaves [24].

### 2.3.2. Canopy openness

Canopy openness was quantified by the visible part of the sky, ranging from 0 to 100% (0 full coverage; 100% open area) measured with an LAI-2000 plant canopy analyzer (Li-Cor, Lincoln, NE, USA). Measurements were performed close to sunset on a clear day at silking and 25 days after silking. Readings were first recorded at the top of the canopy and then at the positions of three layers including (i) upper (>leaf 15), (ii) middle (leaves 13–15; leaf 14 is the ear leaf), and (iii) bottom layer (<leaf 13). All measurements were performed in un-sampled plants with four replicates.

### 2.3.3. Leaf SPAD values

To determine leaf relative chlorophyll content and leaf senescence over time during the late grain filling period, SPAD values of all leaves of 10 plants in each plot were measured with a SPAD-502 chlorophyll meter at silking, 10 days after silking (DAS), 20 DAS, and 40 DAS in 2011.

### 2.3.4. Dry matter and grain yield

At the 6-leaf and 12-leaf, silking, and mid-grain-filling (about 25 days after silking) stages and at harvest, the above ground parts of three randomly selected plants were collected and then leaves, stems, and/or grain were separated. The samples were dried in an oven at 80 °C for 48 h and weighed to determine whole-plant dry matter (DM;  $\text{g plant}^{-1}$ ). DM accumulation per unit area ( $\text{kg ha}^{-1}$ ) = whole-plant DM accumulation  $\times$  plant density.

At harvest, all ears in four adjacent rows 5 m long in the center of each plot were collected and counted. Kernels per ear were counted and kernels were threshed and oven-dried at 80 °C to constant weight. Six samples of 1000 kernels were counted and weighed to measure 1000-kernel weight. The grain yield was adjusted to 14% moisture content.

## 2.4. Model validation and simulation

The relationship between the fraction of incident PAR intercepted by the canopy (fIPAR) and LAI was described by Maddonni et al. [22] as

$$\text{fIPAR} = 1 - e^{-K \times \text{LAI}} \quad (1)$$

where  $K$  is a light attenuation coefficient.

Welles and Norman [23] reported that the penetration rate of incident light could be described as

$$T(\theta, \phi) = \exp[-G(\theta, \phi)\mu S(\theta, \phi)] \quad (2)$$

where  $G(\theta, \phi)$  is the fraction of leaf projected direction (zenith angle  $\theta$ , azimuth angle  $\phi$ ),  $\mu$  is leaf density (leaf area per cubic meter of canopy), and  $S(\theta, \phi)$  is light path length through the canopy. Here, azimuth angle will not be considered in the formula, because the LAI-2000's optical sensor averages over azimuth. The formula for light penetration ratio can be expressed as

$$T(\theta) = \exp[-G(\theta)\mu S(\theta)] \quad (3)$$

Based on (1) and (3),  $T(\theta)$  can be further expressed as

$$T(\theta) = 1 - \text{fIPAR} = e^{-K \cdot \text{LAI}} \text{ or } \exp[-G(\theta, \phi)\mu S(\theta, \phi)] = e^{-K \cdot \text{LAI}} \quad (4)$$

The light attenuation coefficient  $K$  is thus

$$K = \frac{G(\theta, \phi)\mu S(\theta, \phi)}{\text{LAI}} \quad (5)$$

In a homogeneous canopy, leaf density  $\mu$  is expressed as

$$\mu = \frac{\text{LAI}}{H}, \quad (6)$$

where  $H$  is canopy height.

Light path length  $S$  is expressed as

$$S(\theta) = \frac{H}{\cos \theta}, \quad (7)$$

where  $\theta$  is zenith angle.

Substituting Eqs. (6) and (7) into Eq. (5) yields

$$K = \frac{G(\theta)}{\cos \theta}. \quad (8)$$

Projected area  $G$  of a canopy toward the direction of  $\theta$  is expected to be

$$G(\theta) = \begin{cases} \sin \alpha \cos \theta & (\theta - \alpha \leq 0) \\ \frac{2}{\pi} \sqrt{\sin(\alpha + \theta) \sin(\theta - \alpha)} + \left(1 - \frac{2}{\pi}\right) \cos \theta \sin \alpha & (\theta - \alpha > 0) \end{cases} \quad (9)$$

where  $\alpha$  is leaf angle from the vertical [23] and  $\theta$  is zenith angle.

Based on Eqs. (8) and (9), the light attenuation coefficient  $K$  may be expressed as

$$K = \begin{cases} \frac{\sin \alpha}{\cos \theta} & (\theta - \alpha \leq 0) \\ \frac{2}{\pi \cos \theta} \sqrt{\sin(\alpha + \theta) \sin(\theta - \alpha)} + \left(1 - \frac{2}{\pi}\right) \sin \alpha & (\theta - \alpha > 0) \end{cases} \quad (10)$$

fIPAR intercepted by the canopy can be finally expressed as

$$\text{fIPAR} = \begin{cases} 1 - e^{-\sin \alpha \cdot \text{LAI}} & (\theta - \alpha \leq 0) \\ 1 - e^{-K \cdot \text{LAI}} & (\theta - \alpha > 0) \end{cases} \quad (11)$$

## 2.5. Statistical analysis

An analysis of variance of grain yield and grain yield components was performed with PROC MIXED of SAS 9.3 (SAS Institute, Cary, NC, USA). Effects of plant density, plant architecture, and their interaction were treated as fixed and field replicates were treated as random. Correlation between canopy openness and fIPAR was calculated with PROC CORR of SAS. Significance of differences between effects of plant architectures was determined by t test ( $\alpha < 0.05$ ).

## 3. Results

### 3.1. Plant height and leaf length

The plant heights of the triangle, diamond, and original plants were 242, 220, and 258 cm with ear heights of 101, 89, and 121 cm, respectively, at 60,000 plants  $\text{ha}^{-1}$  (Fig. 2). At 90,000 plants  $\text{ha}^{-1}$ , the mean plant height and mean ear height, on average across three plant architectures, were 2–3 cm higher than at 60,000 plants  $\text{ha}^{-1}$ . Across plant densities, plant width of original plants was largest (ca. 120 cm), followed by diamond plants (ca. 110 cm) and triangle plants (ca. 80 cm).

The leaf length of the regulated plants was markedly smaller than that of the original plants, and the difference occurred mainly at leaves 9–15 (Fig. 3). At the high plant density, the difference was more pronounced (Fig. 3-B). The length of leaves 12–15 of the diamond plants was significantly larger than that of the triangle plant. The leaf area of the triangle and diamond plants decreased by 8.2% and 8.8%, respectively, at 60,000 plants  $\text{ha}^{-1}$ , and by 13.9% and 13.1% at 90,000 plants  $\text{ha}^{-1}$ , compared with that of the original plant. The leaf area reduction was concentrated mainly at leaves 9–16 at 60,000 plants  $\text{ha}^{-1}$ , and moved to leaves 14–16 at 90,000 plants  $\text{ha}^{-1}$  (Fig. 4). All the leaves above the ear on the regulated plants were smaller than that of the original plants. The largest single leaf was leaf 12 on original plants, but moved upward to leaf 14 (the ear leaf) for diamond plants and downward to leaf 11 for triangle plants.

### 3.2. Leaf orientation value (LOV)

According to the LOV formula, the larger the LOA, the more erect is the leaf. Across the three canopy layers at both densities, diamond plants showed the smallest mean LOV and original plants the largest (Fig. 5). In the upper canopy layer, triangle plants had the largest LOV and diamond plants the smallest. In the middle layer (leaves 13–15), the LOV values were similar for all three plant architectures at the low density, but LOV of diamond plants was significantly smaller at the high density. In the bottom layer (leaves <13th), the original plants had the largest LOV.

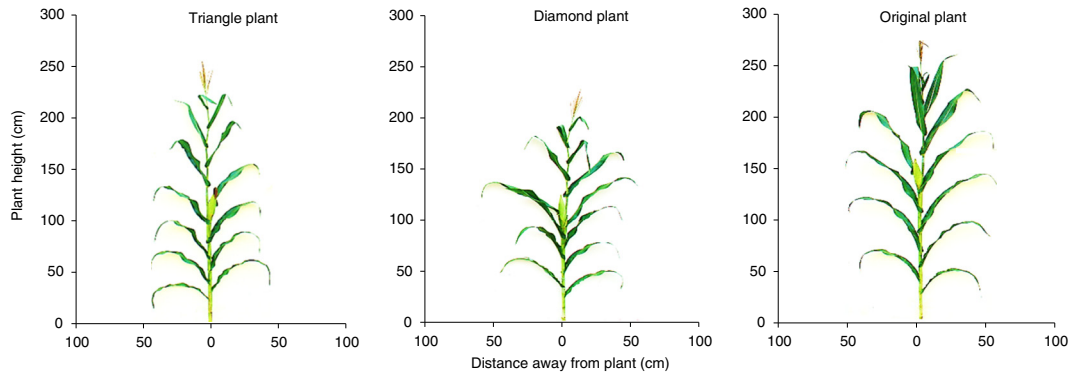
### 3.3. Evaluation of plant architecture

#### 3.3.1. Effect of plant architecture on canopy openness

The original plant had the smallest openness at the bottom of the canopy (measured above the soil surface) at different growing stages (Table 1). The canopy openness of diamond plants was significantly smaller at leaf 13 at the silking and mid-grain-filling stages, but became the largest at leaf 16 among the three plant architectures. Triangle plants had the greatest canopy openness at the canopy bottom and leaf 13, irrespective of plant density or growing stage.

#### 3.3.2. Incident PAR (simulated fIPAR)

At silking stage, diamond plants had a lower mean simulated fIPAR than the original plants at 60,000 plant  $\text{ha}^{-1}$ : that is, 56.0% vs. 58.1% on average across the three canopy layers, but



**Fig. 2 – Vertical and horizontal expansion of triangle, diamond, and original plants at 25 days after silking at 60,000 plants ha<sup>-1</sup>. Plant architectures at 90,000 plants ha<sup>-1</sup> were similar to those at 60,000 plants ha<sup>-1</sup>.**

no difference was found at 90,000 plant ha<sup>-1</sup> (63.4% vs. 63.1%, Fig. 6). The simulated fIPAR of triangle plants was the lowest in all three layers under both densities at silking stage. The diamond plants had a fIPAR very close to that of the triangle plants 25 days after silking, but both values were lower than that of the original plant at 60,000 plants ha<sup>-1</sup>, and the difference was reduced at 90,000 plant ha<sup>-1</sup>.

### 3.3.3. Relationship between canopy openness and fIPAR

The simulated fIPAR was negatively logarithmically related to measured canopy openness (%) at silking stage with  $R^2 = 0.952$ , and at mid-grain-filling stage with  $R^2 = 0.833$  (Fig. 7). The relationships between them at the soil surface and leaf 13 at silking stage were significant, with  $r = -0.95$  and  $-0.93$ , respectively (data not shown), but became weaker at mid-grain-filling stage with  $r = -0.86$  (significant) and  $-0.61$  (not significant).

### 3.3.4. Leaf SPAD values

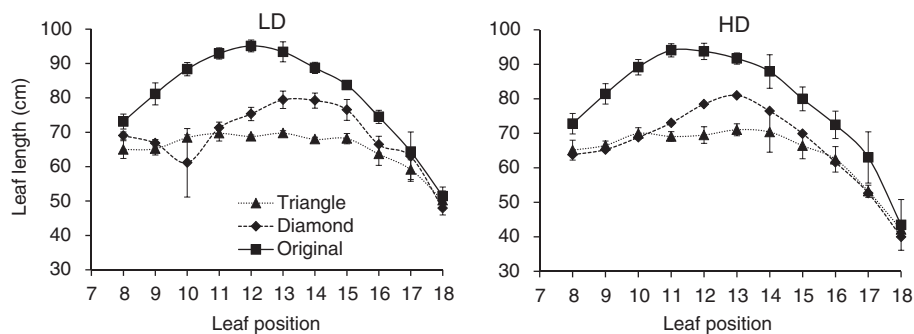
SPAD values of single leaves of triangle plants were higher at silking stage at 60,000 plants ha<sup>-1</sup> and during the entire grain-filling period at 90,000 plants ha<sup>-1</sup>, than those of the diamond and original plants (Fig. 8). The diamond plant had higher leaf SPAD values 10 days after silking (DAS), but this relationship did not persist until 40 DAS. The original plant architecture showed the lowest SPAD values at both densities during the grain-filling period.

### 3.4. Relationship between dry matter and grain yield

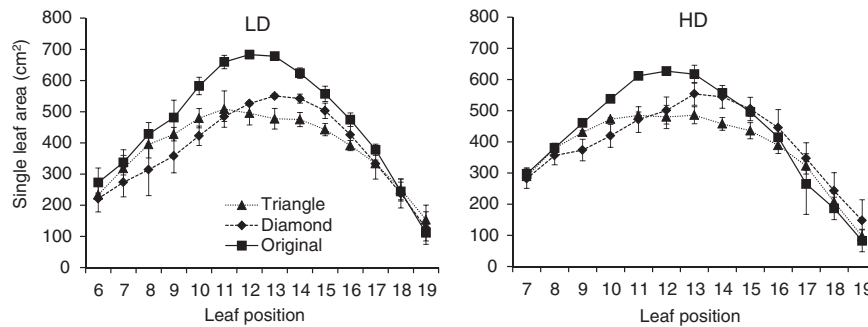
Plant architecture had no significant effects on dry matter (DM) accumulation, except at silking stage at the high density (Fig. 9). The difference in DM between the three plant architectures increased with plant density, but not significantly.

The analysis of variance showed that plant density had significant effects on ear number ha<sup>-1</sup>, kernels per ear, TKW, and harvest index (HI); plant architecture had significant effects on HI; and year had significant effects on kernel number and TKW. The interaction between plant density and architecture had significant effects on yield and ear number, and the interaction of three factors (density, plant architecture, and year) had significant effects on yield, ear number ha<sup>-1</sup>, and kernel number (Table 2).

The triangle and diamond plants produced 428–825 kg ha<sup>-1</sup> lower yield than the original plants at low density, owing to the lower kernel number and TKW. With the increasing density from 60,000 to 90,000 plant ha<sup>-1</sup>, the grain yield of triangle and diamond plants slightly decreased or remained at the same level in 2010, and increased by up to 462 kg ha<sup>-1</sup> (5%) in 2011, whereas the grain yield of original plant decreased by up to 885 kg ha<sup>-1</sup> (10%). The diamond plants set significantly higher kernel number and HI at high density in two years than the triangle and original plants. On average across plant densities and years, the overall mean yield of the original



**Fig. 3 – Single-leaf length of triangle, diamond, and original plants at densities of 60,000 (LD) and 90,000 plants ha<sup>-1</sup> (HD) at silking stage in 2010. Triangle and diamond plants were derived from original plants of maize ZD958 by chemical regulation. Leaf 14th is the ear leaf. Vertical bars represent the standard error of the mean.**



**Fig. 4** – Single-leaf area of triangle, diamond, and original plants at densities of 60,000 (LD) and 90,000 (HD) plants  $\text{ha}^{-1}$  at silking stage in 2010. Triangle and diamond plants were derived from original plants of maize ZD958 by chemical regulation. Leaf 14th is the ear leaf. Vertical bars represent the standard error of the mean.

plants was higher than that of the diamond and triangle plants, owing to its highest TKW. At 90,000 plant  $\text{ha}^{-1}$ , the original and diamond plants had very similar mean yields (8714 vs. 8798 kg  $\text{ha}^{-1}$ ) over the two years (not shown).

## 4. Discussion

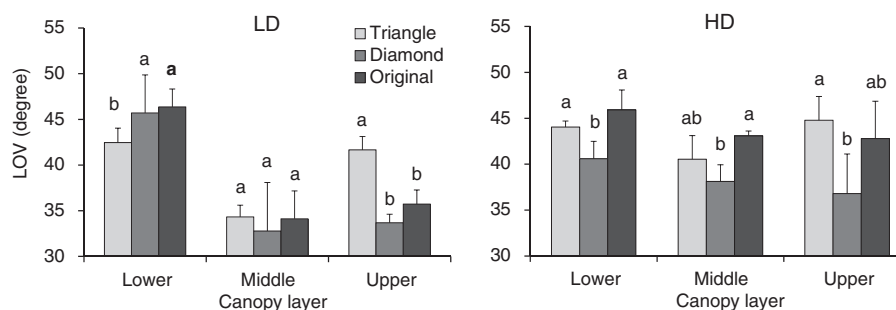
### 4.1. Plant architecture and yield of maize

This study confirmed that the size and distribution of leaf area and leaf orientation can determine light distribution and light interception within maize canopy, thus influencing grain yield. Based on the results of leaf traits, dry matter, and yield (Table 2), the original plants of ZD958 seems to have a preferable canopy architecture, especially at low plant density, as a result of longer, larger, and more vertical leaves (Figs. 3–5). Under high plant densities, however, the advantages in plant architecture of the original plants decreased to some extent, likely as a result of greater intraspecific competition [26,27].

In comparison with the original plants under high plant densities, the triangle plants can make light distribution more uniform within the canopy because of their reduced leaf area, and the diamond plant is able to intercept more incident light in the middle canopy layer (leaves 13–15) as a consequence of the presence of flatter leaves around or above the ear, these

being the most important leaves for grain production [14,16]. The minimized leaves in the middle and upper canopy of the diamond plants can result in larger canopy openness (for example, 56% at leaf 16; Table 1), improving light penetration at high densities (Fig. 6). With these traits, the most important solar resource can be used by the most important leaves of maize, reducing the suppressive effects of limited solar radiation on maize yield [9]. The yield of the diamond plants is consistent with findings of Liu et al. [18] who reported a 12%–15% yield increase in maize resulting from removal of the two uppermost leaves shortly after flowering at high densities. However, the reduced size of leaves, particularly in the middle canopy layer, may have somewhat limited dry matter contribution and yield increases for the triangle and diamond plants, an effect that was more obvious at low density (Table 2, Fig. 9).

Modern maize hybrids are assumed to be more tolerant to high densities than older ones [25], thus producing higher grain yields at increased plant densities [6]. The triangle and diamond plants in this study were expected to show greater tolerance of high densities because of the minimized leaf size in the middle and upper canopy layers. On the other hand, chemical regulation in this study can make the plant architecture more uniform, an effect that can increase tolerance of high densities [26,27]. Along with the smaller plant architecture, particularly in the upper canopy, which can reduce plant competition, the position of the largest leaf



**Fig. 5** – Mean leaf orientation values (LOV) at the lower (leaves < 13th), middle (leaves 13th–15th), and upper canopy layer (leaves > 15th) of triangle, diamond, and original plants at silking stage at 60,000 (LD) and 90,000 plants  $\text{ha}^{-1}$  (HD) in 2010. Triangle and diamond plants were derived from original plants of maize ZD958 by chemical regulation. Values followed by the same letters for the same canopy layer were not significantly different at  $P < 0.05$ .

**Table 1 – Canopy openness (%) measured at soil surface, 13th leaf, and 16th leaf of triangle, diamond, and original plants at 60,000 and 90,000 plants ha<sup>-1</sup> at silking and 25 days after silking (DAS) in 2011.**

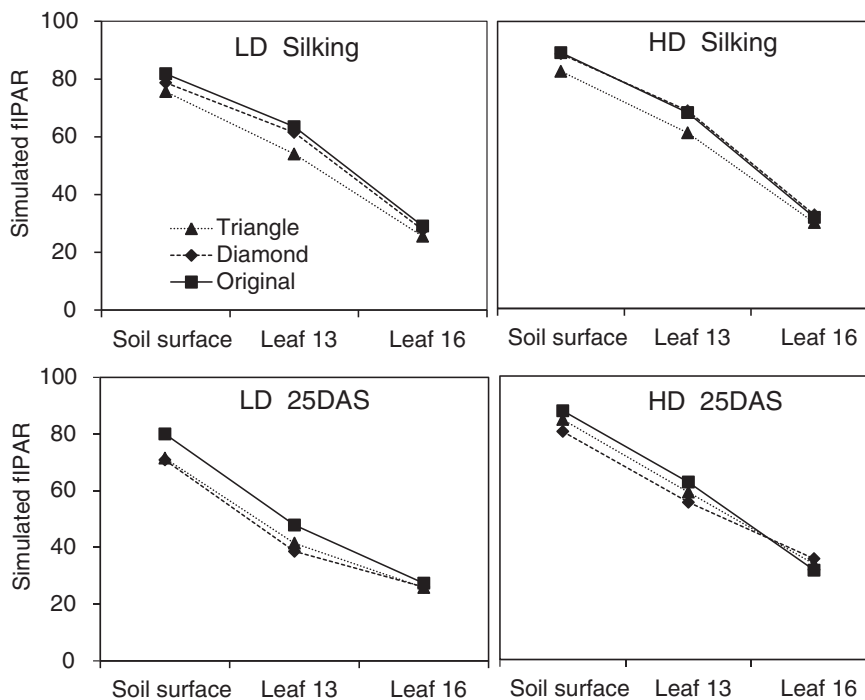
Density (plants ha <sup>-1</sup> )	Plant architecture	Silking stage			25 DAS	
		Soil surface	Leaf 13	Leaf 16	Soil surface	Leaf 13
60,000	Triangle	8.8 a	26.7 a	52.4 ab	8.2 a	20.7 a
	Diamond	7.2 ab	17.1 b	55.1 a	8.1 a	14.6 b
	Original	6.3 b	20.6 ab	48.5 b	7.7 a	22.1 a
90,000	Triangle	4.3 a	16.1 a	54.2 ab	4.6 a	15.1 a
	Diamond	3.8 ab	8.9 c	56.0 a	4.1 a	9.8 b
	Original	3.2 b	11.3 b	46.7 b	3.7 a	9.4 b

Triangle and diamond plants were derived from original plants of maize ZD958 by chemical regulation. Values within each column and at the same density followed by the same letter are not significantly different at  $P < 0.05$ .

area on the plants moved upward to the ear for the diamond plants (Figs. 2, 4), probably accounting for the greater number of kernels per ear (Table 2). This result is consistent with the findings following plant removal or leaf removal experiments in the study of Liu et al. [18], Lizaso et al. [28], and Hashemi et al. [29] who showed that weak interplant competition during the flowering period is of great importance in increasing the kernel number of maize. Moreover, the photosynthates produced by the largest leaf layer, positioned around the ear of diamond plants, are expected to be partitioned to the yield sink more easily, accounting for the relatively higher yield of the diamond plants at the higher density.

The higher yields of modern maize hybrids are also associated with delayed leaf senescence [30], depending on genetic background and external conditions such as solar conditions

[22,31]. Enhanced light attenuation within the canopy can accelerate leaf senescence of maize [31]. Compared with the original plant, the triangle and diamond plants had significantly lower total dry weight at silking stage under high density, in agreement with the findings of Kasele et al. [32] and Shekoofa and Emam [33]. These studies indicated that application of a plant growth retardant such as ethephon at an early growth stage can reduce the total dry weight of maize by up to 30%. However, the significance disappeared after silking in the present study (Fig. 9), an effect that might be attributed to delayed leaf senescence (represented by leaf SPAD values; Fig. 8) of the triangle and diamond plants during the grain-filling period. Delayed leaf senescence, probably resulting from preferable light distribution in the canopy or EC application, may have increased the productivity of the triangle and diamond plants.



**Fig. 6 – Simulated incident photosynthetically active radiation (fIPAR) at the soil surface, 13th leaf, and 16th leaf of triangle, diamond, and original plants at 60,000 (LD) and 90,000 plants ha<sup>-1</sup> (HD) at mid-day (12:00, highest solar elevation) at silking stage and 25 days after silking (DAS) in 2011.**

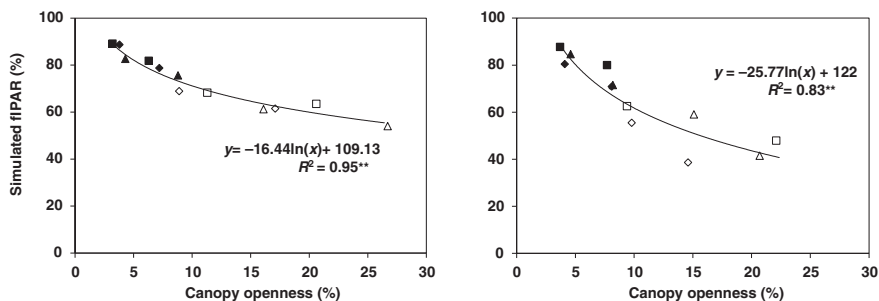


Fig. 7 – Simulated fIPAR against measured canopy openness at the soil surface (filled symbols) and 13th leaf (open symbols) of triangle (▲, △), diamond (◆, ◇), and original (■, □) plants at silking (A) and 25 days after silking (B) at 60,000 and 90,000 plants ha<sup>-1</sup>. \*\* Significant at P < 0.01.

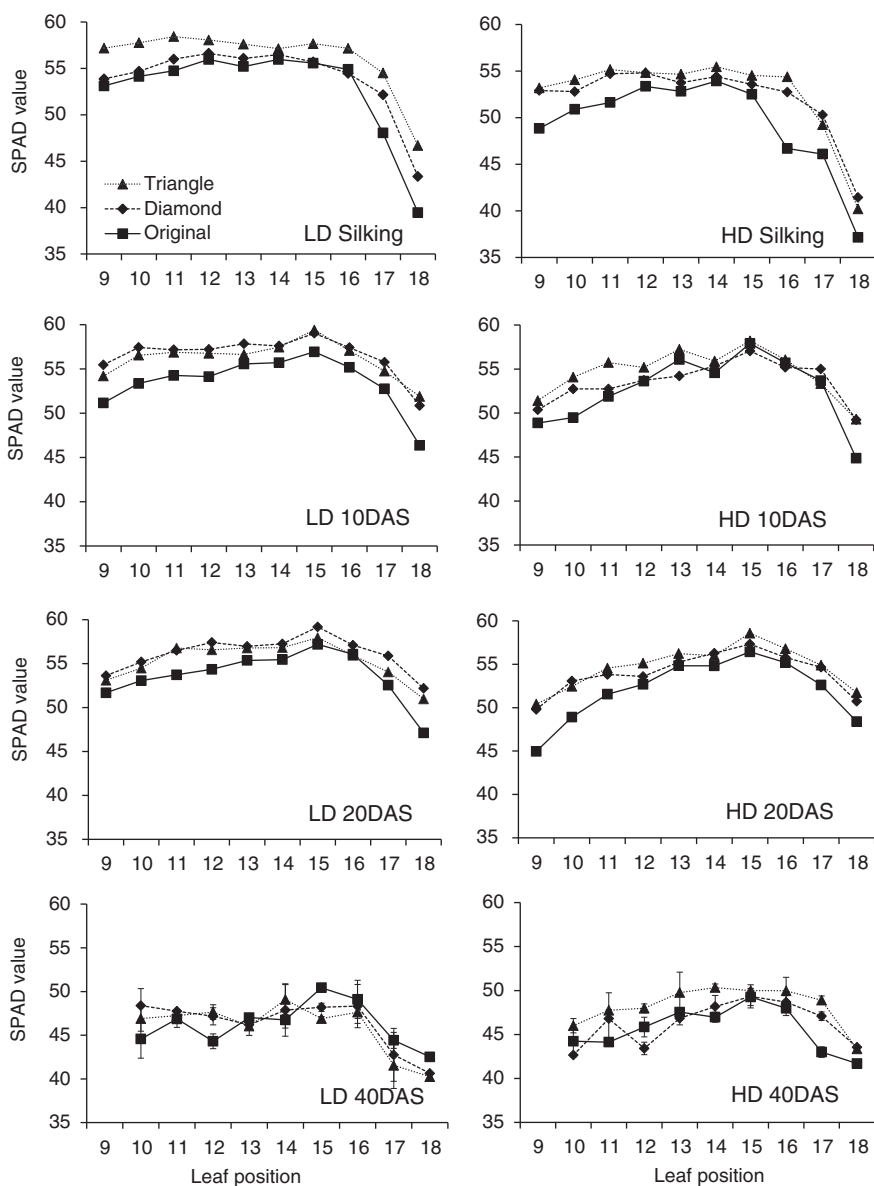
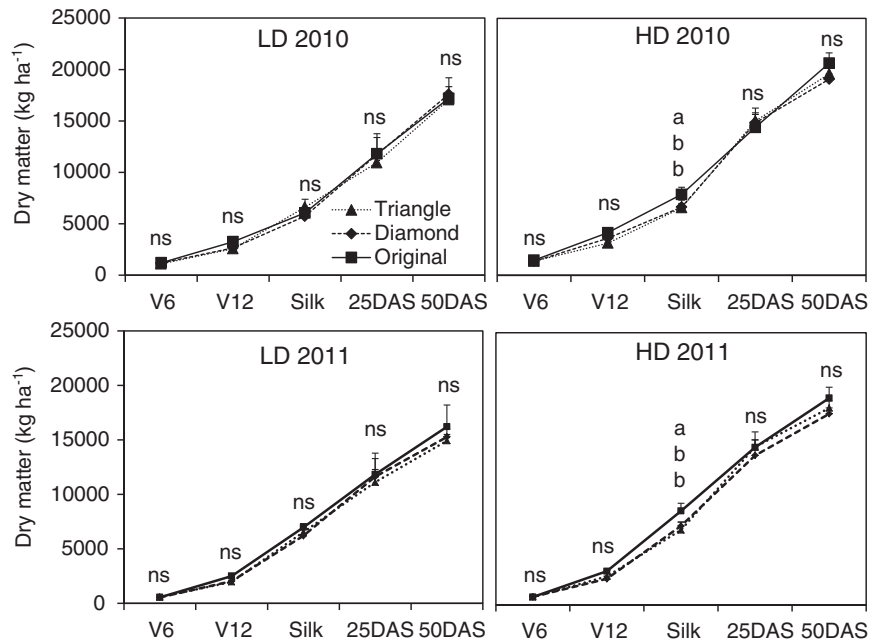


Fig. 8 – Leaf SPAD values of triangle, diamond, and original plants of maize at 60,000 (LD) and 90,000 (HD) plants ha<sup>-1</sup> during seed maturation in 2011. Triangle and diamond plants were derived from original plants of maize ZD958 by chemical regulation. The 14th leaf was the ear leaf. DAS, days after silking stage. Bars, standard error of mean.





**Fig. 9 – Dry matter accumulation (kg ha<sup>-1</sup>) of triangle, diamond, and original plants of maize at 60,000 (LD) and 90,000 plant ha<sup>-1</sup> (HD). Triangle and diamond plants were derived from original plants of maize ZD958 by chemical regulation. V6 and V12 indicate 6-leaf and 12-leaf stage. DAS, days after silking. Values followed by different letters are significant at P < 0.05; ns, not significant.**

The growing period of maize in a double cropping system (winter wheat–summer maize) at the experimental site is about 100 days [34] with a mean daily temperature of 24 °C and mean daily solar radiation of 8 MJ m<sup>-2</sup> (Fig. 1). The growing degree days for ZD958 are about 1600 °C [35],

corresponding to about 130 days in this region. The short growing period is expected to reduce yield potential [36]. For this reason, modern maize hybrids, which possess preferential plant architecture and a short growing period, are expected to be most suitable for yield increase in this area.

**Table 2 – Yield, ear number ha<sup>-1</sup>, kernel number ear<sup>-1</sup>, thousand-kernel weight (TKW) and harvest index (HI) of maize, as an effect of plant density (LD: 60,000; HD: 90,000 plant ha<sup>-1</sup>) and plant architecture (plant).**

Year	Plant	Yield (kg ha <sup>-1</sup> )	Ears (No. ha <sup>-1</sup> )	Kernels (No. ear <sup>-1</sup> )	TKW (g)	HI (%)
2010	LD triangle	8582 a	60,000 a	531.9 b	274.8 b	50.3 b
	LD diamond	8916 a	60,834 a	547.2 ab	279.7 b	50.7 b
	LD original	9407 a	60,277 a	553.2 a	290.3 a	54.7 a
	HD triangle	8030 a	85,278 a	424.3 b	224.9 b	41.0 b
	HD diamond	8461 a	85,833 a	465.6 a	227.1 b	44.5 a
	HD original	8522 a	85,556 a	438.3 b	250.6 a	41.2 b
2011	LD triangle	8748 a	65,559 a	507.0 b	279.5 b	50.4 a
	LD diamond	8673 a	62,226 a	522.6 a	277.4 b	48.9 a
	LD original	9176 a	63,059 a	550.6 ab	289.2 a	51.5 a
	HD triangle	8742 a	87,504 a	404.8 b	269.9 a	40.8 b
	HD diamond	9135 a	90,560 a	421.5 a	253.6 b	45.0 a
	HD original	8907 a	85,283 a	401.0 b	268.6 a	40.3 b
Overall mean	Triangle	8526 a	74,585 a	467.0 b	262.3 b	45.6 a
	Diamond	8796 a	74,863 a	489.2 a	259.5 b	47.3 a
	Original	9003 a	73,544 a	485.8 a	274.7 a	46.9 a
Proc. Mixed	Density (D)	ns	***	***	***	**
	Plant (P)	ns	ns	ns	ns	*
	Year (Y)	ns	ns	**	*	ns
	D × P	*	*	ns	ns	ns
	D × P × Y	*	*	*	ns	ns

Triangle and diamond plants were derived from original plants of ZD958 by chemical regulation. Differences between values with the same letter are not significant at P < 0.05, comparing plant architectures at the same density. \* significant at P < 0.05, \*\* at P < 0.01, \*\*\* at P < 0.001, and ns, not significant.

#### 4.2. Evaluation of light interception model

The light interception model developed in this study is predominately application-oriented, providing an easy way to evaluate plant architecture. The simulated fIPAR could closely reflect the expected advantages of the triangle and diamond plants in canopy architecture (Fig. 6). If robust datasets can be collected, the accuracy of the model can be further increased.

In comparison with previous studies [21,37,38], the input variables of the model, such as LAI and leaf angle, are easily collected. Leaf orientation and leaf azimuth angles are also of great importance to light distribution in a crop canopy [13,15]. In addition, canopy openness, as an integrated parameter, can increase the evaluation of plant architecture. The logarithmic relationship between simulated fIPAR and canopy openness (Fig. 7) should be considered for the improvement of light interception models.

#### 5. Conclusions

The plant architecture of maize determines light distribution in the canopy, which in turn influences plant physiology (such as leaf senescence). A large leaf area is the key to increasing or maintaining maize yield, like that of the original plants of hybrids ZD958 in the present study. Under high plant densities, light interception by the middle canopy layer appears to be most responsible for the yield dynamics of maize. The short growing period of maize in the wheat–maize cropping system also likely accounts for reduced maize yields in the Heilonggang River valley. Selection or breeding for maize cultivars with preferable canopy architecture and short growing period might be a feasible strategy for increasing maize yield in this region. The light interception model developed in the present study provides an easy way to evaluate plant architecture. Combination with canopy openness may improve simulation accuracy.

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