

Morphophysiological responses and tolerance of various sweet corn (*Zea mays* convar. *saccharata*) hybrids to shade stress

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Abstract. Utari VF, Chozin MA, Hapsari DP, Ritonga AW. 2023. Morphophysiological responses and tolerance of various sweet corn (*Zea mays* L. convar. *saccharata*) hybrids to shade stress. *Biodiversitas* 24: 4438-4447. Expanding lands for cultivating sweet corn (*Zea mays* convar. *saccharata*) is a strategy to increase its production. Yet, the available lands for sweet corn extensification might be those with existing tree stands with some extent of shading. Planting sweet corn under tree stands affects its growth and productivity since there is a reduction in light intensity, but some superior varieties might tolerate such stress. This study aimed to determine the growth, yield, and shade-tolerance levels of several sweet corn genotypes under shade stress. The experiment adopted a randomized complete block design consisting of two factors, namely shading (i.e. control or 0% shade and 50% shade) and sweet corn genotype (16 genotypes). The observed parameters included morphological traits (plant height, leaf number, leaf length, leaf width, and stem diameter), physiological traits (stomatal density and trichome density), yield attributes (cob weight with husks, cob weight without husks, cob length, cob diameter, and total soluble solid), and stress tolerance index (STI). The tested genotypes responded differently to shading. In general, 50% shade significantly reduced cob production, with an average decrease of more than 50% compared to the control. Commercial varieties, namely Exotic (G13), Talenta (G14), Paragon (G15), and Golden Boy (G16), had relatively higher STI values compared to the hybrids. Among the hybrids, the highest STI values were observed for genotypes resulting from the crosses SM7-8 × SM12-2 (G11) and SM11-6 × SM12-2 (G12). The results of this study recommend that commercial varieties can be cultivated under tree stands or low light intensity and can be used to develop high-yielding shade-tolerant sweet corn varieties.

Keywords: Light intensity, shade stress, sweet corn, tolerant genotypes

INTRODUCTION

Corn (*Zea mays* L.) is Indonesia's leading secondary food crop and cattle fodder (Rahman et al. 2019). Among several corn varieties, many people prefer to consume sweet corn (*Zea mays* convar. *saccharata*) than other varieties because it has a higher sugar content. As a consequence, the demand for sweet corn has increased dramatically in Indonesia, but production and productivity remain low (Ruswandi et al. 2020). The average production of sweet corn in Indonesia reaches 19.81 tons ha⁻¹ (BPS 2018). This productivity can be increased both in quantity and quality by various improvements in agricultural aspects.

Several factors are responsible for the low sweet corn production in Indonesia, one being the continuing reduction in the extent of cultivating lands (Rondhi et al. 2018). Therefore, one strategy to increase the production of sweet corn in Indonesia can be achieved by expanding the land area for sweet corn cultivation and planting high-yielding varieties (Hamdani and Susanto 2020; Syukur et al. 2023). Nonetheless, in many cases, extensification is conducted by opening up new lands and clearing the existing tree stands

and forests. This approach could have perverse impacts on the environment since vegetation clearance might reduce the ecosystem functions of the landscape. For example, it might trigger soil erosion and alter the hydrological system. The alternative approach of extensification can be done by planting sweet corn under the tree stands, which is often called agroforestry or intercropping system. However, this approach has several obstacles, prominently the reduction of light intensity due to shading, which might cause stress to corn, which is generally known as a light-demanding crop (Hamdani and Susanto 2020).

Light plays an important role in the development and performance of plants (Yan et al. 2016). Plants have different light requirements depending on the species, variety, and type of photosynthesis (Khalid et al. 2019). Some crop species require full light intensity and the reduction of light caused by shading might affect its growth and productivity. For example, shading by more than 50% can reduce productivity in rice (Song et al. 2022), soybean (Bing-Xiao et al. 2020), chili pepper (Masabni et al. 2016), and tomato (Sulistyowati et al. 2016; Ritonga et al. 2019). Nonetheless, several varieties of such crops can also cope with the stress of low light by improving their ability to

continue photosynthesis under light-deficient conditions (Fan et al. 2019). This shows that the use of shade-tolerant varieties is essential for high productivity. In other words, it is necessary to use varieties that can grow, develop, and produce well under shade stress to optimize land use under tree stands (Syafii et al. 2021).

Plant breeders develop new varieties by hybridization processes (Syukur et al. 2023) to enhance productivity (Schroeder et al. 2013). Hybridization is an appropriate strategy to increase the productivity and production of sweet corn (Syafii et al. 2021). For example, Ertiro et al. (2015) developed a hybrid sweet corn by breeding between pure parental lines to produce F1 generation with superior characteristics that can increase production. Such advantageous characteristics include disease resistance and high productivity. In regard to the cultivation of sweet corn under tree stands, hybridization might provide an opportunity to obtain tolerant sweet corn varieties that can maintain productivity under shade stress or low light intensity (Hamdani and Susanto 2020).

The critical light intensity for selecting shade tolerance varieties in many food crops is 50% shading, such as in rice (Song et al. 2022), soybean (Bing-Xiao et al. 2020), chili pepper (Masabni et al. 2016), and tomato (Sulistiyowati et al. 2016). On the other hand, the critical light intensity for corn is at 20% shading (Jauhari et al. 2022) because the relative productivity of the species varies at this level. However, at 40% shading, most crop species experience a significant decrease in production. Therefore, this study aimed to determine the morphophysiological responses of growth, yield, and yield components and the shade-tolerance level of several sweet corn genotypes under shade stress. We hope that the results of this study help to clarify the findings of Jauhari et al. (2022) on the selection of environment for shade-tolerant sweet corn varieties.

MATERIALS AND METHODS

Study area and genotype materials

This study was conducted in July–November 2022 at the Pasir Kuda Experimental Field of IPB University, Bogor, Indonesia. The experiment consisted of two factors. The first factor was shade with two levels: without shade (control) and 50% shading with black plastic shade cloth. The second factor was the sweet corn variety and included 16 hybrids. The seeds used were 12 genotypes (G1–G12) of sweet corn hybrid obtained from the collection of the Plant Breeding and Biotechnology Study Program, IPB University. In addition, we used four commercial sweet corn varieties used by many Indonesian farmers, including Exotic (G13), Talenta (G14), Paragon (G15), and Golden Boy (G16). The genotypes used in this study are described in Table 1. The microclimate variables observed in this study were light intensity, air temperature, and daily air humidity. Microclimate data were recorded in the morning (07:00–09:00 GMT+7 for Jakarta), afternoon (12:00–14:00 GMT+7 for Jakarta), and late afternoon (16:00–18:00 GMT+7 for Jakarta). Light intensity was observed with a lux meter (UNI-T UT383) and temperature and humidity with a thermohygrometer (HTC-1) installed at the center (the point between the east and west sides) of the experimental field.

Experimental procedures

This study adopted a randomized complete block design. Black shade plastic net was used to reduce light intensity by up to 50% (the height of shade plastic net poles was 3 meters). Lime and manure were applied two weeks before planting with respectively 1.5 tons ha⁻¹ of dolomite and 10 tons ha⁻¹ of manure. As much as 300 kg ha⁻¹ of NPK (16:16:16) was applied at the vegetative phase. Weeding was scheduled every week after planting. The irrigation was done every day to prevent drought or water shortages. The crop was protected from insects, pests, and diseases using the recommended pesticide.

Table 1. The sweet corn genotypes used in this study

Genotype	Female parent	Male parent	Cultivar type
G1	F1 T10-3	SM12-2	Hybrid
G2	F1 SM6-3	SM12-2	Hybrid
G3	F1 SB5-1C	XSM12-2	Hybrid
G4	F1 T9-2	SM12-2	Hybrid
G5	F1 SM10-1	SM12-2	Hybrid
G6	F1 T8-2A	SM12-2	Hybrid
G7	F1 SM12-2	F1 SM12-2	Hybrid
G8	F1 SB9-2	SM12-2	Hybrid
G9	SM7-3	SM12-2	Hybrid
G10	F1 T8-2B	SM12-2	Hybrid
G11	SM7-8	SM12-2	Hybrid
G12	SM11-6	SM12-2	Hybrid
G13 (Exotic)	Unknown	Unknown	Commercial variety
G14 (Talanta)	Unknown	Unknown	Commercial variety
G15 (Paragon)	Unknown	Unknown	Commercial variety
G16 (Golden boy)	Unknown	Unknown	Commercial variety

The harvesting of full light plants and 50% shading plants was conducted respectively at 10 weeks after planting (WAP) and 12 WAP. The observation was recorded on five plants per sample, including morphological traits (plant height, leaf number, leaf length, leaf width, and stem diameter), two plants per sample included physiological traits (stomatal density and trichome density), and three plants per sample included yield attributes (cob weight with the husk, cob weight without the husk, cob length, cob diameter, and TSS).

Observation of morphological characters

Sweet corn plant height was measured from the base of the stem to the growing point of the plant using a ruler or tape measure from 2 WAP to 8 WAP. The number of leaves was determined by counting perfectly open leaves from 2 WAP to 8 WAP. Leaf length was measured from the perfectly formed leaf axil to the tip of the leaf at harvest. Leaf width was measured from one edge of the leaf to the other at the center of the leaf at harvest. Stem diameter was measured with calipers at harvest. Three replicates of measurements were obtained for each variable for each of the 160 samples.

Observation of physiological characters

Stomatal density and trichome density were observed in the generative phase at 7 WAP. The third leaf from a fully opened shoot was sampled. Transparent nail polish was applied to the lower surface of the leaves. Transparent nail polish can provide clear, stable, and almost permanent epidermal smears for stomatal enlargement (Wu and Zhao 2017). Clear colored tape was affixed to the nail polish after it was dry. The tape was then removed and affixed to a glass slide and observed under a microscope with an objective lens magnification of 40× and numerical aperture of 0.65 (Heyneke et al. 2013). Stomata were counted using the image-J application. Three replicate measurements of each variable were obtained for each of 64 samples. Stomatal density was determined using the following equation:

$$\text{Stomatal density} = \frac{\text{Number of stomata}}{\text{Area of field of view (mm}^2\text{)}}$$

Trichomes were observed under a microscope at 4× magnification and 0.10 numerical aperture. Trichomes were counted using the image-J application. The density of trichomes was calculated with the equation:

$$\text{Trichome density} = \frac{\text{Number of trichomes}}{\text{Area of field of view (mm}^2\text{)}}$$

Observation of yield characters and yield components

The yield components considered in this study were cob weight with the husk, cob weight without the husk, cob length, cob diameter, and sweet corn total soluble solid (TSS). The yield components were observed at 10 WAP (full light plants) and 12 WAP (50% shading plants). Cobs with husks and cobs without husks were weighed using a scale after the ears were harvested. Cob length, from the

base to the tip of the filled cob, was measured with a ruler after peeling off the husk. The diameter at the midpoint of the cob was measured with calipers. Total soluble solid (TSS) was measured using a digital refractometer (Aliyiqi) to determine the sugar content in sweet corn kernels. Three replicate measurements were taken for each variable for each of 96 samples.

Determination of plant shade-tolerance level

The tolerance index value under shade stress was determined based on cob weight without the husk. The stress tolerance index (STI) was calculated as follows (Fernandez 1982):

$$\text{STI} = \frac{Y_p \times Y_s}{\bar{Y}_p^2}$$

Where: Y_p was the result under normal conditions, Y_s was the result under stressed conditions, and \bar{Y}_p^2 was the average yield under normal conditions.

The shade tolerance of sweet corn genotypes was classified as follows (Fernandez 1982): tolerant = $\text{STI} \geq 1.0$; moderately tolerant = $0.5 \leq \text{STI} < 1.0$; and sensitive = $\text{STI} < 0.5$.

Data analysis

Analysis of variance (ANOVA) of quantitative data was performed using PKBT STAT 3.1 at the 5% significance level. If the ANOVA found a significant or very significant effect, then the post hoc Tuckey's HSD test was performed at the 5% significance level using PKBT-STAT 3.1 (<http://pkbtstat.com/pkbt-stat/>).

RESULTS AND DISCUSSION

Microclimate conditions

The microclimate observations made during the study for sweet corn plants under full light and 50% shade included light intensity, temperature, and humidity (Table 2). Solar radiation greatly influences the microclimate around plants and eventually affects plant growth (Marrou et al. 2013). Table 2 shows that light intensity caused changes in other microclimate parameters, i.e., temperature and humidity. The temperature under full light (35.4°C) at 6 WAP was higher than that under 50% shade (30.4°C). In contrast, under full light conditions, the average air humidity (75.7%) was lower than that under 50% shade (81.7%). In other words, shade increases the humidity around the plants.

The light intensity, temperature, and humidity around plants differed between the full light and 50% shade environments (Table 2). Plants grown under 50% shade experienced a decrease in light intensity, resulting in lower temperatures and higher humidity compared to plants grown under full light conditions.

The differences in microclimate conditions had varying effects on the morphological and physiological responses, growth, and yield components of sweet corn genotypes between plants grown under full light and those grown under 50% shade (Table 3). The shading treatment did not

significantly affect leaf length, leaf number, and TSS (Table 3). In contrast, genotype had a highly significant effect on all variables except for the number of leaves, which was moderately affected. The interaction between shade and sweet corn genotype significantly affected all variables except for plant height, number of leaves, stomatal density, trichome density, and cob diameter. The results of the recapitulation of the analysis of variance showed that the coefficient of variation in this experiment ranged from 3.8% to 24.02%.

Morphological and physiological responses of sweet corn plants

The analysis of variance showed that the interaction between shade and genotype had a highly significant effect on stem diameter, leaf length, and leaf width (Table 4). The largest stem diameters under full light were found in the commercial varieties G13 (Exotic) and G16 (Golden Boy). Under 50% shade, the largest stem diameters were found in genotypes G1 and G2. The stem diameter of the tested sweet corn genotypes showed different responses. The average stem diameter under full light was 2.06 cm, which is greater than that under 50% shade (1.34 cm). Perrin and Mitchell (2013) found that the lack of light due to shading caused changes in the morphophysiology of *Taxus baccata* L. as it led to a reduction in stem diameter. In this study, 50% shading resulted in significantly reduced stem diameter, for example, in the genotype G16, which had a stem diameter of 1.23 cm under 50% shade, which is significantly lower than that under full light (2.75 cm). However, the stem diameter of G6 under full light (1.87 cm) was not significantly different from that under shade (1.37 cm). Therefore, the genotypes tested showed varying stem diameter responses to low light intensity or shading.

In most genotypes tested, there was no significant difference in leaf length between full light and 50% shade, except for G3, G10, and G13. Under 50% shade, the average leaf length of G3 was 65.65 cm, which is significantly lower than that under full light (84.74 cm). In contrast, shade stress increased the leaf length of G10 from 83.86 cm under full light to 91.86 cm under 50% shade and that of G13 from 78.52 cm under full light to 90.63 cm under 50% shade. This could be because some of these genotypes have different adaptation mechanisms. According to Levitt (1980), plant adaptation to low light intensity has two mechanisms: increasing the total light intercepted by increasing leaf area and increasing the percentage of light used in photosynthesis by decreasing the amount of light reflected and transmitted. Supriyono et al. (2017) suggested that increased leaf area is a plant's effort to efficiently capture the light used for photosynthesis, typically under shade. Leaf area is related to leaf length, with leaf area being calculated by measuring the dimensions of all leaf surfaces, including leaf length. The longer leaves under 50% shade allow the capture of as much light as possible with the lowest reflected light.

The interaction between shade and genotype had a highly significant effect on leaf width. The average leaf width under full light was 9.46 cm, which is greater than the 7.85 cm under 50% shade. However, a significant difference between full light and 50% shade was evident only for G16. In this genotype, shading significantly decreased leaf width from 10.67 cm under full light to 8.19 cm under 50% shade. Leaf development is strongly regulated by temperature (Gray and Brady 2016), and the higher environmental temperatures under full light lead to maximum cell division and leaf elongation and as a result, increased leaf width.

Table 2. Average light intensity, temperature, and humidity under full light and under 50% shade

Variable	6 WAP		7 WAP		8 WAP	
	Full light	50% shade	Full light	50% shade	Full light	50% shade
Light intensity (lux)	63,860	34,603	63,867	34,387	49,373	16,213
Temperature (°C)	35.4	30.4	32.3	30.7	32.3	29.7
Humidity (%)	75.7	81.7	79.7	92	86	87.7

Note: WAP: weeks after planting

Table 3. Recapitulation of analysis of variance of morphophysiological characteristics and yield components of several sweet corn genotypes under shade

Variable	Shade	Genotype	Shade × genotype interaction	CV (%)
Stem diameter	**	**	**	12.47
Leaf length	ns	**	**	6.48
Leaf width	**	**	**	6.54
Plant height	**	**	ns	3.8
Number of leaves	ns	*	ns	5.1
Stomatal density	*	**	ns	8.67
Trichome density	*	**	ns	24.02
Cob weight with husks	**	**	**	13.39
Cob weight without husks	**	**	**	12.36
Cob length	**	**	**	9.63
Cob diameter	**	**	ns	8.74
TSS	ns	**	**	8.45

Note: ns: not significant; *: significant ($p < 0.05$); **: highly significant ($p < 0.01$); CV: coefficient of variance

Shade significantly affected plant height, stomatal density, and trichome density (Table 5). Sweet corn genotypes showed significant variation in plant height, number of leaves, stomatal density, and trichome density. The 16 genotypes of sweet corn were of various heights. The tallest genotype was G14 and the shortest was G6. However, the responses of the genotypes to shade stress did not differ. All genotypes were stunted under 50% shade. The average plant height under 50% shade was 179.28 cm, which was lower than that under full light (224.46 cm), a decrease of 20%. According to Taiz and Zeiger (2002), shaded plants show etiolation symptoms in order to obtain more light; thus, by increasing height, plants are able to acquire light of higher quality. Based on such premise, shaded plants are taller due to increased auxin activity, which results in etiolation. However, the result of this study, which found the inhibition of plant height under low light intensity, is not in line with the premise by Taiz and Zeiger (2002). This may be because shade inhibits plant growth, so sweet corn plants become stressed. This could explain the reason for sweet corn plants being taller under full light than under 50% shade.

The results of the analysis of variance showed that genotype had a significant effect on the number of leaves. The genotypes G2, G11, G13, G14, and G15 had significantly more leaves than G4, G6, G7, G9, and G10. The ability to form photosynthates is greater when plants have more leaves; consequently, vegetative growth is higher (Sulistyowati et al. 2019). This adaptive response is one of the strategies for maintaining a high photosynthesis rate by absorbing more light under shaded conditions.

The analysis of variance showed that shade and genotype significantly affected stomatal density and trichome density in sweet corn. However, the genotype and shade interaction had no significant effect. Table 5 shows the average stomatal density and trichome density of sweet corn under full light and under 50% shade. The average

stomatal density of plants under full light was 111.66 stomata mm^{-2} , which was significantly higher than the average under 50% shade (94.87 stomata mm^{-2}). The results of this study indicate that low light intensity causes stomatal density to decrease. This result agrees with the finding of Kim et al. (2011) that the leaf surface exposed to more sunlight had a higher stomatal density than the shaded leaf surface. Stomatal density varied significantly between the genotypes tested. G14 had denser stomata than the other genotypes, while G15 had the lowest stomatal density at 89.29 stomata mm^{-2} .

Unlike stomatal density, trichome density increased under 50% shade. Trichome density was significantly higher under 50% light intensity, with an average of 0.65 trichomes mm^{-2} , than under full light, with an average of 0.50 trichomes mm^{-2} . The results of this analysis indicate that low light intensity causes trichome density to increase and that plants under full light have fewer trichomes.

According to Levitt's (1980) hypothesis, the success of plants in growing and developing under low light intensity depends on the efficiency of light capture, among other factors, by reducing the number of trichomes. Leaves with many trichomes show a 40% reduction in light absorption compared to leaves with few or no trichomes (Taiz and Zeiger 2002).

However, our results do not conform to such statement. This might be because the function of trichomes is to inhibit the rate of transpiration; a high number of trichomes on the leaf surface can prevent excessive transpiration under stress. One of the adaptations that can reduce the rate of transpiration is a large number of hairs or trichomes on the leaf surface (Salisbury and Ross 1992). The tested genotypes varied in trichome density, with G16 having a significantly higher average trichome density of 0.76 trichomes mm^{-2} than G9, G11, and G12.

Table 4. The effects of shading on stem diameter, leaf length, and leaf width of several sweet corn genotypes

Genotype	Stem diameter (cm)			Leaf length (cm)			Leaf width (cm)		
	Full light	50% shade	Genotype average	Full light	50% shade	Genotype average	Full light	50% shade	Genotype average
G1	2.03 ^{a-g}	1.51 ^{c-i}	1.77 ^{ABC}	82.65 ^{def}	83.16 ^{def}	82.90 ^{CDE}	9.60 ^{a-e}	8.13 ^{c-k}	8.87 ^{BC}
G2	2.13 ^{a-e}	1.50 ^{c-i}	1.82 ^{AB}	84.07 ^{de}	81.71 ^{def}	82.89 ^{CDE}	9.09 ^{b-i}	7.26 ^{ijk}	8.17 ^C
G3	2.08 ^{a-f}	1.21 ^{hi}	1.65 ^{ABC}	84.74 ^{de}	65.65 ^f	75.20 ^{DE}	9.41 ^{a-f}	7.82 ^{e-k}	8.61 ^{BC}
G4	1.87 ^{b-i}	1.16 ^j	1.51 ^{BC}	82.74 ^{def}	78.81 ^{def}	80.77 ^{CDE}	8.49 ^{c-j}	7.08 ^{lk}	7.79 ^{CD}
G5	1.90 ^{b-h}	1.38 ^{f-i}	1.64 ^{ABC}	85.01 ^{de}	81.99 ^{def}	83.50 ^{CDE}	9.23 ^{b-h}	7.47 ^{g-k}	8.35 ^{BC}
G6	1.87 ^{b-i}	1.37 ^{f-i}	1.62 ^{ABC}	79.92 ^{def}	80.19 ^{def}	80.06 ^{CDE}	9.39 ^{a-f}	7.81 ^{e-k}	8.60 ^{BC}
G7	1.90 ^{b-i}	1.25 ^{hi}	1.57 ^{ABC}	83.85 ^{def}	78.18 ^{def}	81.01 ^{CDE}	9.23 ^{b-h}	7.36 ^{h-k}	8.30 ^{BC}
G8	1.42 ^{e-i}	1.25 ^{hi}	1.34 ^C	70.66 ^{ef}	76.99 ^{def}	73.82 ^E	7.06 ^{lk}	6.26 ^k	6.66 ^D
G9	2.17 ^{a-d}	1.32 ^{ghi}	1.75 ^{ABC}	84.77 ^{de}	86.60 ^{bode}	85.69 ^{CD}	9.29 ^{b-g}	8.27 ^{c-j}	8.78 ^{BC}
G10	1.95 ^{b-h}	1.29 ^{hi}	1.62 ^{ABC}	83.86 ^{def}	91.86 ^{a-d}	87.86 ^{BC}	9.28 ^{b-g}	8.04 ^{d-k}	8.66 ^{BC}
G11	2.19 ^{a-d}	1.33 ^{ghi}	1.76 ^{ABC}	83.97 ^{de}	85.20 ^{de}	84.59 ^{CDE}	9.67 ^{a-e}	7.89 ^{e-k}	8.78 ^{BC}
G12	2.17 ^{a-d}	1.39 ^{f-i}	1.78 ^{ABC}	85.69 ^{cde}	82.73 ^{def}	84.21 ^{CDE}	9.85 ^{a-d}	7.65 ^{f-k}	8.75 ^{BC}
G13	2.28 ^{ab}	1.33 ^{ghi}	1.80 ^{AB}	78.52 ^{def}	90.63 ^{a-d}	84.58 ^{CDE}	10.03 ^{abc}	8.72 ^{c-j}	9.37 ^{AB}
G14	2.03 ^{a-g}	1.41 ^{e-i}	1.72 ^{ABC}	91.45 ^{a-d}	82.60 ^{def}	87.03 ^{BC}	9.85 ^{a-d}	8.08 ^{d-k}	8.97 ^{BC}
G15	2.23 ^{abc}	1.47 ^{d-i}	1.85 ^{AB}	104.44 ^{ab}	103.67 ^{abc}	104.06 ^A	11.24 ^a	9.59 ^{a-e}	10.42 ^A
G16	2.75 ^a	1.23 ^{hi}	1.99 ^A	105.00 ^a	91.43 ^{a-d}	98.21 ^{AB}	10.67 ^{ab}	8.19 ^{e-j}	9.43 ^{AB}
Shade average	2.06 ^A	1.34 ^B		85.71	83.84		9.46 ^A	7.85 ^B	

Note: Means followed by the same letter in the same row and same upper-case letter in the same column are not significantly different based on the HSD test at the 5% significance level

Yield responses and yield components of sweet corn

The average cob weight with the husk and that without the husk of several sweet corn genotypes are shown in Table 6. Shading significantly reduced the weight of cobs without husks by more than 50%, except in genotypes G1 (44%) and G15 (32%). The effect of the interaction between shade and sweet corn genotype on cob weight was highly significant. In all genotypes tested, 50% shade significantly reduced cob weight. The reduction ranged from 32% to 69%, with an average decrease of 52%. This is because sweet corn is a C4 species that requires high-intensity irradiation (Hryhoriv et al. 2023). The decrease in cob weight of various genotypes under shade was caused by the inhibition of plant growth under low light intensity. Low light intensity during the seed-filling stage is a direct cause of reduced yields (Chen et al. 2019). The lowest reduction in cob weight without the husk was in G15, with a 32% decrease from 250 g under full light to 170 g under 50% shade. The highest reduction was in G8, with a 69% decrease, from 130 g under full light to 40 g under 50% shade (Table 6). Likewise, in the case of cob weight with the husk, G8 showed the highest decrease, from 210 g under full light to 70 g under 50% shade. G15 showed the lowest reduction in cob weight with the husk, from 390 g under full light to 250 g under 50% shade. G13 had the highest cob weight, with a 50% decrease in cob weight without the husk, from 320 g under full light to 160 g under 50% shade.

The interaction between shade and genotype had a highly significant effect on cob length and TSS, but not on cob diameter. In all genotypes, 50% shade decreased cob length. This demonstrates that low light intensity is a stress that can reduce cob length in sweet corn. The longest cobs were found in commercial varieties, i.e. in G13 and G14

under full light and in G15 under 50% shade. G8 showed the highest reduction in cob length, at 41.6%, from 18.23 cm under full light to 10.64 cm under 50% shade. In contrast, G15 showed the lowest reduction, of 6.9%, from 19.47 cm under full light to 18.13 cm under shade.

Shade and genotype had a highly significant effect on cob diameter. However, the interaction between shade and genotype did not have a significant effect. Cob diameter decreased from 4.09 cm under full light to 3.55 cm under 50% shade. G16 had the largest average cob diameter of 4.86 cm and G8 had the smallest cob diameter, with an average of 2.47 cm. Based on the response of yield components, G8 had the lowest cob weight with the husk, cob weight without the husk, cob length, and cob diameter. These results indicate that G8 has poor adaptability to low light conditions compared to the other genotypes.

The total soluble solid (TSS) is used to measure the level of sweetness. The higher the TSS is, the sweeter the taste of sweet corn. In this study, TSS was not significantly affected by shading, but it was highly significantly affected by genotype and the interaction between shade and genotype.

The highest average TSS, 15.13 °Brix, was obtained by G15 under full light. Most of the genotypes tested did not show a significant difference between full light and 50% shade, except for G2. The average TSS of G2 under 50% shade was 13.4 °Brix, which was significantly higher than that under full light (9.33 °Brix). This may be because genetic factors have a more significant influence than environmental factors. This conjecture is in accordance with the statement of Heryanto et al. (2022) that most characters in the sweet corn varieties tested are controlled by different genes.

Table 5. The effects of shade on the morphological and physiological characters of some genotypes of sweet corn

Treatment	Plant height (cm)	Number of leaves (sheet)	Stomatal density (stomata mm ⁻²)	Trichome density (trichomes mm ⁻²)
Shade				
Full light	224.46 ^a	11.12	111.66 ^a	0.50 ^b
50% shade	179.28 ^b	10.73	94.87 ^b	0.65 ^a
Genotype				
G1	196.62 ^{b-e}	10.97 ^{ab}	107.99 ^{a-d}	0.56 ^{ab}
G2	196.81 ^{b-e}	11.40 ^a	103.32 ^{a-d}	0.49 ^{ab}
G3	200.06 ^{a-e}	10.77 ^{ab}	102.47 ^{a-d}	0.65 ^{ab}
G4	201.10 ^{a-e}	10.70 ^b	98.21 ^{a-d}	0.60 ^{ab}
G5	200.53 ^{a-e}	10.83 ^{ab}	90.99 ^{cd}	0.55 ^{ab}
G6	191.97 ^e	10.43 ^b	109.27 ^{abc}	0.65 ^{ab}
G7	193.51 ^{cde}	10.33 ^b	112.24 ^{ab}	0.65 ^{ab}
G8	193.09 ^{de}	11.03 ^{ab}	106.29 ^{a-d}	0.53 ^{ab}
G9	203.43 ^{a-e}	10.63 ^b	103.74 ^{a-d}	0.46 ^b
G10	199.13 ^{a-e}	10.70 ^b	110.97 ^{ab}	0.55 ^{ab}
G11	209.11 ^{a-d}	11.13 ^a	99.49 ^{a-d}	0.47 ^b
G12	198.49 ^{a-e}	11.00 ^{ab}	104.17 ^{a-d}	0.44 ^b
G13	209.62 ^{abc}	11.17 ^a	103.32 ^{a-d}	0.53 ^{ab}
G14	213.48 ^a	11.50 ^a	116.92 ^a	0.62 ^{ab}
G15	211.06 ^{ab}	11.27 ^a	89.29 ^d	0.71 ^{ab}
G16	211.87 ^{ab}	10.87 ^{ab}	93.54 ^{bcd}	0.76 ^a

Note: Numbers followed by the same letter in the same column are not significantly different for each character based on the HSD test at the 5% significance level

Shade tolerance levels of sweet corn under shade stress

Figure 1 shows that the sweet corn genotypes differed in their level of tolerance to shade. According to the tolerance level (STI) values used by Fernandez (1982), genotypes G1 to G12 were sensitive, G14 was moderately tolerant, and G13, G15, and G16 were tolerant to 50% shade stress.

Plants under shade stress generally show a reduction in yield, with different genotypes showing different rates of

reduction depending on their adaptability to shade stress. Shading affects the amount of incident solar irradiation, which in turn affects yield, including crop weight and plant biomass (Sekiyama and Nagashima 2019). The environmental conditions of 50% shade stress led to cob weights with husks ranging from 70 g to 250 g, while full light led to weights of 210-460 g (Table 6). G13 showed the highest STI index (1.226 ± 0.327) and G8 the lowest (0.119 ± 0.079).

Table 6. The effect of shade on cob weight with or without the husk of several sweet corn genotypes

Genotype	Cob weight with the husk (g)			Cob weight without the husk (g)		
	Full light	50% shade	Genotype average	Full light	50% shade	Genotype average
G1	320 ^{c-h}	150 ^{k-o}	230 ^{CD}	180 ^{cde}	100 ^{f-j} (44%)	140 ^{BCD}
G2	280 ^{e-j}	130 ^{mno}	200 ^{CDEF}	180 ^{cde}	90 ^{hij} (50%)	140 ^{BCD}
G3	360 ^{a-e}	140 ^{mno}	250 ^{BC}	210 ^{bcd}	100 ^{f-j} (52%)	150 ^B
G4	260 ^{e-j}	100 ^{no}	180 ^{DEF}	160 ^{c-f}	60 ^{ij} (62%)	110 ^{CDE}
G5	290 ^{d-i}	110 ^{mno}	200 ^{CDEF}	180 ^{cde}	70 ^{ij} (61%)	120 ^{BCDE}
G6	210 ^{g-m}	110 ^{mno}	160 ^{EF}	140 ^{d-h}	70 ^{ij} (50%)	110 ^{DE}
G7	260 ^{e-k}	100 ^{no}	180 ^{DEF}	150 ^{e-h}	60 ^{ij} (60%)	110 ^{DE}
G8	210 ^{h-m}	70 ^o	140 ^F	130 ^{e-i}	40 ^j (69%)	90 ^E
G9	300 ^{d-i}	120 ^{mno}	210 ^{CDE}	190 ^{b-e}	90 ^{hij} (53%)	140 ^{BCD}
G10	280 ^{d-j}	120 ^{mno}	200 ^{CDEF}	180 ^{cde}	90 ^{hij} (50%)	140 ^{BCD}
G11	330 ^{b-f}	120 ^{mno}	230 ^{CD}	220 ^{bc}	90 ^{hij} (59%)	150 ^B
G12	320 ^{b-g}	140 ^o	230 ^{CD}	200 ^{b-e}	100 ^{f-j} (50%)	150 ^{BC}
G13	460 ^a	210 ^{g-m}	330 ^A	320 ^a	160 ^{c-g} (50%)	240 ^A
G14	430 ^{ab}	170 ^{j-o}	300 ^{AB}	290 ^a	130 ^{e-i} (55%)	210 ^A
G15	390 ^{a-d}	250 ^{f-l}	320 ^A	250 ^{ab}	170 ^{cde} (32%)	210 ^A
G16	420 ^{abc}	200 ⁱ⁻ⁿ	310 ^{AB}	300 ^a	150 ^{c-h} (50%)	230 ^A
Shade average	320 ^A	140 ^B		210 ^A	100 ^B (52%)	

Note: Numbers followed by the same upper-case letter in the same row or the same column are not significantly different and numbers followed by the same lower-case letter in the same column and row for each character are not significantly different based on the HSD test at the 5% significance level. Numbers within parentheses are percentages relative to the control (full light)

Table 7. Effects of shade on cob length, cob diameter, and TSS of several sweet corn genotypes

Genotype	Cob length (cm)			Cob diameter (cm)			TSS (°Brix)		
	Full light	50% shade	Genotype average	Full light	50% shade	Genotype average	Full light	50% shade	Genotype average
G1	20.73 ^{abc}	15.64 ^{c-i}	18.18 ^{AB}	3.76	3.32	3.54 ^{DE}	12.33 ^{a-d}	13.07 ^{abc}	12.70 ^{AB}
G2	20.10 ^{abc}	13.13 ^{ghi}	16.62 ^{BC}	4.00	3.82	3.91 ^{CDE}	9.33 ^d	13.40 ^{abc}	11.37 ^B
G3	21.07 ^{ab}	14.51 ^{d-i}	17.79 ^{ABC}	4.06	3.45	3.76 ^{CDE}	10.97 ^{bcd}	11.47 ^{bcd}	11.22 ^B
G4	19.37 ^{a-f}	12.11 ^{hi}	15.74 ^{BC}	3.79	3.07	3.43 ^E	14.27 ^{ab}	12.07 ^{a-d}	13.17 ^{AB}
G5	19.65 ^{a-d}	13.94 ^{ghi}	16.80 ^{BC}	4.00	3.12	3.56 ^{DE}	12.73 ^{abc}	11.73 ^{bcd}	12.23 ^{AB}
G6	20.92 ^{ab}	13.95 ^{ghi}	17.44 ^{ABC}	3.98	3.07	3.53 ^{DE}	11.77 ^{a-d}	12.67 ^{a-d}	12.22 ^{AB}
G7	19.50 ^{a-e}	12.44 ^{hi}	15.97 ^{BC}	3.75	3.18	3.46 ^E	11.27 ^{bcd}	11.40 ^{bcd}	11.33 ^B
G8	18.23 ^{a-g}	10.64 ⁱ	14.43 ^C	2.75	2.19	2.47 ^F	10.83 ^{cd}	11.80 ^{a-d}	11.32 ^B
G9	19.97 ^{abc}	14.15 ^{f-i}	17.06 ^{BC}	4.08	3.84	3.96 ^{BCDE}	12.10 ^{a-d}	11.77 ^{a-d}	11.93 ^{AB}
G10	21.53 ^{ab}	14.66 ^{d-i}	18.10 ^{AB}	3.78	3.62	3.70 ^{DE}	10.93 ^{bcd}	12.60 ^{a-d}	11.77 ^{AB}
G11	21.53 ^{ab}	13.82 ^{ghi}	17.68 ^{ABC}	4.18	3.36	3.77 ^{CDE}	12.73 ^{abc}	13.00 ^{abc}	12.87 ^{AB}
G12	19.97 ^{abc}	14.27 ^{e-i}	17.12 ^{BC}	4.05	3.66	3.85 ^{CDE}	11.40 ^{bcd}	11.17 ^{bcd}	11.28 ^B
G13	22.03 ^a	16.37 ^{b-h}	19.20 ^{AB}	5.01	4.3	4.66 ^{AB}	11.00 ^{bcd}	11.93 ^{a-d}	11.47 ^B
G14	22.23 ^a	14.57 ^{d-i}	18.40 ^{AB}	4.45	3.99	4.22 ^{ABCD}	11.40 ^{bcd}	11.90 ^{a-d}	11.65 ^{AB}
G15	19.47 ^{a-e}	18.13 ^{a-g}	20.80 ^A	4.72	4.18	4.45 ^{ABC}	15.13 ^a	12.30 ^{a-d}	13.72 ^A
G16	20.90 ^{abc}	16.67 ^{b-h}	18.79 ^{AB}	5.09	4.62	4.86 ^A	10.80 ^{cd}	11.70 ^{bcd}	11.25 ^B
Shade average	20.45 ^A	14.81 ^B		4.09 ^A	3.55 ^B		11.81	12.12	

Note: Numbers followed by the same upper-case letter in the same row or the same column are not significantly different and numbers followed by the same lower-case letter in the same column and row for each character are not significantly different based on the HSD test at the 5% significance level

Under full light conditions, the highest average cob weight without the husk was obtained by G13 with 320 g, but it decreased significantly by 50% to 160 g under 50% shade (Table 6). G15 showed the lowest reduction in weight of 32%, from 250 g under full light to 170 g under 50% shade. This shows that although G13 was highly productive, it was sensitive to shade, while G15 was less productive but relatively more shade tolerant. The selection of stress-tolerant sweet corn genotypes based on STI may allow for the screening of tolerant genotypes with high yield potential (Moradi et al. 2012). The tolerance level determined with the Fernandez (1982) equation is based on weight rather than weight reduction, which may explain why G13 had a higher STI index than G15. A high STI value also indicates the genotype's level of shade tolerance.

Figure 2 shows the phenotypic differences of sweet corn genotypes under 50% shade and full light conditions. The genotypes were grouped into three categories: sensitive (A2), moderately tolerant (B2), and tolerant (C2). The G2 genotype in the sensitive group showed a relatively higher reduction in cob size due to shade stress compared to the other two genotypes in the moderately tolerant and tolerant groups (Figure A2). The G14 genotype, which was moderately tolerant, had larger and heavier cobs than the sensitive genotype, but these cobs were smaller and less heavy than the cobs of the tolerant genotype (Figure B2). G13 was the shade-tolerant genotype and had the largest, fullest, and heaviest cobs compared to the sensitive and moderately tolerant genotypes (Figure C2). The results of this study confirmed that 50% shading of sweet corn plants did not increase relative production.

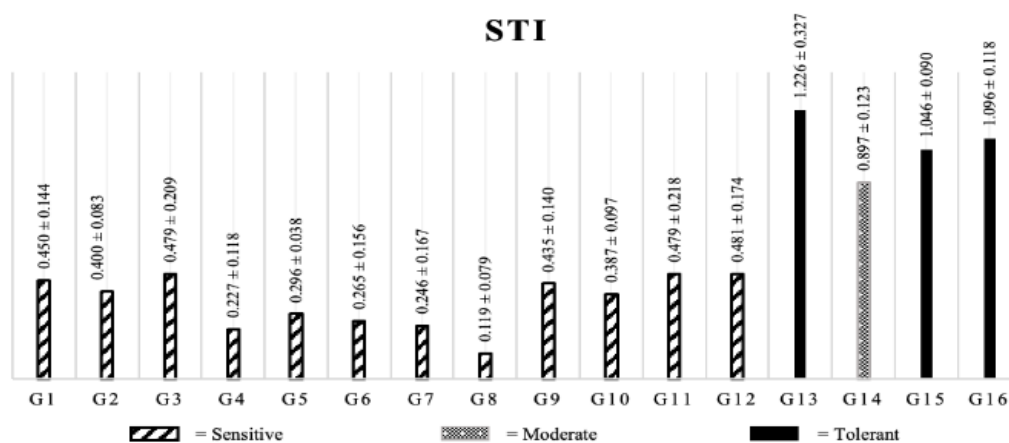


Figure 1. The shade tolerance of various sweet corn genotypes

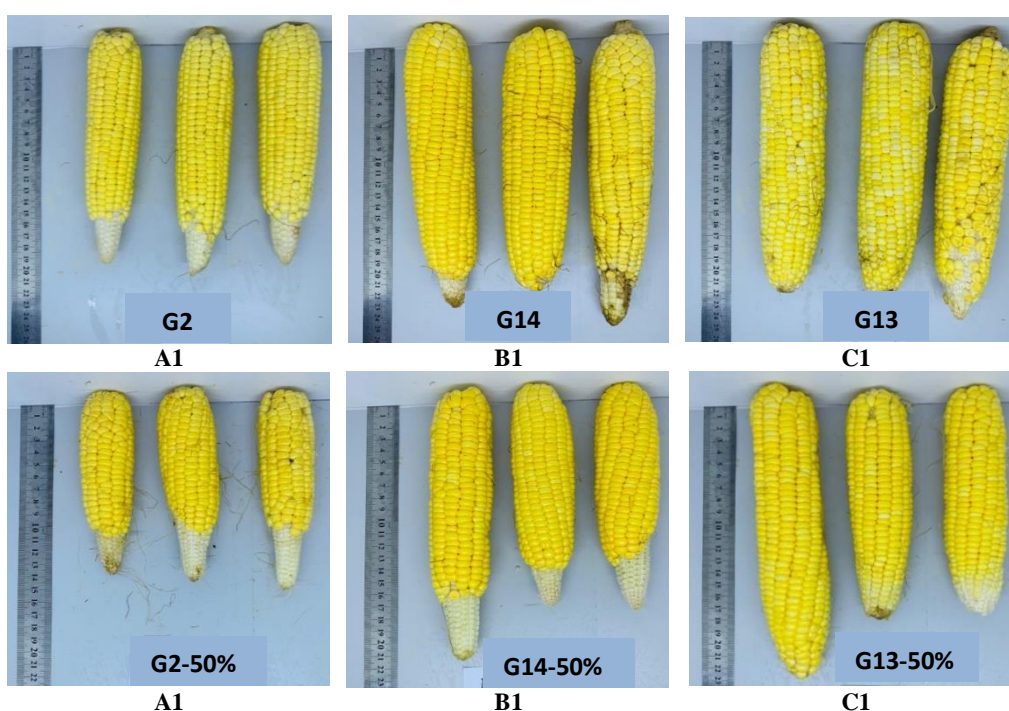


Figure 2. Cobs of (A1) a sensitive sweet corn genotype under high light; (A2) a sensitive genotype under 50% shade; (B1) a moderately tolerant genotype under high light; (B2) a moderately tolerant genotype under 50% shade; (C1) a tolerant genotype under high light; and (C2) a tolerant genotype under 50% shade

In conclusion, the sixteen genotypes of sweet corn tested showed variation in growth, production, and responses to low light intensity or shade. The stress tolerance index value is influenced by the cob weight of sweet corn. All commercial varieties, G13 (Exotic), G14 (Talenta), G15 (Paragon), and G16 (Golden Boy), showed relatively high STI values. Of the genotypes resulting from crosses, the highest STI values were found for G11 (SM7-8 × SM12-2) and G12 (SM11-6 × SM12-2). The results of this study recommend that commercial varieties can be cultivated under tree stands or low light intensity and can be used to develop high-yielding shade tolerant sweet corn varieties.

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