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Effect Mechanism of Solar Radiation on Maize Yield Formation

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Abstract: Solar dimming due to global climate change is becoming increasingly more common in some agricultural areas. Such low-light stress inhibits maize ear number, kernel number per unit area (KN), and kernel weight (KW) as vital yield components. However, which yield component factors are most important for yield formation under low-light stress remains unknown. In this study at Qitai Farm in Xinjiang, China, in 2019 and 2020, we planted three maize (*Zea mays* L.) cultivars (Denghai 618 (DH618), Xianyu 335 (XY335), and Zhengdan 958 (ZD958)) at two densities (7.5×10^4 (D1) and 12×10^4 (D2) plants ha^{-1}). We used four shading treatments (85% (S1), 70% (S2), and 50% (S3) natural light and no shading (CK)) from the three-leaf stage until maturity to create different light conditions. KN was the key factor that directly affected yield under low-light stress. For every 100 MJ m^{-2} decrease in photosynthetically active radiation (PAR), the KN decreased by 803.2 kernels per m^2. When the PAR was >674.3 MJ m^{-2}, KW tended to stabilize at 36.2 g/hundred kernels and the growth rate was 5.82 g/100 MJ m^{-2} per hundred kernels. DH618 and XY335 KNs were more sensitive to lowered solar radiation than ZD958. When density increased, DH618 required fewer light resources than the other cultivars to produce an equivalent amount of photosynthates for kernels. Therefore, in the face of climate change, particularly solar dimming, there is an urgent need to breed maize cultivars, such as DH618, with low-light stress tolerance and high grain yield.

Keywords: maize cultivar; solar radiation; planting density; quantitative relationship; yield components

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1. Introduction

Mean climatic conditions and their fluctuations substantially impact field harvests [1]. Adequate solar radiation, the energy source for crops, such as maize (*Zea mays* L.), is vital for ensuring food security [2,3]. However, a previous study found that air pollution [4] tends to dim surface solar radiation in China [5,6]. Western and Northern China have relatively rich solar resources, but that resource in Eastern and Southern China is seriously affected by aerosol-based pollution and Eastern China has 30–50% less insolation than Western China does [7]. Previous studies in China found that aerosols negatively affect maize biomass and yield, which have subsequently decreased by 23.7% and 15.1%, respectively [8–12]. Additionally, recurrent cloud cover and rainy climates were dominant factors that diminished solar radiation, thus, causing a 3–6% maize yield loss [6,11,13]. Because China is a major maize producer and consumer, maize production in this country figures importantly in global food security [14–16]. Therefore, it is crucial to understand and quantify the relationships between solar radiation and maize yield, as well as that of other major agronomical characteristics in China.

Light limitation plays an important role in suppressing crop growth and productivity. To investigate that, researchers often use shading to simulate low-light stress in fields [5,6,17,18] and many studies have reached conclusions about how the effects of shading result in lower maize yields [19,20]. To that end, some studies have proposed mechanisms (e.g., yield components [11,21], genotypes [21,22], planting density and biomass [23], photosynthetic characteristics [24,25], chlorophyll fluorescence [26–28], and endosperm qualities [11]) that may explain yield decreases due to low-light stress.

Yield components are the key for maize yield formation. As early as 1923, Engledow [29] divided yield components into ear number, kernel number per ear, and kernel weight (KW). Such yield components have accounted for approximately 40% to 60% and 35.5% of the maize grain yield increases in the United States and China, respectively [30]. While examining the responses of maize yield components to low-light stress, previous studies demonstrated that ear weight, number of kernels per row, and KW per ear were positively correlated with maize yields under shading conditions [21]. Other studies found that low-light stress [31] raised the number of abortive kernels and retarded kernel dry weight [32–34]. Zhong et al. [35] reported that shading (low-light stress) could increase both the number of abortive grains and the rates of barren stalks. Additionally, shading in different developmental stages affected maize yield and yield components differently [11,36,37]. For instance, the yield component that decreased the most from shading during silking to maturity was the 1000-kernel weight [37,38], and Chen et al. [39] found that the grains per ear, 1000-kernel weight, and yield all decreased to varying degrees. Additionally, under shading conditions, the resulting bare tips and barrenness decreased maize yield [35], and a 20–50% grain abortion rate caused reduced yield due to reduced grain number per ear [40]. However, previous studies have compared only the effects on each yield component index after shading [11,17,20], but none have investigated which yield component factor is most important for yield formation. Therefore, the quantitative relationships between solar radiation and yield components remain poorly reported.

China is divided into six maize-cultivation regions [41,42] based on their different climatic conditions. One of the most important of those conditions is solar radiation, and differences in solar radiation cause differences in maize yields among the different regions [8,9]. For instance, solar radiation in Huanghuaihai is lower than that in the other regions [3,43]. Further, previous shading experiments in China were often conducted in lower-solar-radiation areas, such as Huanghuaihai [13,32]. In this study, we combined various shading and planting density schemes to simulate different solar-radiation environments in Xinjiang, the maize cultivation region with the most abundant solar radiation in China. We further confirmed which yield component factor was most important for yield formation under low-light stress and the quantitative relationships between solar radiation and yield components. Our results provide a reference for low-light stress-tolerant cultivar selection and breeding and for achieving high and stable yields under the coming adverse climate conditions caused by global climate change.

2. Materials and Methods

2.1. Experimental Design

We conducted field experiments at Qitai Farm (89°48′ E, 43°49′ N) in Xinjiang, China, from 2019 to 2020. We sowed three maize cultivars (Denghai 618 (DH618), Xianyu 335 (XY335), and Zhengdan 958 (ZD958)) on 19 April 2019 and 18 April 2020, at two planting densities: 7.5×10^4 (D1) and 12×10^4 (D2) plants ha^{-1}. Then, for all cultivars at all planting densities, we conducted shading experiments from the three-leaf stage until maturity to create different solar-radiation conditions. The shading treatments were 50% (S3), 70% (S2), and 85% (S1) natural light and no shading (CK). Every experimental plot was 110 m^2 (11 m × 10 m) and adjacent plots were spaced 1 m apart. We built shade nets using temporary scaffolding and nylon nets, and during shading, we left a 1.5 m space between the top of the maize canopy and the shade nets to maintain the same microclimate conditions, except for solar radiation, as those of the unshaded portions of the field.

Base fertilizers, applied before sowing to all treatments, included 150 kg ha^{-1} N from urea, and 225 kg ha^{-1} P_2O_5 (Superphosphate) and 75 kg ha^{-1} K_2O from potassium sulfate.

To ensure a non-limiting supply of nutrients, we applied additional urea (300 kg ha^{-1} N) via drip irrigation in alternate irrigations during the growing seasons. Weeds, diseases, and pests were well controlled in all treatments.

2.2. Sampling and Measurement

At physiological maturity, a 3.3 m × 5 m area (in an alternating wide–narrow row planting pattern (70 + 40 cm)) was manually harvested from the center of each plot and all plants and ear numbers were counted. With earless plants defined as plants having no ears or having less than 10 kernels per ear, we then calculated the earless plant rate as earless plants/all plants. We then selected 10 representative ears from each sample to count the grain number per ear at silking and at maturity and to calculate the kernel rows per ear and the number of kernels per row [44]. We then calculated the kernel number per unit area (KN) as the ear number per unit area × grain number per ear [45] and the grain abortion rate as (grain number per ear at silking − grain number per ear at maturity)/grain number per ear at silking. Using vernier calipers, we measured the lengths of bare tips on the ears. At 10 d intervals from silking until maturity, we collected six tagged ears from each plot and sampled 100 grains from the middle of each ear. Those kernels were oven dried at 85 °C to a constant weight. Using a SunScan (Delta-T Devices, Cambridge, UK) with a diagonal orientation on clear days, we measured the photosynthetically active radiation (PAR) in both the wide and narrow row widths [23,44]. The KW change process was analyzed using a logistic model: $y = A/(1 + Be^{-Cx})$, where A is the ultimate kernel growth mass, B is the initial parameter, and C is the growth rate parameter. The PAR when the KW tended to be stable (stable PAR) was calculated as (lnB + 4.59512)/C [46]. We determined grain moisture content using a PM8188 portable moisture meter (Kett Electric Laboratory, Tokyo, Japan), and grain yield was determined at 14% moisture content.

2.3. Statistical Analysis

Statistical calculations were performed and charts were generated in Excel 2016 (Microsoft, Redmond, WA, USA) and Origin 2018 (OriginLab, Northampton, MA, USA), respectively. SPSS (version 18.0) (IBM SPSS, Chicago, IL, USA) was used to conduct one-way ANOVAs followed by Duncan's multiple range tests at $p < 0.05$ to test the differences between different treatments. Using SPSS stepwise regression analysis and path analysis, we analyzed the relationships between maize yields and the main agronomic traits in different treatments in the two study years.

3. Results

3.1. Effects of Shading on Maize Yields under Different Planting Densities

Shading (low light) sharply reduced maize yields in 2019 and 2020 (Figure 1). Compared with CK's yield, the average yields for treatments S1, S2, and S3 were 9.0%, 18.4%, and 67.9% lower, respectively, at all planting densities in both years. The average yields for DH618, XY335, and ZD958 under shading (averaging S1, S2, and S3 yields) decreased by 30.0%, 35.0%, and 27.2% at D1, and 29.8%, 34.0%, and 36.3% at D2, respectively, compared to the CK yields. The grain yields for all shading conditions and planting densities for the three cultivars decreased in the order of XY335 > ZD958 > DH618. Under shading conditions and at D1, DH618 and XY335 were more sensitive to shading than ZD958 was, but the DH618 and XY335 yield decreases were smaller than those of ZD958 at D2, indicating that DH618 and XY335 better tolerated low light under high-density planting.

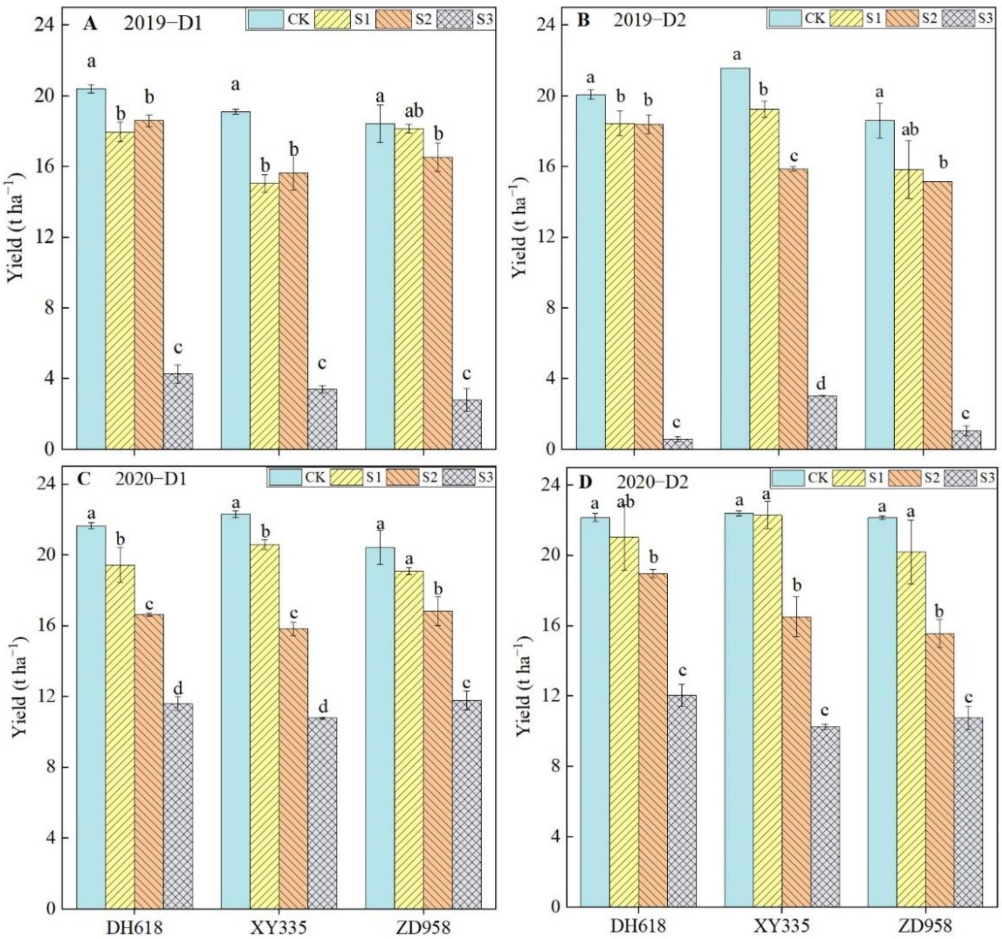

Figure 1. Effects of different shading levels (CK: 100% natural light; S1: 85% natural light; S2: 70% natural light, S3: 50% natural light) and planting densities (D1: 7.5×10^4 plants ha^{-1}, D2: 12×10^4 plants ha^{-1}) on the yields of three maize cultivars: Denghai 618 (DH618), Xianyu 335 (XY335), and Zhengdan 958 (ZD958) over two years (2019 and 2020). (**A**) 2019−D1, (**B**) 2019−D2, (**C**) 2020−D1, (**D**) 2020−D2. Data are means (SD). Means with different lowercase letters are significantly different at $p < 0.05$.

3.2. Effects of Shading on Maize Ear Number and Barrenness

Shading significantly increased the earless plant rate and decreased the ear number, and the greatest ear number decreases and the earless plant rate increases were at the highest shading level (Table 1). On average, under S1, S2, and S3 (both years averaged), ear number decreased by 3.4%, 4.0%, and 29.2%, respectively, compared with the CK, and the earless plant rate was 0.5%, 1.6%, and 18.5%, respectively, higher than CK. Among the three cultivars, ear number decreased in the order of DH618 > XY335 > ZD958, and the earless plant rate increased by 9.6%, 7.8%, and 3.6% for DH618, XY335, and ZD958, respectively. Among the two planting densities, ear number decreases and earless plant rate increases were both less at D1 than at D2 after shading.

Table 1. Ear numbers, the rates of ear number decreases, and earless plant rates under different shading levels (CK: 100% natural light, S1: 85% natural light, S2: 70% natural light, S3: 50% natural light) and planting densities (D1: 7.5 × 10^4 plants ha^{-1}, D2: 12 × 10^4 plants ha^{-1}) of three maize cultivars (Denghai 618 (DH), Xianyu 335 (XY), and Zhengdan 958 (ZD)) over two years. Means with different lowercase letters are significantly different at $p < 0.05$.

Treatment	2019			2020		
	Ear Density (10^4 ha^{-1})	**Decrease Rate (%)**	**Earless Plant Rate (%)**	**Ear Density (10^4 ha^{-1})**	**Decrease Rate (%)**	**Earless Plant Rate (%)**
DH−D1−CK	7.7 a		0.0 b	7.8 a		0.8 a
DH−D1−S1	7.6 a	0.8	1.6 b	6.8 b	12.4	0.0 a
DH−D1−S2	7.4 a	3.9	1.6 b	7.5 ab	4.7	0.7 a
DH−D1−S3	4.7 b	38.6	29.2 a	6.7 c	14.0	3.2 a
DH−D2−CK	11.2 a		0.0 b	11.7 a		4.3 b
DH−D2−S1	10.9 a	2.7	3.4 b	11.0 a	6.5	2.0 ab
DH−D2−S2	11.0 a	2.2	8.1 b	11.3 a	3.9	1.0 ab
DH−D2−S3	2.0 b	82.0	73.6 a	10.2 b	12.7	6.1 a
XY−D1−CK	7.6 a		0.0 b	7.7 a		0.8 a
XY−D1−S1	7.4 a	3.6	2.4 b	7.5 a	2.4	1.6 a
XY−D1−S2	7.1 a	7.1	4.3 b	7.5 a	3.1	0.8 a
XY−D1−S3	4.4 b	42.1	17.2 a	7.0 b	8.7	2.3 a
XY−D2−CK	10.0 a		0.0 b	11.5 a		0.4 b
XY−D2−S1	10.0 a	0.0	0.0 b	11.6 a	−0.8	1.0 b
XY−D2−S2	10.0 a	0.0	0.0 b	10.9 b	5.5	4.4 b
XY−D2−S3	3.4 b	66.1	46.7 a	10.1 c	12.9	12.2 a
ZD−D1−CK	8.8 a		0.0 b	8.1 a		0.8 a
ZD−D1−S1	8.5 a	2.8	0.0 b	7.9 a	3.0	0.8 a
ZD−D1−S2	8.0 a	9.0	0.8 b	7.8 a	3.7	0.8 a
ZD−D1−S3	4.5 b	48.3	14.1 a	7.4 b	9.0	0.0 a
ZD−D2−CK	11.3 a		0.0 b	12.3 a		0.5 b
ZD−D2−S1	10.6 a	5.6	1.1 b	12.1 ab	1.5	0.0 b
ZD−D2−S2	11.1 a	1.6	2.8 b	11.8 ab	3.7	1.5 ab
ZD−D2−S3	2.8 b	82.0	22.1 a	11.5 b	5.9	4.3 a

3.3. Effects of Shading on Maize Ear Traits and the Relationships between PAR and Both the Number of Kernels Per Row and the Grain Abortion Rate

As the shading level increased, the number of kernels per row decreased and the lengths of bare tips and the grain abortion rates increased while the kernel rows per ear were less affected by any shading treatment (means of both years, Table 2). Compared with CK, the number of grains per row of S1, S2, and S3 decreased by 7.2%, 17.2%, and 36.8% and bald tip lengths were 1.4-, 1.6-, and 2.7-times higher, respectively. Meanwhile, the grain abortion rates under CK, S1, S2, and S3 were 25.4%, 30.7%, 37.9%, and 54.2%, respectively. Therefore, as the proportion of shading increased, the number of kernels per row decreased, the bald tip length increased, and the grain abortion rate worsened. Among the three cultivars and under low-light stress (averaging S1, S2, and S3), the number of kernels per row decreased by 22.0%, 26.1%, and 14.7% and the bald tip lengths increased by 2.8-, 1.4-, and 1.4-times for DH618, XY335, and ZD958, respectively, compared to those measures for CK. Further, the grain abortion rates (averaging CK, S1, S2, and S3) for DH618, XY335, and ZD958 were 35.6%, 41.0%, and 34.6%, respectively. As planting density increased from D1 to D2 under low-light stress, the kernel rows per ear reduction rate increased from 15.9% to 24.5% and those of the CK bald tip lengths decreased from 2.2- to 1.3-times, respectively. Additionally, the mean grain abortion rate of the three shading levels increased from 30.9% to 43.3% for D1 and D2, respectively.

Table 2. Row numbers per ear, kernel numbers per row, lengths of bald tips, and kernel abortion rates of three maize cultivars grown at different densities and under different shading levels. See Table 1 for treatment definitions. Means with different lowercase letters are significantly different at $p < 0.05$.

	2019				2020			
Treatment	No. of Rows Per Eear	No. of Kernels Per Row	Bald Tip Length (cm)	Kernel Abortion Rate (%)	No. of Rows Per Ear	No. of Kernels Per Row	Bald Tip Length (cm)	Kernel Abortion Rate (%)
DH−D1−CK	16.0 a	35.8 a	0.6 c	9.2 b	15.7 a	38.5 a	0.7 c	29.1 c
DH−D1−S1	16.0 a	35.4 a	2.0 bc	5.4 b	15.7 a	37.2 ab	1.4 bc	34.4 b
DH−D1−S2	15.0 a	35.0 a	1.5 b	9.9 b	15.3 a	34.5 b	2.0 b	44.4 a
DH−D1−S3	15.2 a	16.8 b	3.6 a	52.3 a	15.7 a	27.8 c	5.6 a	46.8 a
DH−D2−CK	15.0 ab	31.2 a	2.1 c	27.2 c	15.3 a	33.7 a	2.9 b	39.1 b
DH−D2−S1	15.5 a	25.5 b	3.0 ab	25.9 c	16.0 a	31.8 a	3.6 b	40.8 b
DH−D2−S2	14.4 ab	26.0 b	3.1 a	33.2 b	16.3 a	24.8 b	4.3 ab	54.1 a
DH−D2−S3	12.6 b	14.4 c	2.4 bc	60.6 a	16.4 a	18.2 c	5.9 a	57.5 a
XY−D1−CK	16.0 a	38.3 a	1.4 b	19.2 c	16.0 a	40.3 a	2.0 b	26.4 b
XY−D1−S1	16.8 a	39.0 a	1.1 b	22.2 c	17.7 a	35.5 b	2.3 b	32.9 ab
XY−D1−S2	16.8 a	34.0 b	1.7 ab	32.0 b	17.7 a	29.0 c	4.2 a	37.2 a
XY−D1−S3	16.4 a	18.4 c	2.7 a	60.2 a	16.8 a	25.2 d	5.0 a	38.8 a
XY−D2−CK	16.0 a	36.6 a	2.2 b	19.5 c	17.3 a	33.6 a	4.4 bc	44.1 b
XY−D2−S1	16.0 a	32.4 b	2.7 ab	41.4 b	15 a	30.0 a	4.3 c	44.3 b
XY−D2−S2	15.2 ab	29.4 b	2.4 ab	43.5 b	16 a	23.8 b	5.2 ab	56.0 a
XY−D2−S3	14.8 b	17.2 c	3.5 a	79.9 a	17 a	16.5 c	5.5 a	58.8 a
ZD−D1−CK	17.2 a	34.0 a	0.9 a	12.7 a	15.0 a	37.2 a	1.8 b	30.7 b
ZD−D1−S1	15.6 ab	34.8 a	1.3 a	14.5 a	16.3 a	38.0 a	2.0 b	32.8 b
ZD−D1−S2	17.2 a	32.8 a	0.8 a	19.5 a	15.7 a	31.7 a	2.8 b	43.0 a
ZD−D1−S3	15.0 b	26.0 b	2.0 a	43.9 a	15.3 a	24.8 b	4.1 a	44.0 a
ZD−D2−CK	16.0 a	33.8 a	1.8 a	26.3 b	16.0 a	31.8 a	2.4 b	21.6 b
ZD−D2−S1	14.8 a	30.0 a	1.8 a	41.1 a	15.3 a	29.3 ab	2.3 b	33.1 a
ZD−D2−S2	14.8 a	29.8 a	1.2 a	42.6 a	15.0 a	26.8 b	3.3 ab	39.5 a
ZD−D2−S3	15.0 a	16.7 b	1.6 a	72.0 a	15.7 a	26.7 b	4.1 a	36.0 a

At both D1 and D2, KN was significantly positively correlated with PAR (Figure 2). With every 100 MJ m^{-2} decrease in PAR, KN decreased by 637.7 kernels per m^2 at D1 and 968.7 per m^2 kernels at D2. As planting density increased by 60% (from D1 to D2), the KN slopes for DH618 and XY335 each increased by 35.4% and by 31.2% for ZD958, thus, showing that, after densities increased, DH618 and XY335′s KN changes were more sensitive to changes in light radiation than ZD958′s.

KN was significantly negatively correlated with grain abortion rate and bald tip length (Figure 3). When the grain abortion rate increased by 10%, the KN decreased by 576 kernels m^{-2}, and when the average bald tip length increased by 1 cm, the KN decreased by 205 kernels m^{-2} (Figure 3).

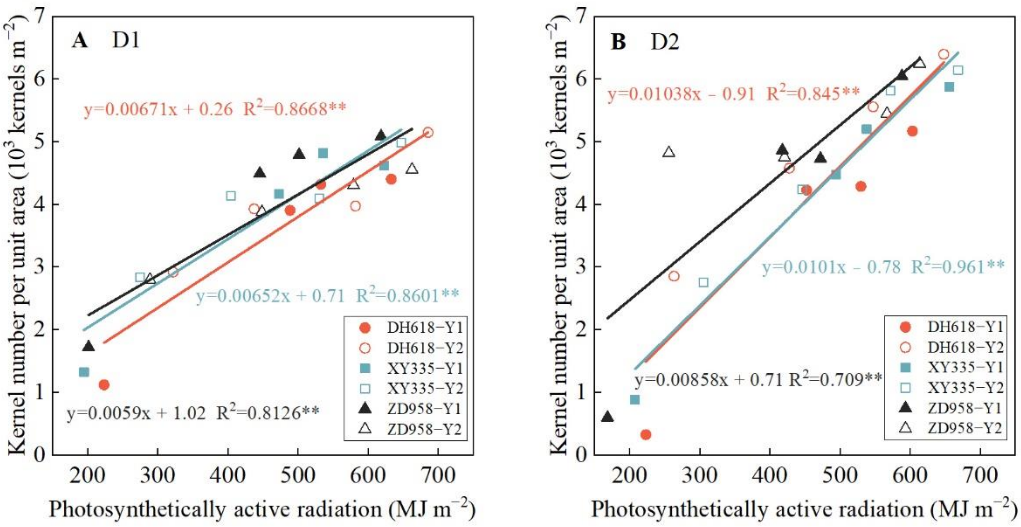

Figure 2. Relationships between kernel number per unit area and photosynthetically active radiation from the silking to maturity stages of three maize cultivars in 2019 (Y1) and 2020 (Y2). Planting densities: D1, 7.5 × 10^4 plants ha^{-1} (A) and D2, 12 × 10^4 plants ha^{-1} (B). See Figure 1 for cultivar names. **, $p \leq 0.01$.

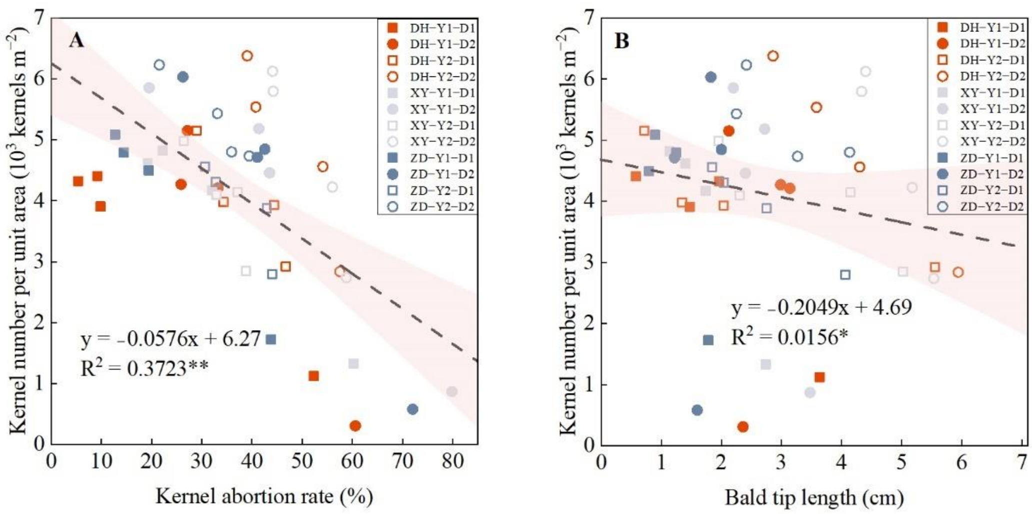

Figure 3. Relationships between the kernel number per unit area and the kernel abortion rate (**A**) and bald tip lengths (**B**). Cultivars: DH, DH618; XY, XY335; ZD, ZD958. Planting densities: D1, 7.5 × 10^4 plants ha^{-1} and D2: 12 × 10^4 plants ha^{-1}. The experimental years, 2019 (Y1) and 2020 (Y2), are indicated by solid and empty symbols, respectively. * $p \leq 0.05$, ** $p \leq 0.01$.

3.4. Quantitative Relationships between Grain Weights and Accumulated Solar Radiation

The relationships of KW to PAR for each cultivar, as well as for the three cultivars combined, displayed positive S-curve responses; by taking the first derivative of those logistic curves, the rates of KW change with PAR all had single-peaked curves (Figure 4). When the PAR was greater than 634.7, 674.8, and 681.0 MJ m^{-2} for DH618, XY335, and ZD958, the KWs tended to stabilize at 37.6, 34.7, and 35.6 g, respectively. Further, the average hundred KW growth rates with PAR were 5.46, 4.93, and 5.26 g/100 MJ m^{-2} for DH618, XY335, and ZD958, respectively. Overall, when PAR was >674.3 MJ m^{-2}, KW tended to stabilize at 36.2 g/100 kernels, and the hundred-kernel weight growth rate was 5.82 g/100 MJ m^{-2} (Figure 4).

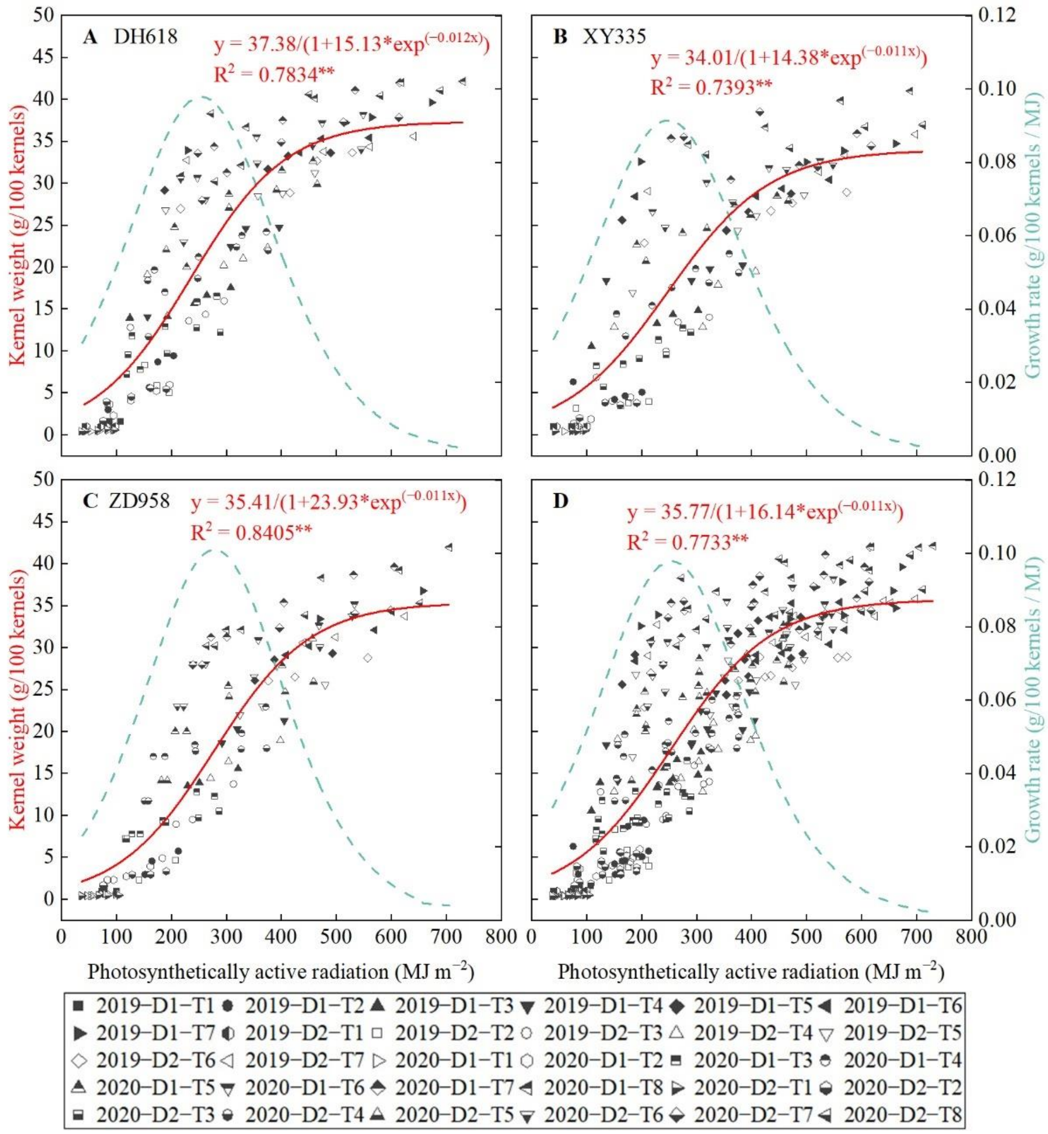

Figure 4. Relationships between kernel weights and growth rate and photosynthetically active radiation from the silking to maturity stages for three cultivars (**A**–**C**) and all cultivars combined (**D**). Planting density: D1, 7.5×10^4 plants ha^{-1} and D2, 12×10^4 plants ha^{-1}. Each T represents a 10−d interval sampling of kernel weight. ** $p \leq 0.01$.

3.5. Relationships between Ear Characteristics and Maize Yields

Maize yields are affected by many factors, so we used path analysis to calculate and analyze the relative importance of ear characteristics to maize yield (Figure 5). Through a path analysis of simple correlation coefficients, we found that maize yield was significantly positively correlated with ear density, KN, KW, and number of kernels per row, and was significantly negatively correlated with grain abortion rate and bald tip length. The order of the direct path coefficient of each trait from large to small was KN > KW > ear density > number of kernels per row > bald tip length > grain abortion rate. These results showed that KN is the key factor that directly affected yield. The indirect path coefficient showed that the effects of ear density and KW on yield were caused primarily by the indirect KN effect. The indirect number of kernels per row and grain abortion rate path coefficients through KN were 0.28 and −0.29, respectively, indicating that number of kernels per row and grain abortion rate greatly influenced yield through KN.

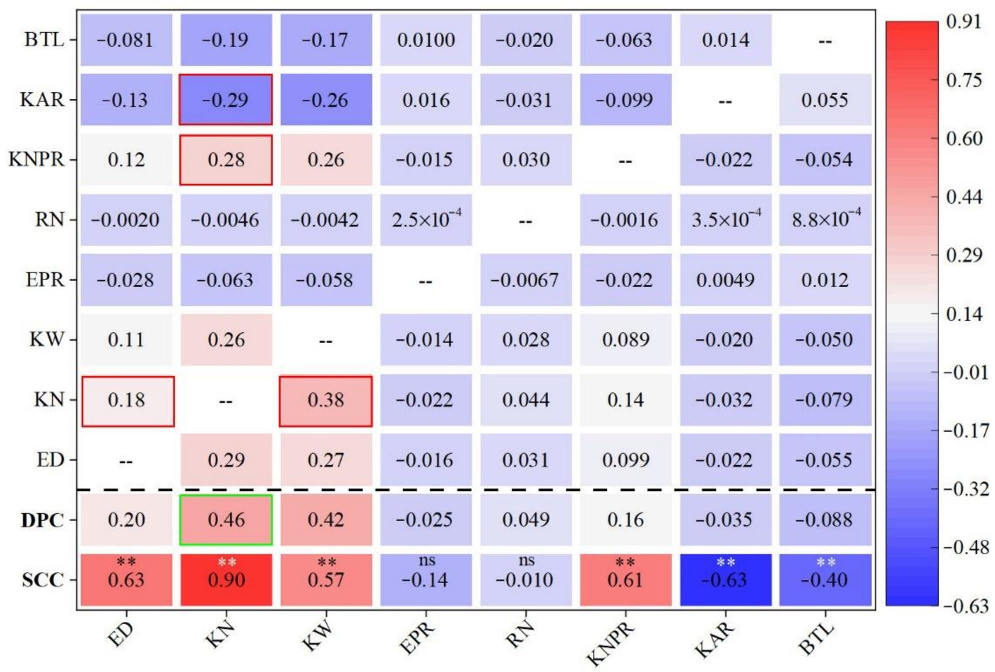

Figure 5. Path analysis of grain yield and ear density (ED), kernel number per unit area (KN), kernel weight (KW), earless plant rate (EPR), number of rows per ear (RN), number of kernels per row (KNPR), kernel abortion rate (KAR), and bald tip length (BTL). The results above the dotted line are the indirect path coefficients, and the direct path coefficients (DPC) and simple correlation coefficients (SCC) are below the dotted line. ** $p < 0.05$, ns indicates no significance.

4. Discussion

Maize is a typical C4 plant; the high productivity of maize is closely related to the differentiation and development of parenchyma and very sensitive to light restriction [13]. Many studies have shown that maize yields are significantly reduced under low-light conditions [19,20,47]. Yang et al. [25] reported that light deprivation decreased kernel set by decreasing photosynthate flux and the activity of enzymes involved in starch synthesis, resulting in kernel yield loss. Previous studies demonstrated 92–96% yield decreases after shading (40% of ambient sunlight) [17,20], a higher amount than in this study, in which yield decreased by 18.4–67.9% under 30–50% shading. Those yield differences may be because the previous studies were conducted at different sites and environments than our study. This suggests that the same degree of shading can lead to greater yield loss in regions where solar radiation is already inadequate. Yield components are key for maize yield formation [29]. Previous studies showed that the change in ear number ha^{-1} under shading conditions significantly affected yield [13,23], findings that are consistent with those of our study. We found that when the solar radiation was reduced by 15%, 30%, and 50% compared with CK, ear number decreased by 3.4%, 4.0%, and 29.2% and the earless plant rate was 0.5%, 1.6%, and 18.5% higher than CK, respectively. This indicates that when solar radiation is minimally decreased, ear number does not change much, but a large enough reduction in solar radiation leads to a sharp decrease in ear number.

Both kernel number and weight are mainly related to most yield variations [11,32,40,48]. Inadequate solar radiation inhibits kernel number and weight increases, ultimately lowering crop yields [6,20]. As with our results, previous studies have found that low-light stress affected maize yield mainly by reducing the number of kernels per row and the 1000-grain weight, without affecting kernel rows per ear [21,49]. That may be because kernel rows per ear are controlled mostly by genetic factors rather than by environmental factors, such as shading [21,31]. In this study, maize yield decrease induced by low-light stress was due mainly to decreased KN, not decreased KW (Figure 5). Previous studies reporting similar results concluded that KN was the major trait that directly affected yield [50–53]. Further, primarily under low-light stress, the grain abortion rate and bald tip length worsened and, thus, contributed to the KN decrease [20,35]. Although many studies have examined the effects of shading on maize kernel number and KW [11,13,21,32,49], little is known about the quantitative relationships between solar radiation and kernel number and weight.

Quantifying the relationship between basic agricultural traits and environmental factors plays a fundamental role in the application of process-oriented maize simulation models [5,54] and agricultural information technology and precision agriculture [55]. One such relationship, that between KN and PAR, was investigated by Andrade, Frugone, and Uhart (1993), who demonstrated that the slope of this relationship was 5.39 grains MJ^{-1} of intercepted PAR. In our study, for every 100 MJ m^{-2} decrease in PAR, KN decreased by 803.2 kernels per m^2 (averaged at D1 and D2). That result was higher than that observed by Andrade et al. (1993), likely because of different cultivars and PAR ranges. However, in our study, the KN was significantly negatively correlated with the grain abortion rate and bald tip length, results consistent with previous studies [20,37,56]. Beyond that, we found that with a 10% increase in the grain abortion rate and a 1 cm increase in the bald tip length, the KN decreased by 576 and 205 kernels, respectively (Figure 3). These results may be attributed to the high heritability of ear and tassel differentiation [20], which are key players in breeding low-light-resistant maize cultivars [38].

Another important relationship, that between KW and PAR, was investigated by Chen et al. [39] who subsequently showed that at a 50% shading level, the thousand-kernel weight was reduced by 6.8% on average compared with that of the control. One study concluded that shading applied during reproductive development alone decreased KW to 79% (shading level: 40% of ambient sunlight) [20]. Jia et al. [11] and Naseer et al. [18] also reported that the KWs in all treatments were significantly less than those of the control. In the present study, the quantitative relationship between PAR and KW was accurately described. When the PAR was >674.3 MJ m^{-2}, KW tended to stabilize at 36.2 g/100 kernels, and the KW growth rate was 5.82 g/100 MJ m^{-2} per hundred kernels (Figure 4D). Altogether, the results of these quantitative relationships may provide a reference for verifying crop growth modeling parameters, especially in low-light conditions [54,57,58].

Maize yield is significantly affected by cultivar and density [14], and solar radiation significantly affects the optimum maize planting density [8]. In this study, the different responses to changes in solar radiation among cultivars and densities were obvious. As shown in Figure 2, with a 60% increase in planting density, from D1 to D2, the KNs of DH618 and XY335 each increased by 35.4% and by 31.2% for ZD958. This shows that at increased densities, the KN changes in DH618 and XY335 were more sensitive to solar-radiation changes than that of ZD958. Further, less accumulated PAR was required to stabilize the hundred-kernel weight for DH618 than for XY335 and ZD958 (Figure 4). In addition, as PAR decreased, the rate of DH618′s KW decrease was less than that of the other cultivars. That indicated that among the three cultivars, DH618 needs fewer light resources than the other cultivars to produce an equivalent amount of photosynthates for kernels (Figure 4). The type of cultivar exemplified by DH681 should be used to improve resource utilization efficiency and, thus, help reduce the regional yield gap in China [41,59].

5. Conclusions

Low-light stress inhibits ear number, kernel number per unit area, and kernel weight production, and kernel number per unit area is a key factor that determines maize yield formation under low-light stress. Further, there were significant quantitative relationships between photosynthetically active radiation and kernel number per unit area, kernel weight, and kernel growth rate. The types of cultivars exemplified by DH681 should be used to improve resource utilization efficiency and, thus, help reduce the regional yield gap in China. However, in the broader picture and in a future facing diminishing solar resources due to global climate change, new maize cultivars that possess both low-light stress tolerance and high grain yield must be bred.

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