

Full Length Research Paper

Shading effects on the yield, quality, and sucrose-metabolizing enzyme activity of sweet corn during filling stage

Fu-cheng Zhao^{1*}, He-ping Tan¹, Li-quan Jing², Hai-liang Han¹, Fei Bao¹, Wei-ping Lu² and Gui-yue Wang¹

¹Institute of Maize and Featured Upland Crops, Zhejiang Academy of Agricultural Sciences, Dongyang, 322100, Zhejiang, China.

²Jiangsu Key Laboratory of Crop Genetics and Physiology/Jiangsu Key Laboratory of Crop Cultivation and Physiology/Jiangsu Co-Innovation Center for Modern Production Technology of Grain Crops, Agricultural College of Yangzhou University, Yangzhou 225009, Jiangsu, China.

Received 21 December, 2021; Accepted 8 February, 2022

Two low-light sensitive varieties of sweet corn (*Zea mays* L.), cultivars Xiantian 5, and Huazhen, were subjected to different shading-intensity treatments during the grain-filling stage in a field experiment in order to clarify physiological mechanisms of lowlight effects on the yield, quality, and sucrose-metabolizing enzyme activity of sweet corn. The results showed that under weak light stress (50% light transmittance), the ear length and diameter, fresh ear yield, grains per row and grain weight, weight per ear and sugar content of the grains decreased sharply, while the bald length and water content of the fresh grains increased significantly. The 50% shading decreased the fresh ear yield, max weight per 100 fresh grains, and soluble sugar content of Xiantian 5 by 40.5, 31.3, and 19.5%, respectively, whereas those of Huazhen were decreased by 17.5, 19.8 and 10.1%, respectively. Shading furthermore suppressed the activities of sucrose phosphate synthase (SPS) and sucrose synthetase (SS), and delayed the emergence of peak SPS activity.

Key words: Sweet corn, shading condition, yield, quality, sucrose-metabolizing enzyme.

INTRODUCTION

Corn (*Zea mays* L.) is a typical C₄ crop that can hardly reach its light saturation point under sunshine but its yield and quality can be improved with ample light (Wenzel et al., 1989; McLachlan et al., 1994). In the past 50 years, the sunshine duration in China decreased significantly, especially in East and North China (Zeng et al., 2001) where the mean sunshine duration decreased by 74.2 h

every 10 years during 1961 to 2010 (Zhang, 2012). The mean sunshine duration decreased significantly at the rate of -40.7 h every 10 years over mainland China, the decline rate in sunshine duration was the largest in summer (-16.8 h every 10 years), and the decline trend in sunshine duration was significantly higher in the eastern region than in the western region, especially in North

*Corresponding author. E-mail: encliff@163.com.

China (Feng et al., 2019).

There have been many reports on the adverse effects of weak light on the growth and morphogenesis of corn. For example, shading reduced the plant height, stem diameter, and effective leaf area of corn (Early et al. 1967; Hashemi and Herbert, 1992; Ma et al., 1996; Kobata et al. 2000; Martin et al., 2004; Lambert et al., 2014; Harbur and Owen, 2016), reduced photosynthetic capacity (Ward and Woolhouse, 1986; Fernando et al., 1993; Setter et al., 2001; Jia et al., 2007a), caused less tassel branches and filaments (Warrington and Kanemasu, 1983), decreased pollen fertility (Andrew et al., 1988; He et al., 1998), rows per ear, grains per row (Reed et al. 1988; Kiniry et al., 1992; Andrade et al., 1993), and yield (Jia et al., 2007b; Zhang et al., 2009). Weak light also inhibited the starch synthase activity, which hindered starch synthesis and reduced starch content (Mengel and Judel, 1982; Hawker and Jenner, 1993; Morell et al., 1995). In contrast to intensive studies of shading effects on common corn, those on sweet corn were still rare (Feng et al., 2007), especially on the issue of sugar accumulation and sucrose-metabolizing enzyme activity (Frans et al., 2021).

In this study, the effects of shading on the yield, quality, and sucrose-metabolizing enzyme activity of sweet corn under field conditions were determined. The present study also provided a theoretical basis for adapting the sweet corn production to the current climate changes in the region of study and breeding new shade-tolerant varieties.

MATERIALS AND METHODS

Experimental design

The experiment was performed in a farm of the Maize Research Institute which is located in Dongyang (120° 18' E, 29° 11' N), Zhejiang Province, China in 2013. The experimental plot was of red soil with good irrigation and drainage facilities. The soil contained in the upper 20 cm 22.5 g kg⁻¹ organic matter, 1.43 g kg⁻¹ total N, 1.31 g kg⁻¹ total P, 15.8 g kg⁻¹ total K, 96.7 g kg⁻¹ soil-available N, 9.87 g kg⁻¹ soil-available P, and 83.92 g kg⁻¹ soil-available K. The pH value of the soil was 5.64. N, P₂O₅, and K₂O were applied during soil preparation at 75 kg ha⁻¹ as base fertilizers. At the jointing stage, 150 kg ha⁻¹ N fertilizer was additionally applied. In this study, two sweet corn cultivars, Xiantian 5 and Huazhen were used, which purchased them from market. Two sweet corn cultivars were cultivated with a population density of 52 500 plants ha⁻¹.

The experimental design was a split-plot with three replicates, with varieties in the main plots and shading in the sub-plots. After pollination, a dark net (light transmittance: 50%, ST) was set up with stainless steel frames, forming a removable combined shade (H × L × W: 4 m × 24 m × 8 m). The dark nets were hung from top to bottom of only two sides, east and west to ensure good ventilation. No shading set was set as the control (CK).

Monitor of microclimate change

Geothermometers were placed 5 cm underneath the soil surface and ordinary thermometers were placed at ear position of the corn plants for measuring temperature. LI-6400 (LI-COR, USA) portable

photosynthetic analyzers were used for detection at 11:00 am of the plant photosynthesis efficiency (Yang et al., 2019).

Sampling method

For the two cultivars in different cells, ears of a similar growth stage were marked with tags before silking. The female ears were bagged for artificial pollination at the silking stage. At days 10, 14, 18, 22, 26, and 30 after pollination, five of the tagged ears were respectively taken, and grains of the middle parts were picked off. Parts of the grains were de-enzymed for 30 min in an oven at 105°C and dried at 70°C to a constant weight. The other parts were stored in an ultralow-temperature refrigerator at -80°C.

Data collections

The yield was measured at the milk stage with the water content of grain between 70 and 75%. Both cultivars were harvested under natural light on day 22 after pollination, however, under shading, Xiantian 5 was harvested on day 25 after pollination, and Huazhen was harvested on day 23 after pollination.

The physical properties (hardness, fracturability, adhesiveness, springiness, cohesiveness, chewiness and resilience) were determined with a texture analyzer (TA. XT Plus, UK Stable Micro Systems Inc). The sweet corn ears with bractal leaves removed were placed in a rice cooker, and steamed for 20 min. One full row grain on the middle part of each ear was peeled off from the steamed corn ears when the temperature dropped naturally to 60°C. Eight grains with consistent quality were chosen for texture profile analysis (TPA) by conventional method.

Residue rate was measured by the method proposed by Liu et al. (2009); the grain moisture content was determined by weighing before and after drying to constant weight; the contents of soluble sugar and starch were determined by the use of anthrone colorimetry, and the sucrose content was measured using m-dihydroxybenzene (Li, 2000). The enzymes were extracted following the methods proposed by Doehlert et al. (1988). Enzyme activity was determined by the method presented by Wardlaw (1971) with slight modification (Zhao et al., 2013).

Data analysis

The data were processed with Microsoft Excel 2007. All the other data were subjected to the split-plot design analysis of variance (ANOVA), and the Duncan's Multiple Range Test at the 5% probability level was used to determine the significance of differences between treatments using SPSS 21.0 for Windows. Figures were processed with Sigma Plot 12.5.

RESULTS

Effects of shading on microclimate in the field

The effects of shading on the microclimate in the field are shown in Table 1. It was clear that shading changed largely the light intensity but very little the other climate factors tested.

Effects of shading on the yield of sweet corn

As shown in Table 2, the fresh ear yield of sweet corn

Table 1. Effects of shading on some factors of microclimate in the experimental field.

Treatment	Light intensity ($\mu\text{mol (m}^2\text{-s)}^{-1}$)	CO ₂ concentration ($\mu\text{mol mol}^{-1}$)	Relative humidity (%)	Temperature (°C)	Ground temperature (°C)
CK	1640.94±49.28 ^a	346.14±4.88 ^a	65.24±0.86 ^a	27.90±0.48 ^a	25.36±0.51 ^a
ST	771.71±26.61 ^b	327.84±7.23 ^a	67.04±1.00 ^a	27.06±0.43 ^a	24.84±0.43 ^a

Data followed by different letters are significantly different ($P < 0.05$).

Table 2. Effects of shading on the field yield and some related traits of sweet corn.

Cultivar	Treatment	Ear length (cm)	Ear diameter (cm)	Bald length (cm)	Rows per ear	Grains per row	Weight per ear (g)	Barrenness (%)	Yield (kg ha ⁻¹)
<i>Xiantian 5</i>	CK	18.1 ^a	5.0 ^a	0.9 ^b	16.6 ^a	35.7 ^a	342.0 ^a	6.7 ^b	16832.7 ^a
	ST	13.8 ^b	3.9 ^b	6.8 ^a	16.2 ^a	24.2 ^b	227.8 ^b	16.6 ^a	10022.0 ^b
<i>Huazhen</i>	CK	19.3 ^a	4.2 ^a	1.1 ^b	13.0 ^a	42.0 ^a	285.6 ^a	3.9 ^a	14291.6 ^a
	ST	17.1 ^b	3.8 ^b	3.8 ^a	12.6 ^a	28.2 ^b	212.8 ^b	4.5 ^a	11795.4 ^b

Data followed by different letters are significantly different ($P < 0.05$).

Table 3. Effects of shading on some physical properties of fresh sweet corn grains.

Cultivar	Treatment	Hardness (g)	Fracturability (g)	Adhesiveness	Springiness	Cohesiveness	Chewiness	Resilience
<i>Xiantian 5</i>	CK	22678.53 ^a	5849.93 ^a	-2.52 ^a	0.53 ^a	0.45 ^a	5454.13 ^a	0.37 ^a
	ST	9193.91 ^b	2281.52 ^b	-2.24 ^a	0.41 ^a	0.25 ^b	1616.63 ^b	0.16 ^b
<i>Huazhen</i>	CK	13273.99 ^a	4982.47 ^a	-2.64 ^a	0.49 ^a	0.34 ^a	2332.22 ^a	0.29 ^a
	ST	9986.79 ^b	2943.45 ^b	-1.89 ^a	0.40 ^a	0.32 ^a	1254.45 ^b	0.22 ^a
		F-Value						
Cultivar		46.15*	0.12	2.77	0.18	1.72	10.03†	0.09
Treatment		175.04*	90.37*	7.65	3.79	29.43*	19.96†	24.93†
Cultivar×Treatment		64.71*	6.72†	4.04	0.07	19.77†	6.29†	6.25†

Data for a same variety followed by different letters in the same column are significantly different at the 5% level. * $P < 0.01$; † $P < 0.05$.

under shading was appreciably less than that of the controls. However, the yield reductions of the two cultivars were quite different: the two-year average yields of *Xiantian 5* and *Huazhen* decreased by 40.5 and 17.5%, respectively, in comparison with the controls. On the other hand, the ear length, ear diameter, grains per row, and weight per ear of the two varieties after shading were also appreciably less than those of the controls. The bald length is significantly longer than that of the controls. Considering the barrenness, *Xiantian 5* was significantly longer than the controls. No significant differences were observed between *Huazhen* and the control group.

Effects of shading on the physical properties of sweet corn grain

The two cultivars had significantly different physical

properties of hardness and chewiness (Table 3). In the shading treatment, significant differences were observed between the two cultivars in hardness, fracturability, cohesiveness, chewiness, and resilience, with only one exception in the adhesiveness or springiness. The two cultivars under shading were significantly lower in comparison with the controls in hardness, fracturability, and chewiness. With regard to cohesiveness and adhesiveness, significant differences were observed only in *Xiantian 5* with the controls.

Effects of shading on the weight per 100 fresh grains, moisture content, and residue rate of sweet corn

For the two cultivars, the weight per 100 fresh grains increased and then declined with the number of days after pollination (Figure 1A and B). Their peaks of the

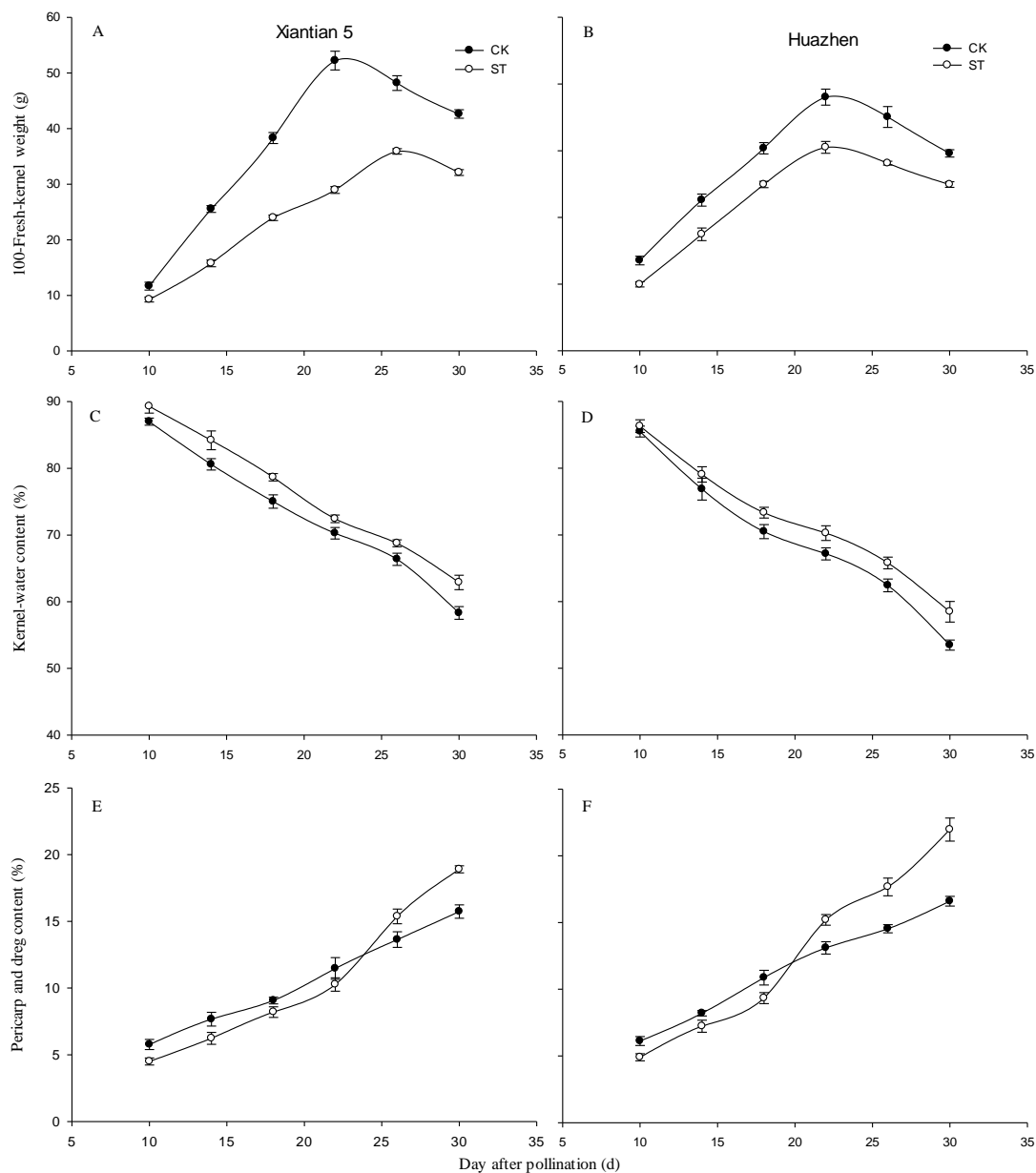


Figure 1. Dynamics of the 100-fresh-kernel weight, water-content, pericarp and dreg content in grains of sweet corn after pollination.

max weight per 100 fresh grains emerged differently. For Xiantian 5 under weak light stress, the peak appeared on day 26 after pollination, four days less than the control group. While for Huazhen, the maximal weight per 100 fresh grains appeared 22 days after pollination under two light conditions. The maximal weight per 100 fresh grains under weak light stress was significantly lower than that of the controls, with decreases by 31.3 and 19.8% for Xiantian 5 and Huazhen, respectively.

The grain moisture content showed a decreasing trend with the number of days after pollination (Figure 1C and D), and on day 30 after pollination, the grain moisture

content of the two varieties was significantly lower than that of the controls.

The weight per 100 dry grains of Xiantian 5 under weak light stress decreased by 33.0% in comparison with the controls while that of Huazhen the decrease was by 27.8%, while the residue rate of sweet corn grains increased gradually with the number of days after pollination (Figure 1E and F). The residue rates of the two cultivars were lower than those of the controls during the early and middle filling stages; however, at the late filling stage the residue rates of the two varieties were significantly higher than those of the controls.

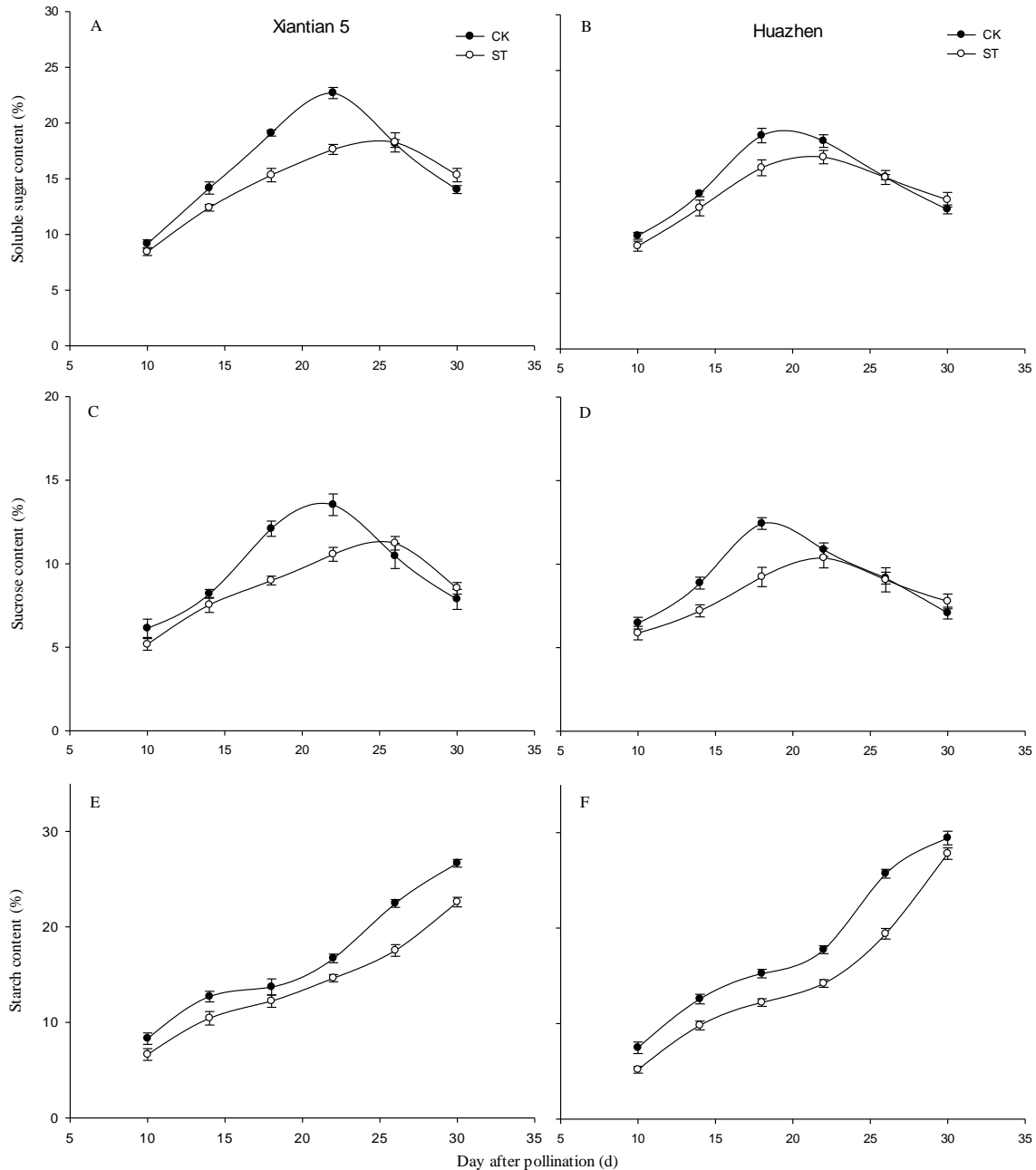


Figure 2. Dynamics of the contents of soluble sugar, sucrose and starch in grains of sweet corn after pollination.

Effects of shading on the contents of soluble sugar, sucrose, and starch in sweet corn grains

The contents of soluble sugar (Figure 2A and B) increased while sucrose (Figure 2C and D) decreased after pollination, forming a unimodal curve. The peaks of both the soluble sugar and sucrose of Xiantian 5 under natural light reached the peak values 22 days after pollination. But the peaks of shading treatment appeared on day 26. The contents of soluble sugar and sucrose of

Huazhen under natural light reached peak values 18 days after pollination, and those under weak light stress appeared 22 days after. Sweet corn is generally harvested on day 22 after pollination. During these 22 days period, the content of soluble sugar decreased by 22.3% and that of sucrose decreased by 21.9% in Xiantian 5 under weak light stress; the content of soluble sugar decreased by 7.7% and that of sucrose decreased by 4.6% in Huazhen. The starch contents of the two cultivars increased after pollination (Figure 2E and F), but

were always lower than those of the controls.

Effects of shading on the sucrose-metabolizing enzyme activity of sweet corn grains

Sucrose phosphate synthase (SPS) which presents in the cytoplasm is a key rate-limiting enzyme to synthesize sucrose, and the catalytic reaction is reversible. As shown in Figure 3A and B for the two cultivars, the changing trend of the SPS activity was quite similar to the contents of soluble sugar and sucrose. During the development of grains, the SPS activity under weak light stress was lower than that of the controls, and the peak value of the SPS activity appeared later than that of the controls. The catalytic reaction of sucrose synthetase (SS) is reversible, and it can catalyze the synthesis and decomposition of sucrose. During the development of sweet corn grains, the changes in SS activity in the direction of synthesis (Figure 3C and D) also show a unimodal curve. In SS synthesis, those of the two cultivars under weak light stress are lower than those of the controls, and peak values of the two varieties appear at different time points. However, those of Xiantian 5 appeared on day 22 after pollination in both the treatment and the control, whereas those of Huazhen appeared on day 18. The SS activity in the direction of decomposition (Figure 3E and F) increased slowly at the early filling stage and increased sharply at the middle and late filling stages. Throughout the entire grain filling process, the SS activity in the direction of decomposition under weak light stress was lower than that of the controls.

DISCUSSION

Light is an important environmental factor influencing the growth and development of all the crops. Corn yield chiefly depends on the transport of organic matter in stems and leaves before flowering and the accumulation of photosynthetic products in the leaves and bracts after flowering. The total solar radiation during the growth of corn reduces by 1 kJ cm^{-2} , with an indicative reduction of 337.5 kg hm^{-2} biological yield in the corn mean population density (Wang et al., 2008). Haze weather is not uncommon because of serious air pollution in recent years. In South China, the plum rain season significantly influences sweet corn during filling stage. Insufficient light conditions also affect the yield and quality of sweet corn. As have been reported by Jia et al. (2010), the dry weights of photosynthetic products during filling stage contribute 78 to 84% of the grain yield. At the early filling stage, weak light stress appreciably reduces the grains per ear and the thousand-kernel weight, and at the middle and late stage, it mainly affects the degree of grain filling (Frans et al., 2021).

Setter and Flannigan (1989) have claimed that shading

slows down the development process of corn with significant differences in genotypes. In the present study, the shading throughout the filling stage reduced about 50% sunlight under field conditions, and in terms of the maximal weight per 100 fresh grains, both the cultivars investigated under natural light conditions reached their peaks 22 days after pollination. However, under weak light stress, Xiantian 5 reached its peak 26 days after pollination, whereas Huazhen reached its peak 22 days after. The weight per 100 fresh grains under weak light stress is lower than that of the controls throughout the growth period. The maximal weight per 100 fresh grains of Xiantian 5 was reduced by 31.3% in comparison with the control group, whereas that of Huazhen decreased by 19.8%. With regard to the maximal weight per 100 dry grains, the two cultivars, Xiantian 5 and Huazhen decreased by 33.0 and 24.8% in comparison with the control group, respectively. For ordinary corn varieties, weak light stress reduced the number of ears and that of grains, but the grain weight remained unchanging or increases (Uhart and Andrade, 1995; Reed and Singletary, 1989)

Weak light stress increases the protein contents in the grains of wheat, rice, and corn (Mengel and Judel, 1982; Struik 1983; Setter et al., 2001; Li et al., 2005), with the starch content reduced and the quality deteriorated. In the regional tests on new varieties of sweet corn in the country, the quality evaluation has been based on the appearance, steaming (including sweetness, tenderness, skin thickness, and taste) and nutrition, and the result of quality evaluation has mainly been in the form that several authoritative experts give marks after tasting. This method is subjective and affected by environmental conditions. For avoiding the evaluation results from subjective bias, the aforementioned texture analyzer was first adopted to determine TPA (Bourne, 2002), and is now widely applied in vegetables and fruits (Liu and Li, 2010; Zhang et al., 2011). In the present experiments, significant differences were observed between the two sweet corn cultivars in terms of hardness and chewiness. Under weak light stress, the hardness, fracturability, and chewiness declined, affecting negatively the palatability (Zhang et al., 2011).

It is a common sense that the content of soluble sugar decides the sweetness of corn, and sucrose is a principal part of soluble sugar. The contents of soluble sugar and sucrose of Xiantian 5 reach peak values 22 days after pollination under natural light and 26 days under weak light stress, respectively. However, those of Huazhen reached peak values on day 18 after pollination under natural light and on day 22 under weak light stress. The highest contents of soluble sugar in Xiantian 5 and Huazhen under weak light stress decreased by 19.5 and 10.1%, respectively in comparison with the controls. By judging from the fresh ear yield, grain yield and sugar content in the best harvest time (for Xiantian 5 and Huazhen under natural light, 22 days after pollination; for

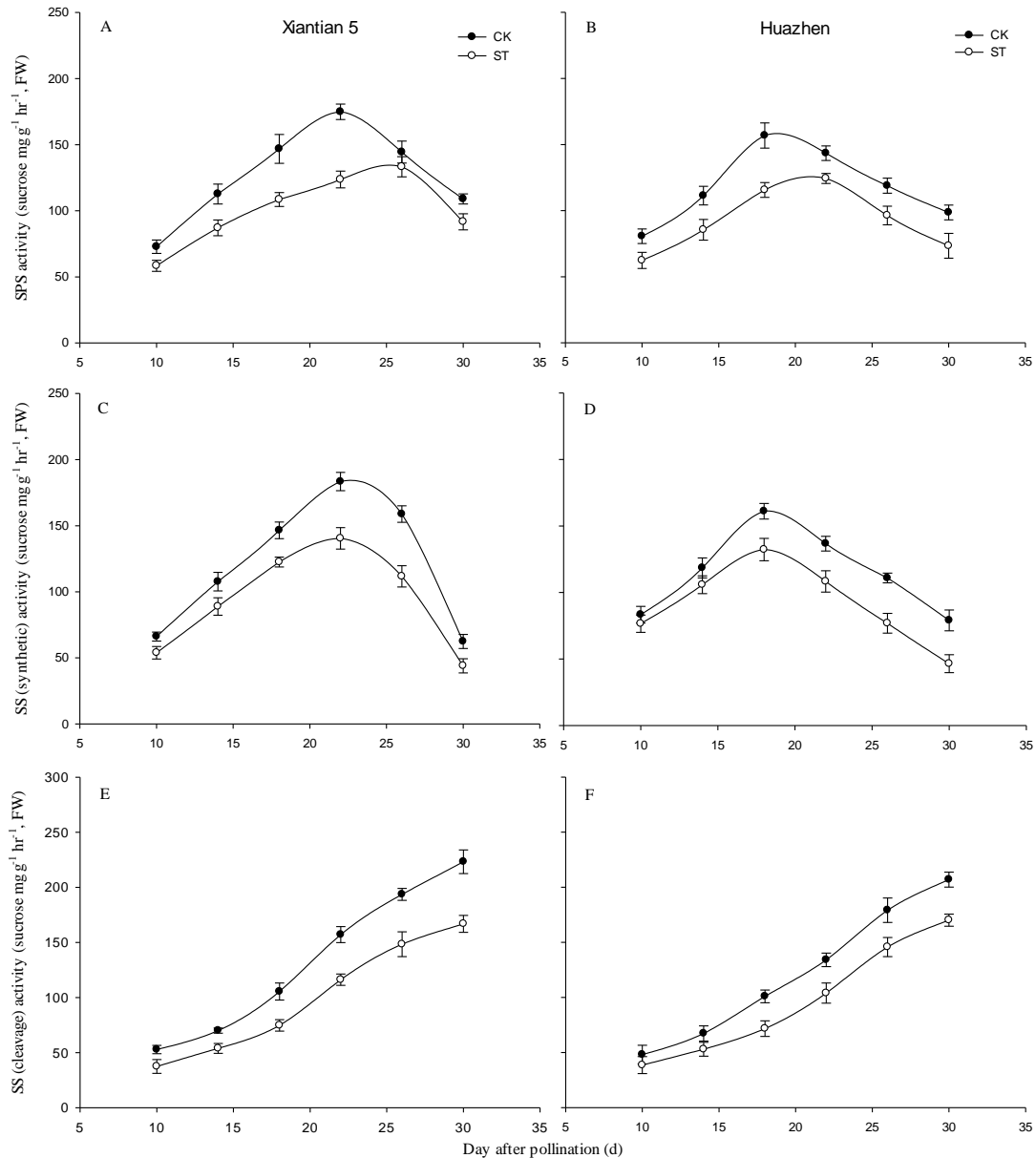


Figure 3. Dynamics of the activities of SPS, SS (synthetic), and SS (cleavage) in grains of sweet corn after pollination.

Xiantian 5 weak light stress, 25 days after pollination; and for Huazhen, 22 days after pollination), the shade tolerance of Huazhen was better than that of Xiantian 5.

Sucrose is the main form of storage and transportation of carbohydrates in crops. In sweet corn, the synthesis of sucrose is catalyzed by SPS and SS, whereas the decomposition of sucrose is driven by SS. Our previous studies (Zhao et al., 2013) showed that from the early and middle filling stages, the SPS/SS activity in the direction of the synthesis of sucrose is higher than that in the decomposition direction, leading to an increase in the sucrose content. At the late filling stage, the SS activity in

the decomposition direction increases rapidly and was also higher than the SPS/SS activity in the synthesis direction of sucrose.

The activities of metabolizing enzymes are seriously affected by weak light stress. Mengel and Judel (1982) and Zhang et al. (2008) have pointed out that because of the lack of supply of assimilates, weak light stress reduces the activities of starch synthases, including adenosine diphosphoglucose pyrophosphorylase, uridine diphosphate-glucose pyrophosphorylase, granule-bound starch synthase, and soluble starch synthase. In the present study, shading reduced the SPS/SS activity in

the directions of synthesis and decomposition and slowed down the emergence of the peak SPS activity. It was found that the reduction in synthesis was greater than that in the decomposition, and the sucrose content declined. On the other hand, the reduction in SPS/SS activity in the synthesis direction under weak light stress at the middle filling stage was greater than that at the early filling stage. In addition, the SPS/SS activity in Xiantian 5, a low-light-sensitive cultivar, decreased faster than that of Huazhen, a low-light-insensitive variety. Therefore, it could be said that weak light stress highly affects the grain yield and quality of sweet corn during the filling stage. This phenomenon is attributed not only to the poor photosynthesis which results in a reduction in photosynthetic products but also mainly the poor SS activity in the grains which results in the accumulation of less sucrose.

Conclusion

Weak light stress slows down the development process of sweet corn, lowering the fresh ear yield, weight per 100 fresh grains, contents of soluble sugar and sucrose, and the quality. Weak light stress also weakens the activities of sucrose-metabolizing enzymes (in the directions of synthesis and decomposition of SPS/SS) and slows down the emergence of the peak SPS activity. The synthesis of sucrose declines faster than the decomposition, thus resulting in a reduction in sucrose content. Genotypic differences are observed in the responsiveness of the yield/quality of sweet corn to weak light stress during the filling stage. Under weak light stress, the yield and sugar content of Xiantian 5, a low-light-sensitive variety, decreased faster than those of Huazhen, a low-light-insensitive variety. In practical production, low-light-insensitive varieties are recommended to properly slow down the harvesting time. Thus, the effects of weak light stress on the yield and quality of sweet corn are mitigated.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

ACKNOWLEDGEMENTS

The research was funded by Major Agriculture Science Foundation of Upland Grain Crops Breeding of Zhejiang Province (grant No. 2021C02064-4) and supported by China Agriculture Research System of MOF and MARA.

REFERENCES

Andrade FH, Frugone MI, Uhart SA (1993). Intercepted radiation at flowering and kernel number in maize: shade versus plant

- density effects. *Crop Science* 33(3):482-485.
- Andrew JR, Singletary GW, Schussler JR (1988). Shading effects on dry matter and nitrogen partitioning kernel number and yield of maize. *Crop Science* 28(5):819-825.
- Bourne MC (2002). *Food Texture and Viscosity: Concept and Measurement* (A Volume in the Food Science and Technology International Series). Academic Press, American pp. 42-82.
- Doehlert DC, Kuo TM, Felker FC (1988). Enzymes of sucrose and hexose metabolism in developing kernels of two inbreds of maize. *Plant Physiology* 86(4):1013-1019.
- Early EB, McIlrath WO, Seif RD, Hageman RH (1967). Effects of shade applied at different stages of plant development on corn (*Zea mays* L.) production. *Crop Science* 7(2):151-156.
- Fernando HA, Sergio AU, Mariano IF (1993). Intercepted radiation at flowering and kernel number in maize: shade versus plant density effects. *Crop Science* 33(3):482-485
- Feng YZ, Xie ZW, He LH, Yu T, Chen HY (2007). Effects of light regimes on photosynthesis and yield components in sweet and waxy maize. *Acta Agriculturae Boreali Sinica* 3:132-136.
- Feng ZH, Guo B, Ren SJ, Li Y (2019). Reduction in sunshine duration and related factors over mainland China during 1961-2016. *Energies* 12(24):4718.
- Frans M, Aerts R, Ceusters N, Luca S, Ceusters J (2021). Possibilities of modified atmosphere packaging to prevent the occurrence of internal fruit rot in bell pepper fruit (*Capsicum annuum*) caused by *Fusarium* spp. *Postharvest Biology and Technology* 178(8):111545.
- Harbur MM, Owen DK (2016). Light and growth rate effects on crop and weed responses to nitrogen. *Weed Science* 52(4):578-583.
- Hashemi DA, Herbert SJ (1992). Intensifying plant density response of corn with artificial shade. *Agronomy Journal* 84(4):547-551.
- Hawker JS, Jenner CF (1993). High temperature affects the activity of enzymes in the committed pathway of starch synthesis in developing wheat endosperm. *Functional Plant Biology* 20(2):197-209.
- He ZY, Tan SY, Lin L, Hong DK, Bai CY (1998). Study on various light intensity and its quality affecting the fertility of maize staminate flower. *Scientia Agricultura Sinica* 14(4):6-8.
- Jia S F, Dong S T, Wang KJ, Zhang JW, Liu P (2007b). Effect of shading on grain quality at different stages from flowering to maturity in maize. *Acta Agronomica Sinica* 33(12):1960-1967.
- Jia SF, Dong ST, Wang KJ, Zhang JW, Liu P (2007a). Effects of weak light stress on grain yield and photosynthetic traits of maize. *Chinese Journal of Applied Ecology* 18(11):2456-2461.
- Jia SF, Li CF, Dong ST, Zhang JW (2010). Effects of shading at different stages after anthesis on maize grain weight and quality at cytology level. *Scientia Agricultura Sinica* 43(5):911-992.
- Kiniry JR, Tischler CR, Rosenthal WD, Gerik TJ (1992). Nonstructural carbohydrate utilization by sorghum and maize shaded during grain growth. *Crop Science* 32(1):131-137.
- Kobata T, Sugawara M, Takatu S (2000). Shading during the early grain filling period does not affect potential grain dry matter increase in rice. *Agronomy Journal* 92(3):411-417.
- Lambert RJ, Mansfield BD, Mumm RH (2014). Effect of leaf area on maize productivity. *Maydica* 59(1):58-63.
- Li HS (2000). *The Principles and Techniques of Plant Physiological and Biochemical*. Beijing: Higher Education Press, pp. 24-35.
- Li T, Ohsugi R, Yamagishi T (2005). Effects of weak light on rice starch accumulation and starch synthesis enzyme activities at grain filling stage. *Chinese J Rice Science* 19(6):545-550.
- Liu P, Lu WP, Lu DL (2009). Quality differences and physicochemical index screening for quality evaluation in waxy corn. *Journal of Yangzhou University* 30(3):16-21.
- Liu YP, Li HB (2010). Review on the application of texture analyzer and TPA in the assessment for fruits and vegetables texture. *Journal of Shanxi Agricultural University (Natural science edition)*, 30(2):188-192.
- Ma BL, Morrison MJ, Dwyey LM (1996). Canopy light reflectance

- and filed greenness to assess nitrogen fertilization and yield of maize. *Agronomy Journal* 88(6):915-920.
- Martin SA, Darrah LL, Hibbard BE (2004). Divergent selection for rind penetrometer resistance and its effects on European corn borer damage and stalk traits in corn. *Crop Science* 44(3):711-717.
- McLachlan SM, Tollenaar M, Swanton CJ, Weise SF (1994). Effect of corn-induced shading on dry matter accumulation, distribution, and architecture of redroot pigweed (*Amaranthus retroflexus*). *Weed Science* 41(4):568-573.
- Mengel K, Judel GK (1982). Effect of shading on nonstructural carbohydrates and their turnover in culms and leaves during the grain filling period of spring wheat. *Crop Science* 22(5):958-962.
- Morell MK, Rahman-Sabrahams SL, Appel SR (1995). The biochemistry and molecular biology of starch synthesis in cereals. *Australian Journal of Plant Physiology* 22(4):647-660.
- Reed JA, Singletary GW (1989). Roles of carbohydrate supply and phytohormones in maize kernel abortion. *Plant Physiology* 91(3):986-992.
- Reed JA, Singletary GW, Schussler JR (1988). Shading effects on dry matter and nitrogen partitioning, kernel number, and yield of maize. *Crop Science* 28(5):819-825.
- Setter T L, Brian A F, Melkonian J (2001). Loss of kernel set due to water deficit and shade in maize. *Crop Science* 41(5):1530-1540.
- Setter TL, Flannigan BA (1989). Relationship between photosynthate supply and endosperm development in maize. *Annals Botany* 64(4):481-487. Available at: <https://doi.org/10.1093/oxfordjournals.aob.a087867>
- Struik PC (1983). The effect of short and long shading, applied during different stages of growth, on the development, productivity and quality of forage maize (*Zea mays* L.). *Netherlands Journal of Agricultural Science* 31(2):101-124.
- Uhart SA, Andrade FH (1995). Nitrogen and carbon accumulation and remobilization during grain filling in maize under different source, sink ratios. *Crop Science* 35(1):183-190.
- Wang Y, Qi XN, Shao JF, Liu ZY, Li ZX (2008). Effects of light intensity at full growing stage on the growth and yield of different maize varieties. *Journal of Jilin Agricultural University* 30(6):769-773.
- Ward DA, Woolhouse HW (1986). Comparative effects of light during growth in the photosynthetic properties of NADP- ME type C4 grasses from open and shade habitats. I. Gas exchange, leaf anatomy and ultrastructure. *Plant Cell and Environment* 9(4):261-270.
- Wardlaw IF (1971). The early stages of grain development in wheat: Response to water stress in a single variety. *Australian Journal of Biological Science* 24(4):1047-1055.
- Warrington IJ, Kanemasu ET (1983). Corn growth response to temperature and photoperiod I. seedling emergence, tassel initiation, and anthesis. *Agronomy Journal* 75(5):749-754.
- Wenzel CL, McCully ME, Canny MJ (1989). Development of water conducting capacity in the root systems of young plants of corn and some other C4 grasses. *Plant Physiology* 89(4):1094-1101.
- Yang QR, Pan JQ, Shen GA, Guo, BL (2019). Yellow light promotes the growth and accumulation of bioactive flavonoids in *Epimedium pseudowushanense*. *Journal of Photochemistry and Photobiology B: Biology* 197:111550.
- Zeng Z, Yan Z, Ye D (2001). The regions with the most significant temperature trends during the last century. *Advances in Atmospheric Sciences* 18(4):481-496.
- Zhang DL, Zhang HX, Min WH, Zheng MZ, Liu JS (2011). Physical properties and optimum consumption temperature of steamed corn on the cob. *Food Science* 32(9):111-113.
- Zhang JW, Dong ST, Wang KJ, Hu CH, Liu P (2008). Effects of shading in field on key enzymes involved in starch synthesis of summer maize. *Acta Agronomica Sinica* 34(8):1470-1474.
- Zhang JW, Wu HX, Dong ST, Wang KJ, Hu CH, Liu P (2009). Effects of shading on yield and quality of summer maize. *Journal of Maize Sciences* 17(5):124-129.
- Zhang L (2012). Spatiotemporal change of sunshine hour and its affecting factors in Zhejiang province in recent 50 years. *Journal of Zhejiang Agricultural Science* (10):1448-1452.
- Zhao FC, Jing LQ, Yan FB, Lu DL, Wang GY, Lu WP (2013). Effects of nitrogen fertilization on yield, quality and enzyme activity associated with sucrose metabolism of sweet corn. *Journal of Plant Nutrition and Fertilizer* 13(1):45-53.