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Effect of gibberellic acid on photosynthesis and oxidative stress response in maize under weak light conditions

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Gibberellin (GA) is an important endogenous hormone involved in plant responses to abiotic stresses. Experiments were conducted at the Research and Education Center of Agronomy, Shenyang Agricultural University (Shenyang, China) in 2021.We used a pair of near-isogenic inbred maize lines comprising, SN98A (light-sensitive inbred line) and SN98B (light-insensitive inbred line) to study the effects of exogenous gibberellin A3 (GA_3) application on different light-sensitive inbred lines under weak light conditions. The concentration of GA_3 was selected as 20, 40 and 60 mg L^{-1}. After shade treatment, the photosynthetic physiological indexes of SN98A were always lower than SN98B, and the net photosynthetic rate of SN98A was 10.12% lower than SN98B on the 20th day after shade treatment. GA_3 treatments significantly reduced the barren stalk ratios in SN98A and improved its seed setting rates by increasing the net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs), photosynthetic pigment contents, photochemical efficiency of photosystem II (PS II) (Fv/Fm), photochemical quenching coefficient (qP), effective quantum yield of PSII photochemistry (Φ_{PSII}), and antioxidant enzyme activities, where the most effective treatment was 60 mg $L^{-1}GA_3$. Compared with CK group, the seed setting rate increased by 33.87%. GA_3 treatment also regulated the metabolism of reactive oxygen species (ROS) and reduced the superoxide anion (O_2^-) production rate, H_2O_2 content, and malondialdehyde content. The superoxide anion (O_2^-) production rate, H_2O_2 content and malondialdehyde content of SN98A sprayed with 60 mg L^{-1} GA_3 decreased by 17.32%,10.44% and 50.33% compared with CK group, respectively. Compared with the control, GA_3 treatment significantly ($P < 0.05$) increased the expression levels of *APX* and *GR* in SN98A, and *APX*, *Fe-SOD*, and *GR* in SN98B. Weak light stress decreased the expression of *GA20ox2*, which was related to gibberellin synthesis, and the endogenous gibberellin synthesis of SN98A. Weak light stress accelerated leaf senescence, and exogenous GA_3 application inhibited the ROS levels in the leaves and maintained normal physiological functions in the leaves. These results indicate that exogenous GA_3 enhances the adaptability of plants to low light stress by regulating photosynthesis, ROS metabolism and protection mechanisms, as well as the expression of key genes, which may be an economical and environmentally friendly method to solve the low light stress problem in maize production.

KEYWORDS

maize, low light stress, GA3, barren stalk, photosynthesis

Introduction

Under suitable cultivation conditions, the productivity of different crops is strongly related to the amount of light radiation intercepted in the crop canopy (Slattery and Ort, 2021), where excessive or insufficient amounts of light energy will have adverse effects on photosynthesis by crops (Ferrante and Mariani, 2018). Maize (*Zea mays* L.) is a light-loving and light-sensitive crop (Wang et al., 2016; Xue et al., 2019), but due to frequent extreme weather events in recent years, maize plants have experienced continuous low-temperature and rainy weather in the booting stage. These conditions can severely affect ear development and grain formation in maize, thereby resulting in large areas which high proportions of hollow straw and severe bald tip in some varieties (Huang et al., 2022), which are extremely unfavorable for agricultural production. Light is necessary for photosynthesis and it is the basis of plant life. Insufficient light will lead to decreases in the net photosynthetic rate (Pn) and partial chlorophyll fluorescence parameters in leaves (Qu et al., 2017; Wegrzyn and Mazur, 2020; Feng et al., 2021; Zahra et al., 2022). During this process, plant leaf cells undergo complex changes in physiological processes and cell metabolism, such as chloroplast decomposition, loss of photosynthetic activity, decomposition of chlorophyll and macromolecular compounds, and programmed cell death (Asad et al., 2019). These changes are associated with increases in intracellular reactive oxygen species (ROS) (Ramel et al., 2009). Insufficient light will accelerate leaf senescence and result in the excessive accumulation of ROS, oxidative damage to proteins, nucleic acids, and membrane lipids (Jbir-Koubaa et al., 2015), and decreases or losses of the activities of various enzymes (Mittler, 2002; Gill and Tuteja, 2010). As a consequence, the integrity of the cell membrane can be disrupted (Benlloch-Gonzalez et al., 2015), and the normal functions of chloroplast and mesophyll cells are eventually damaged, with decreased photosynthetic electron transport efficiency (Feng et al., 2021). Plants have a complete protective system of antioxidant enzymes that remove excessive ROS to protect the photosynthetic system and enhance adaptation to stress (Li et al., 2020).These enzymes include superoxide dismutase (SOD), and peroxidase (POD) (Dvorak et al., 2021). Thus, the antioxidant enzyme activity is an important indicator for evaluating whether the redox balance of plant cells is disrupted under adverse conditions (Gill et al., 2013).

The changes in the dependence of plant growth and development on light are regulated by plant hormones (Zhong et al., 2012). The changes in levels of plant hormones under shading are active responses by plants to adverse environments, and they provide the physiological basis that allows plants to make better use of assimilation products (Jiang et al., 2021). Gibberellin (GA) is necessary for the shade avoidance response in plants (Djakovic-Petrovic et al., 2007). In a previous study, we measured the changes in the contents of various hormones in two different light-sensitive inbred lines under shade treatment and in a control group without shade. According to the activities of the hormones, we found that the change in the gibberellin A_3 (GA_3) content was the most important. GA_3 is a type of tetracyclic diterpene plant hormone that can regulate many plant growth and development processes (e.g., seed germination, stem elongation, pollen maturation and fruit development), and one of its important functions is regulating the

flowering time (Vicente and Plasencia, 2011). Previous studies of *Arabidopsis* showed that endogenous GA was necessary for flowering under non-induced conditions, and the flowering time was generally delayed in a GA synthesis defect mutant and GA signal transduction mutant (Rood et al., 1989; Ni and Bradford, 1993; Magome et al., 2004). Exogenous GA application can also promote flowering in *Arabidopsis thaliana* (Ezura and Harberd, 1995; Sauret-Gueto et al., 2012; Bao et al., 2020). It should also be noted GA is an excellent antioxidant that can enhance the tolerance of various biological and abiotic stresses by plants (Yamaguchi et al., 2014; Khan et al., 2015). GA_3 can also increase the number of cell divisions by activating the intermediate meristems to promote cell division (Mcatee et al., 2013). Guo et al. (2022) showed that spraying GA_3 could improve photosynthesis and the antioxidant defenses to increase the yield in salted wood pea. The exogenous application of GA_3 can delay the degradation of chlorophyll and protein, reduce the malondialdehyde (MDA) content, and delay plant senescence (Yu et al., 2009; Wang et al., 2015). Under low light stress, the abscisic acid (ABA) and zeatin (ZT) contents of soybean leaves decreased, whereas the indole acetic acid (IAA) and gibberellin (GA_3) contents increased. Similar results were obtained in previous studies of maize leaves under low light conditions, thereby suggesting that the response of this hormone to low light is an active stress response that allows plants to adapt to low light environments. Therefore, it is of great theoretical and practical significance to study the regulatory effects of exogenous GA_3 on different light-sensitive inbred maize lines under low light condition.

During the breeding of inbred maize lines over numerous years, we found and bred two inbred maize lines called SN98A and SN98B with extreme differences in their culms. In particular, the distinction, SN98A is called the "ear differentiation and sensitive to low light intensity inbred line"(ESL) and SN98B is called the "ear differentiation and insensitive to low light intensity near isogenic line" (EISL-NIL). Under low light stress condition, the hollowing rate in SN98A was 98% and that in SN98B was 0. Thus, in the present study, we used these weak light sensitive near-isogenic lines as experimental materials. By applying GA_3 to leaves, the regulation effect of exogenous GA_3 on empty stalk of maize under low light condition was analyzed. Through the analysis of photosynthetic response, antioxidant enzyme activity and other indexes, the purpose was to find out which physiological indexes of maize were affected by low light stress to induce maize stalk emptying. The regulatory effect of exogenous GA_3 on maize hollows under low light conditions and its regulatory mechanism were discussed, so as to provide solutions for poor maize yield under bad weather conditions.

Materials and methods

Plant materials and experimental design

The maize varieties used in this study were SN98A and SN98B, which are inbred maize lines with extreme differences in the frequency of hollow culms. Under certain low light conditions, the hollow culm rate in SN98A is as high as 98%, whereas SN98B exhibits a normal ear setting. A field experiment was conducted at the South Experimental Base of Shenyang Agricultural University (41°48′N, 123°34′E) in July 2021. The normal light intensity from late July to

early August in the Northern Test Field at Shenyang Agricultural University was usually between 1100–1500 µmol m^{-2} s^{-1}, with an average light intensity of about 1300 µmol m^{-2} s^{-1}. Soil characteristics for temperate subhumid continental climate, the climate belongs to the temperate monsoon climate. A split block design was applied in the experiment. The concentration of GA$_3$ was the main influence factor and the inbred line was the secondary influence factor. The length of the plot was 5 m, the row spacing was 0.6 m, and each plot had 15 rows. In the first three days of the tasseling period, 38% shading was applied with a black shade net, and different concentrations of GA$_3$ were applied by spraying (Beijing Merida Technology Co., Ltd, China), 20mg L^{-1}, 40mg L^{-1}, and 60mg L^{-1} or water as the control. Samples were taken at five, 10, 15, and 20 days after shading, which were frozen in liquid nitrogen and then stored at -80°C. Each treatment was repeated three times.

Phenotypic evaluations

The number of plants, number of bearing plants (with more than 20 grains), and the number of plants with empty stems under each treatment determined during the harvest period. The seed setting rate (%) and empty stalk rate (%) were calculated. Seed setting rate (%) = number of seeds/total number of plants *100%. Empty stalk rate (%) = number of empty culms/total number of plants *100%.

Gas-exchange parameters

Net photosynthetic rate, stomatal conductance, transpiration rate and intercellular carbon dioxide concentration of panicle leaves under different treatments were measured by Li-6400 (US-COR) portable photosynthesometer at 5, 10, 15 and 20 days after shading (Zhou et al., 2022). The measuring time was 9:00-11:00 a.m. The measured environment was 400mol (CO$_2$) mol^{-1} and 50% relative humidity. Ten replicates per process.

Photosynthetic pigment contents

To determine the photosynthetic pigment contents (chlorophyll a (Chl a) and chlorophyll b (Chl b)), 0.1g of fresh leaves were crushed, soaked in 10 mL of acetone, and kept in the dark for 48 h. Chl was extracted and analyzed according to the methods reported by Lichtenthaler and Wellburn (1983). The absorbance values were then recorded at 645 and 663 nm by using a spectrophotometer (Multiskan GO, Thermo Fisher Science, USA), with acetone as a blank control. The following formulae were used to calculate the photosynthetic pigment contents:

Chl a [mg g^{-1} (FM)] = (12.7 × OD663–2.69 × OD645) ×V/ M (1000×M)

Chl b [mg g^{-1} (FM)] = (22.9 × OD645–4.68 × OD663) × V/ M (1000×M)

Chl (a+b) [mg g^{-1}(FM)] = Chl a + Chl b

where OD645 and OD663 represent the absorbance values for Chl a/b at the corresponding wavelengths, V represents the total volume of the extract, and M represents the mass of the sample. Each treatment was repeated three times.

Determination of chlorophyll fluorescence parameters

The panicle leaves were removed 20cm from the tip, placed in wet gauze, and stored for 30 min under certain humidity in the dark and away from light. The FluorCam (Czech PSI) chlorophyll fluorescence imaging system was used to determine the photochemical efficiency of photosystem II (PS II) (Fv/Fm). Chlorophyll fluorescence parameters were determined comprising the photochemical quenching coefficient (qP) and non-photochemical quenching coefficient (NPQ) and images were collected. Each treatment was repeated three times.

Determination of H$_2$O$_2$ content and antioxidant enzyme activities

POD (extinction coefficient = 25.2 mm^{-1} cm^{-1}) was determined at 470 nm in a 1.0 mL reaction mixture containing 100 mM potassium phosphate buffer (pH 6.0), 16 mM guaiacol, 5 µL 10% (v/v) H$_2$O$_2$, and enzyme extract. The SOD activity was measured based on its capacity to inhibit blue light in the chemical reduction of nitrotetrazolium, which was monitored at 560 nm (Abedi and Pakniyat, 2010). Three biological replicates were tested for each sample.

Determination of MDA and superoxide radical contents

The MDA content was determined by using the thiobarbituric acid method to evaluate the level of lipid peroxidation. Leaf tissue (0.5 g) was homogenized in 5.0 mL of 10% trichloroacetic acid and centrifuged at 4°C and 10,000×g for 10 min. The supernatant was assessed as described by Hodges et al. (1999). According to the method of Xia et al. (2009), with some modifications. The panicle leaves were sampled, cleaned with distilled water, and sucked dry. They were then placed in 50 mL 0.5 mg mL−1 NBT reaction solution (potassium phosphate buffer, pH 7.8) and incubated in darkness at 25°C for 2 h to detect O$_2^-$. Three biological replicates were tested for each sample.

Real-time fluorescence quantitative PCR detection of expressed of target genes

The *ZmActin* gene in maize was used as the internal reference gene and SYBR Green Real-time PCR Master Mix was used as the fluorescent dye. The samples were tested after shading for 15 days. The template comprised cDNA diluted 20 times and it was repeated three times. The total reaction system volume was 20 µL and the reaction conditions comprised: 95°CC for 30 s, and 45 cycles at 60°CC for 30 s and 72°CC for 30s (Xu et al., 2023). After PCR, the dissolution curve was analyzed. The primers used are shown in Tables 1, 2.

TABLE 1 Primers used real-time fluorescence quantitative PCR.

Primer name	Primer (5′-3′)
ZmActin	F:GTTAAAGATTGCGCCACCT.R:GCCTGACGTACCATGTCGAAC
APX	F:CGCGCATTTCCAGATCTTTG.R:GATCGATGCGAGATCAGGGG
Fe-SOD	F:CGACTGTCCCTTCTCACAAA.R:ATCCGGTAAGGGACCTTCTT
GR	F:TTGGCAATGAACCTACCAAA.R:CAATTGCCTGCTCCTCAGTA

TABLE 2 Primers used real-time fluorescence quantitative PCR.

Primer name	Primer(5′-3′)
DELLA1	F:GCAAATCAAGCCATCCTC. R:AGCAAACGGCACTCTAACT
DELLA2	F:CAGGCGGTCCTCCTTCATTCC.R:GCTATCGCTTCTGGTTCCTCGTCGG
DELLA3	F:CAGCAACAGCAAGCCACA.R:CCACTTCTTCCACGCAATAC
GID1C1	F:CCCAATGGGAATGATCTCAA.R:ACAATTAGAACTCACAAAACCCTT
GID1C2	F:TCAACCCCACCCGAATCC.R:AGGTCGCCGTTGCATGTT
GID1C3	F:CAATTCACCCAATTCTAACC.R:AAATGCCTTCCAATACCAA
GA20ox2	F:CCCTCACCATTCTCCAACA.R:CCCGGACCACCTTATCTTC
KAO1	F:TTTGAAGGCAAGAAAGACG.R:TGTGATATGACCCGAAGAT
KAO2	F:ATGATTGACTTCTTGTGGTGCTT.R:TTAGACATCGCCGTAACCCCTT

Statistical analysis

DPS (version 9.01) was used for multiple comparative analysis between treatments, the confidence level was 0.05, and one-way ANOVA was used. Data are expressed as mean standard deviation. Chart using Origin 2021 software.

Results

Seed setting rate and hollow stalk rate

Figure 1A shows that after spraying GA$_3$, the seed setting rate increased in the two inbred lines and the hollow stalk rate decreased. The seed setting rates were highest in the 60 mg L^{-1} GA$_3$ treatment groups, where those in SN98A and SN98B were 23.56% and 14.68% higher than that in the control group sprayed with water, respectively (Fig 1A).Treatment with GA$_3$ at 60 mg L^{-1} obtained the lowest hollowing rates, where the rates were 14.25% and 12.34% lower in SN98A and SN98B than the controls, respectively (Figure 1B).

Photosynthetic parameters

Figure 2 shows that in the control group under low light weak light conditions, Pn continued to decrease in SN98A, whereas Pn in SN98B tended to decrease initially before then increasing. Among the two inbred lines, Pn was always higher in SN98B than SN98A. After GA$_3$ treatment, Pn and the transpiration rate (Tr) were significantly higher in SN98A compared with the control. After shading for 20 days, the mean Pn and Tr values in the three treatment groups were

10.88% and 68.43% higher than those in the control, respectively. Thus, GA$_3$ treatment had a positive regulatory effect on Pn in the low light-sensitive inbred line SN98A. Treatment with 40 mg L^{-1} GA$_3$ had the greatest effect but the difference between the treatments was not significant (Figure 2). After GA$_3$ treatment, the stomatal conductance (Gs) was generally higher in the two inbred lines than the control, and the external application of 60 mg L^{-1} GA$_3$ had the greatest effect. The intercellular CO$_2$ concentrations in the two inbred lines were also lowest at this concentration. Thus, the external application of GA$_3$ under low light conditions increased Gs for the maize leaves and enhanced the photosynthetic activity of the mesophyll cells according to the Pn results. Pn increased under low light conditions in SN98A.

Chlorophyll fluorescence parameters

After shading treatment, Fv/Fm, the effective quantum yield of PSII photochemistry (Φ_{PSII}), and qP were significantly lower in the SN98A control group than SN98B, whereas the NPQ values were significantly higher compared with SN98B. Compared with the control, GA$_3$ significantly improved the PSII photosynthetic characteristics of maize leaves, where treatment with 60 mg L^{-1} GA$_3$ had the greatest effect, and SN98A had the highest Fv/Fm, Φ_{PSII} and qP values. On day 20 under 60 mg L^{-1} GA$_3$ treatment, the Fv/Fm, Φ_{PSII}, and qP values in SN98A were 6.9%, 16.39%, and 14.75% higher, respectively, compared with those in the control, and the NPQ value was 22.89% lower compared with the control (Figure 3). The effect of GA$_3$ treatment on SN98B was not significant, but the photosynthetic activity of PSII was higher than that in SN98A, thereby indicating that GA$_3$ was involved in the shading reaction by maize leaves and it had a positive role in maintaining the photosynthetic efficiency of maize leaves under low light stress.
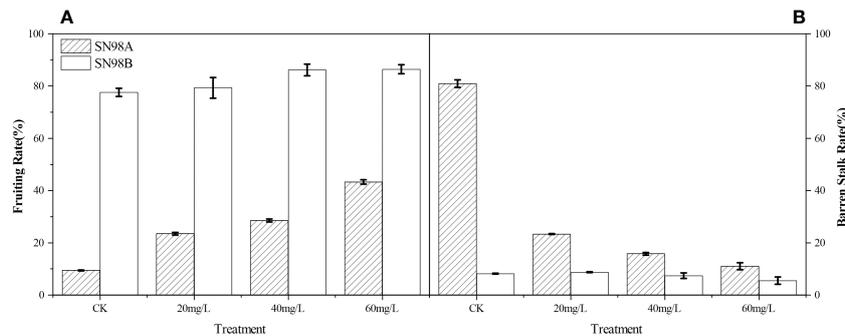
FIGURE 1
Effects of exogenous GA$_3$ on seed setting rate and hollow stalk rate in different light-sensitive inbred maize lines under low light-stress. **(A)** Seed setting rates in different light-sensitive inbred maize lines sprayed with different concentrations of GA$_3$ and water. **(B)** Hollow stalk rates in different light-sensitive inbred maize lines sprayed with different concentrations of GA$_3$ and water. CK is the control water spraying treatment under shade. The numbers 20, 40, and 60 denote GA$_3$ concentrations of 20 mg L^{-1}, 40 mg L^{-1}, and 60 mg L^{-1}, respectively. SN98A is the shade intolerant line and SN98B is the shade tolerant line. Values are expressed as mean $\pm$ SD of three replicates. Lower-case letters indicate the mean difference of different treatments in the same period, which is statistically significant (P<0.05).

Chlorophyll contents

Figure 4 shows that under shading treatment, the Chl a, Chl b and Chl (a+b) contents in the SN98A control group tended to increase initially and then decrease, whereas the Chl content in SN98B did not significantly and it was always higher than that in SN98A. Compared with the control, GA$_3$ had a significant positive regulatory effect on the photosynthetic pigment contents of the low light-sensitive inbred line SN98A, and the Chl a, Chl b and Chl (a+b) contents increased under all three GA$_3$ treatments. The effect of treatment with 60 mg L^{-1} GA$_3$ was most obvious, and the photosynthetic pigment contents increased on days 5, 10, 15, and 20 after treatment, where the Chl (a+b) contents increased by 25.7%, 19.6%, 2.9% and 17.3%, respectively. The photosynthetic pigment content of SN98B was the same as that of the control and it was always higher than that of SN98A, where the content was significantly higher in SN98B on day 10 after treatment with 60 mg L^{-1} GA$_3$.

ROS contents and membrane lipid peroxidation

Under shading, the H$_2$O$_2$ and O$_2^-$ contents increased initially and then decreased in the SN98B control group, whereas the H$_2$O$_2$ and O$_2^-$ contents continued to increase in the hollowing line SN98A and the contents were always higher than those in SN98B (Figure 5). After GA$_3$ treatment, the H$_2$O$_2$ and O$_2^-$ contents of the two inbred lines were lower compared with those in the control group. After shading for 15days, treatment with 60 mg L^{-1}GA$_3$ significantly reduced the O$_2^-$ production rate and H$_2$O$_2$ content of SN98A by 17.3% and 10.4%, respectively. In the control and treatment groups, the H$_2$O$_2$ and O$_2^-$ contents were always higher in SN98A than SN98B, and the ROS contents were always lower in SN98B. The changes in the ROS contents (H$_2$O$_2$ and O$_2^-$) were basically the same. GA$_3$ treatment significantly reduced the MDA contents of the two inbred lines under low light. The MDA contents were higher in SN98A than SN98B in both the control and treatment groups (Figure 6). The effects of short-term shading were similar under the three treatments, but the effect of treatment with 20 mg L^{-1} GA$_3$ decreased as the shading period

continued. In conclusion, the application of GA$_3$ could have reduced the peroxidation of membrane lipids caused by the accumulation of ROS in maize leaves to delay leaf senescence and enhance the tolerance of shading in maize. Treatments with 40 mg L^{-1} and 60 mg L^{-1} GA$_3$ were most effective.

Antioxidant enzyme activities

After shading and treatment with different concentrations of GA$_3$, the SOD and POD activities increased initially and then decreased in the SN98A control group, where the activities were highest after shading for 10 days. The POD activities continued to increase in SN98B and did not peak until 20 days. During short-term shading the antioxidant system was activated to remove ROS and maintain crop growth. Crops can avoid damage caused by short-term adverse conditions by activating their stress response mechanisms, but they cannot prevent damage under long-term adverse conditions. After treatment with GA$_3$ at different concentrations, the antioxidant enzyme activities were significantly higher in SN98A than the control (Figure 7), where treatment with 60 mg L^{-1} GA$_3$ had the most significant effect. After shading for 20 days, the SOD and POD enzyme activities in SN98A were 17% and 31.7% higher compared with the control, respectively, and the difference was significant (Figures 7A, C).

Antioxidant-related genes

Real-time fluorescence quantitative PCR analysis was performed to quantify the expression levels of three genes related to antioxidant stress, and the results are shown in Figure 8. Compared with the control, after GA$_3$ treatment, the expression levels of *APX* (Figure 8A) and *GR* (Figure 8C) were significantly higher in SN98A under treatment with different GA$_3$ concentrations, where the expression levels were highest under treatment with 60 mg L^{-1} GA$_3$, i.e., 6.73 and 2.75 times than those in the control, respectively. The expression levels of *APX* and *GR* under treatment with 40 mg L^{-1} GA$_3$ were 5.41 times and 1.93 times those in the control, respectively. The expression of *Fe-SOD* (Figure 8B) did not increase significantly in SN98A, where
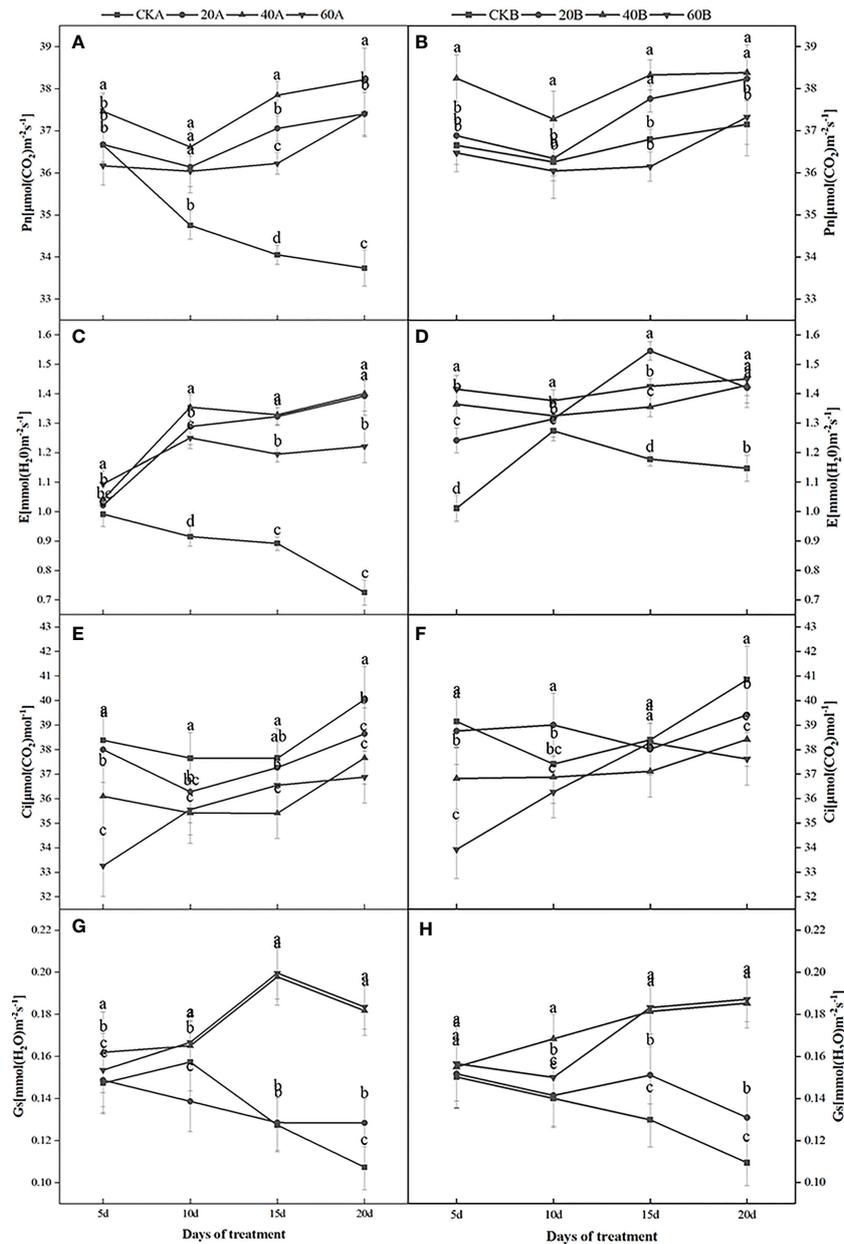
FIGURE 2
Effects of GA_3 on net photosynthetic rate (Pn), transpiration rate (Tr), intercellular CO_2 concentration, and stomatal conductance (Gs) in different light-sensitive inbred maize lines under low light stress. **(A, B)** show the Pn values; **(C, D)** show the Tr values; **(E, F)** show the intercellular carbon dioxide concentrations; and **(G, H)** show the Gs values. In the figure panels, 20A, 40A, and 60A denote SN98A sprayed with 20 mg L^{-1}, 40 mg L^{-1}, and 60 mg L^{-1} GA_3, respectively, and 20B, 40B, and 60B denote SN98B sprayed with 20 mg L^{-1}, 40 mg L^{-1}, and 60 mg L^{-1} GA_3. CKA denotes the SN98A control group sprayed with water and CKB denotes the SN98B control group sprayed with water. Values are expressed as mean $\pm$ SD of three replicates. Lower-case letters indicate the mean difference of different treatments in the same period, which is statistically significant (P<0.05).

the expression level was highest under treatment with 40 mg L^{-1} GA_3 i.e., 1.62 times that in the control. All three genes responded positively to exogenous GA_3 in SN98B, whereas only *APX* and *GR* responded positively in SN98A.

GA-related gene

In this experiment, the relative expressions of gibberellin receptors *GID1C1*, *GID1C2* and *GID1C3* decreased after exogenous GA_3 treatment, and the relative expressions of $GA20ox$, *KAO1* and

KAO2 genes related to gibberellin synthesis and degradation decreased in plants (Figure 9). The expression levels of signal transduction related genes *DELLA1*, *DELLA2* and *DELLA3* were not significantly changed. These results indicated that exogenous GA_3 could inhibit the synthesis of endogenous gibberellin in maize.

Discussion

Northeast China is the most important maize-producing area in China, where the maize output in this region account for more than
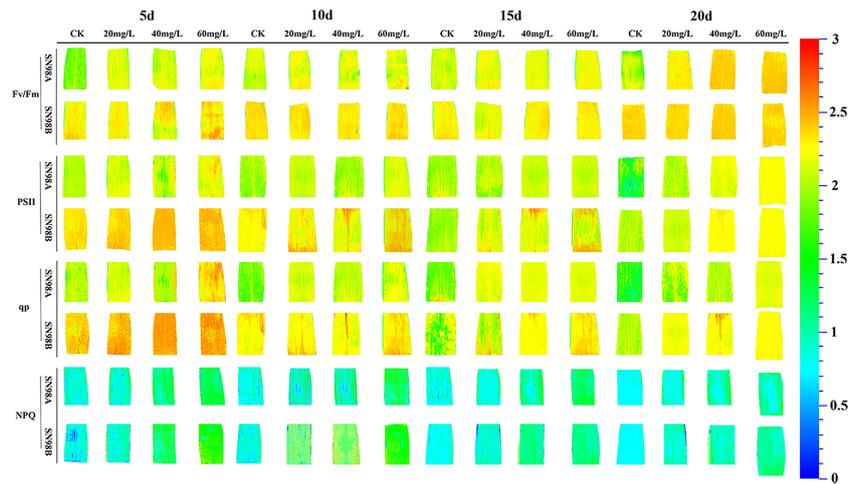
FIGURE 3
Effects of GA$_3$ application on chlorophyll fluorescence according to *in situ* imaging of inbred maize lines with differences in light sensitivity under low light stress conditions. In the figure panels, 5d, 10d, 15d, and 20d denote the number of days under shading treatment; 20, 40, and 60mg L^{-1} denote the GA$_3$ concentrations applied; and CK denotes the water control treatment.

30% of the national maize output. In this region, light, heat, and water resources are generally abundant in the growing period. However due to global climate change, extreme weather events have become more frequent during the maize growing season, The frequency of overcast weather with high rain and low radiation during the withering and silking stage has recently increased each year (Yang et al., 2020), thereby adversely affecting the stability of the maize yield in Northeast China. Light is essential for photosynthesis by plants and the basis for plant growth and development (Jiang et al., 2021). Maize is a light-loving crop with no obvious light saturation point and it is very sensitive to changes in the light intensity. A lack of light during tasseling will inhibit the normal physiological activities, decrease photosynthesis in the leaves, and cause cell metabolism disorders and REDOX homeostasis damage, thereby leading to problems such as ear bald tip, yield reductions, and even hollow stalks. Low light stress can accelerate the excessive accumulation of ROS in maize leaves and cause the peroxidation of membrane lipids. Colebrook et al. (2014) indicated that hormones can effectively help plants to cope with abiotic stress, where stress responses are regulated mainly by activating specific hormones *via* signal transduction and crosstalk in different developmental environments (Verma et al., 2016). Therefore, how to increase the yield and reduce the empty stalk rate under the condition of insufficient light has become an important problem.

GA$_3$ is a plant growth regulator and it is involved in the response to many abiotic stresses in plants, with positive regulatory effects on plant growth and development (Bao et al., 2020). Exogenous GA$_3$ application can reduce the effects of nickel stress (Wiszniewska et al., 2018) and increase the plant cell length independent of biosynthesis (Rizza et al., 2017). In addition, GA and photoperiod pathways have been shown to synergistically regulate crop flowering under long sunshine conditions (Fukuda et al., 2012; Wang et al., 2016). In the present study, GA$_3$ treatment reduced the hollow stem rate in maize by regulating the flowering interval between male and female ears, where treatment with 60 mg L^{-1} GA$_3$ had the greatest effect, followed by treatment with 40 mg L^{-1} GA$_3$ and 20 mg L^{-1}GA$_3$. Under shading treatment, the H$_2$O$_2$ and O$_2^-$ contents continued to increase in the

SN98A control group, and the contents were always higher than those in SN98B. After GA$_3$ spraying treatment, the O$_2^-$ production rate and H$_2$O$_2$ contents still increased in SN98A and SN98B, but the increases were significantly smaller than those in the control group, and the O$_2^-$ production rate and H$_2$O$_2$ contents were always lower in SN98B than SN98A due to the photoprotective capacity of the shade-tolerant inbred line SN98B. Low light stress can induce oxidative stress in maize, but GA$_3$ treatment can enhance the ability of maize to resist low light stress and reduce the oxidative pressure caused by insufficient light. Numerous studies have shown that membrane lipid peroxidation leads to the accumulation of MDA. Low light stress can disrupt the dynamic equilibrium between ROS production and scavenging in plants, thereby resulting in the accumulation of ROS and increased membrane permeability. As a consequence, membrane lipid peroxidation lead to the accumulation of MDA and exacerbates maize aging (Wang et al., 2021). In this study, GA$_3$ treatment significantly reduced the MDA contents of the two inbred lines under low light. The MDA contents were higher in SN98A than SN98B in both the control and treatment groups. The antioxidant enzyme system in plants protects against the toxic effects of ROS. SOD and POD are important antioxidant enzymes in the plant defense mechanism. GA$_3$ may have reduced the ROS contents in maize by enhancing the activities of POD and SOD in the light-sensitive inbred line SN98A, as also suggested by Ali et al. (2021). *APX*, *Fe-SOD* and *GR* are important genes related to the activities of antioxidant enzymes (Lee et al., 2007). Studies have shown that the overexpression of *APX*, *Fe-SOD*, and *GR* significantly improved the tolerance of abiotic stresses by transgenic tall fescue plants. In the present study, we found that exogenous GA$_3$ treatment significantly upregulated the expression levels of *APX* and *GR* in SN98A and SN98B compared with the control group, thereby indicating that exogenous GA$_3$ could enhance the activities of antioxidant enzymes to resist external abiotic stress by increasing the expression of antioxidant-related genes. Therefore, exogenous GA$_3$ may improve the tolerance of stress in plants by regulating antioxidant metabolism and reducing the lipid peroxidation of cell membranes (Gilroy and
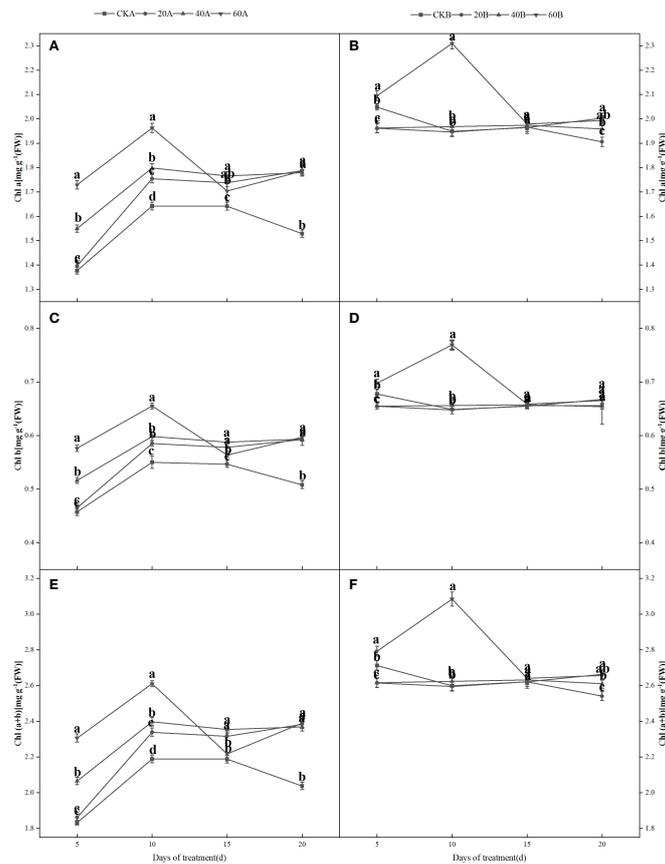
FIGURE 4

Effects of GA₃ application on the Chl a **(A, B)**, Chl b **(C, D)**, and Chl a+b **(E, F)** contents of different light-sensitive inbred maize lines under low light stress. Values are expressed as mean ± SD of three replicates. Lower-case letters indicate the mean difference of different treatments in the same period, which is statistically significant (P<0.05).

Jones, 1992; Jiang and Huang, 2001) to decrease the damage due to low light stress in plants. According to the expression level of GA-related genes, the gene pathway of gibberellin signaling is GA-GID1-DELLA signaling pathway. When gibberellin is at a high level, GID1 can sense the GA signal and combine with it to form GA-GID1. Then it binds to DELLA protein to form GID1-GA-DELLA complex trimer (Zentella et al., 2007), so that ubiquitin ligase SCF in F-Box protein can bind to DELLA protein GRAS region (Fleet and Sun, 2005). The rapid degradation of DELLA protein through ubiquitin proteomic channels resulted in the release of its repression and normal gibberellin response in plants. Therefore, the reduction of gibberellin receptor GID1 may also affect the degradation of DELLA protein at the protein level. After exogenous GA₃ was applied, the expression of *GA20ox2*, a gene related to gibberellin synthesis, decreased (FIG 9G). *GA20ox2* plays an important role in the synthesis of gibberellin in higher plants, and the decreased expression of *GA20ox* gene may decrease the production of endogenous gibberellin. In CK group, the expression level of gibberellin-synthesis-related genes in SN98A was lower than that in SN98B, and CKA of degradation-related genes was higher than that in CKB. Therefore, low light stress inhibited the synthesis of gibberellin by decreasing the expression of genes related to gibberellin synthesis and enhancing the expression of genes related to degradation, resulting in empty culms.

The responses of photosynthetic organs to low light stress and the associated mechanisms are important for understanding the adaptation of crops to different light environments. Thus, many studies have investigated the self-regulation mechanism and light energy conversion process in maize under low light conditions (Zivcak et al., 2014; Hazrati et al., 2016; Yamori, 2016). Chloroplasts are the site of photosynthesis in plants. Weak light stress can significantly damage the anatomical structure of plants to directly affect normal photosynthetic electron transport and the photosynthetic rate (P_n) (Du et al., 2011; Feng et al., 2021). Under low light, the oxidative pressure is intensified in maize leaves and the accumulation of large amounts of ROS leads to changes in the spatial configurations of various enzymes in chloroplasts, thereby adversely affecting their function, decreasing the chlorophyll content, and inhibiting photosynthesis. In the present study, under shading treatment, the Chl a, Chl b and chlorophyll (a+b) contents, tended to increase initially and then decrease in SN98A, whereas the Chl contents did not change greatly in SN98B and they were always higher than those in SN98A. After GA₃ treatment, the photosynthetic pigment contents increased significantly in SN98, and the Pn, Tr, and Gs values were also significantly higher compared with those in the control. PSII is one of the primary sites in photosynthetic organs damaged by stress, and it plays important roles in the light energy conversion and electron transport processes. (Zhang et al., 2020). The
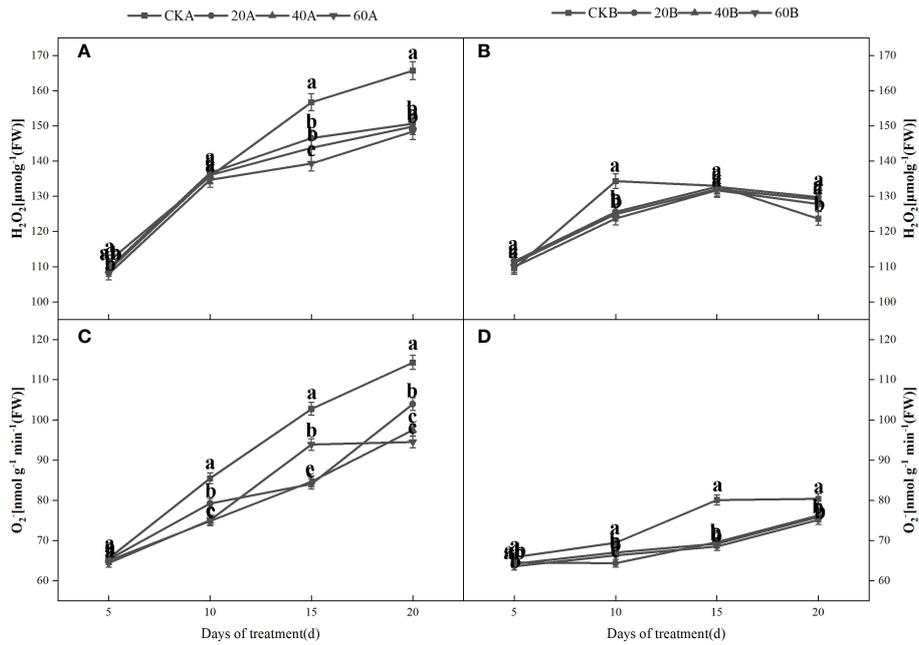
FIGURE 5
Effects of GA$_3$ on H$_2$O$_2$ contents and O$_2^-$ production rate in light-sensitive inbred maize lines after different periods under low light stress. In the figure panels, 20A, 40A, and 60A denote SN98A sprayed with 20 mg L^{-1}, 40 mg L^{-1}, and 60 mg L^{-1} GA$_3$, respectively, and 20B, 40B, and 60B denote SN98B sprayed with 20 mg L^{-1}, 40 mg L^{-1}, and 60 mg L^{-1} GA$_3$. CKA denotes the SN98A control group sprayed with water and CKB denotes the SN98B control group sprayed with water. In the figure, **(A**, **C)** represent the changes of H$_2$O$_2$ and O$_2^-$ after SN98A is treated with GA$_3$. **(B**, **D)** are the changes of H$_2$O$_2$ and O$_2^-$ after SN98B is treated with GA$_3$. Values are expressed as mean $\pm$ SD of three replicates. Lower-case letters indicate the mean difference of different treatments in the same period, which is statistically significant (P<0.05).

photoreaction requires coordination of the photosynthetic system in order to complete the normal linear electron transfer and provide the homogeneity for the fixation and reduction of CO$_2$ in the dark reaction. (Qian et al., 2017). In the present study, Pn, qP, and Φ_{PSII} continued to decrease during shading in SN98A, whereas they tended to increase initially and then decrease in SN98B, but the values were always higher than those in SN98A, thereby indicating that the normal photosynthetic physiological process was maintained in SN98B. GA$_3$ treatment could have increased the stomatal

conductivity of the maize leaves, enhanced the photosynthetic activity of mesophyll cells, and improved the photosynthetic capacity of maize leaves (Verma et al., 2016), where 60 mg L^{-1} GA$_3$ treatment had the greatest effect, and thus GA$_3$ may be involved in the shade protection response process in maize leaves. GA$_3$ had a positive effect on the photosynthetic efficiency of maize leaves under low light stress.

Plant photosynthesis is an extremely complex physiological process and it is negatively affected by both biological and abiotic
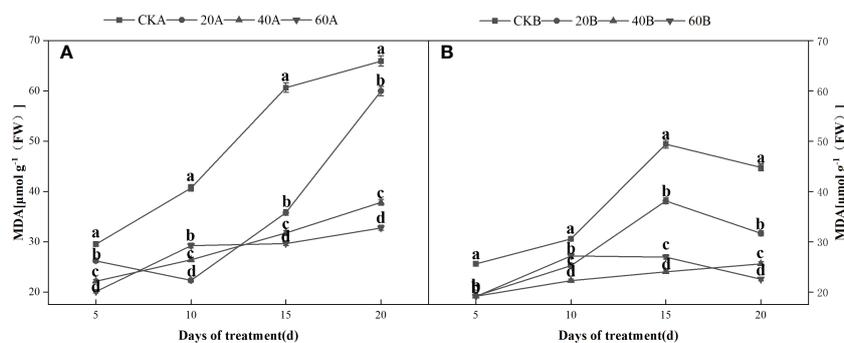

FIGURE 6
Effects of GA$_3$ on MDA content of light-sensitive maize inbred lines at different periods under low light stress. In the figure panels, 20A, 40A, and 60A denote SN98A sprayed with 20 mg L^{-1}, 40 mg L^{-1}, and 60 mg L^{-1} GA$_3$, respectively, and 20B, 40B, and 60B denote SN98B sprayed with 20 mg L^{-1}, 40 mg L^{-1}, and 60 mg L^{-1} GA$_3$. CKA denotes the SN98A control group sprayed with water and CKB denotes the SN98B control group sprayed with water. In the figure, **(A)** is the change of MDA in SN98A after GA$_3$ treatment, and **(B)** is the change of MDA in SN98B after GA$_3$ treatment. Values are expressed as mean $\pm$ SD of three replicates. Lower-case letters indicate the mean difference of different treatments in the same period, which is statistically significant (P<0.05).
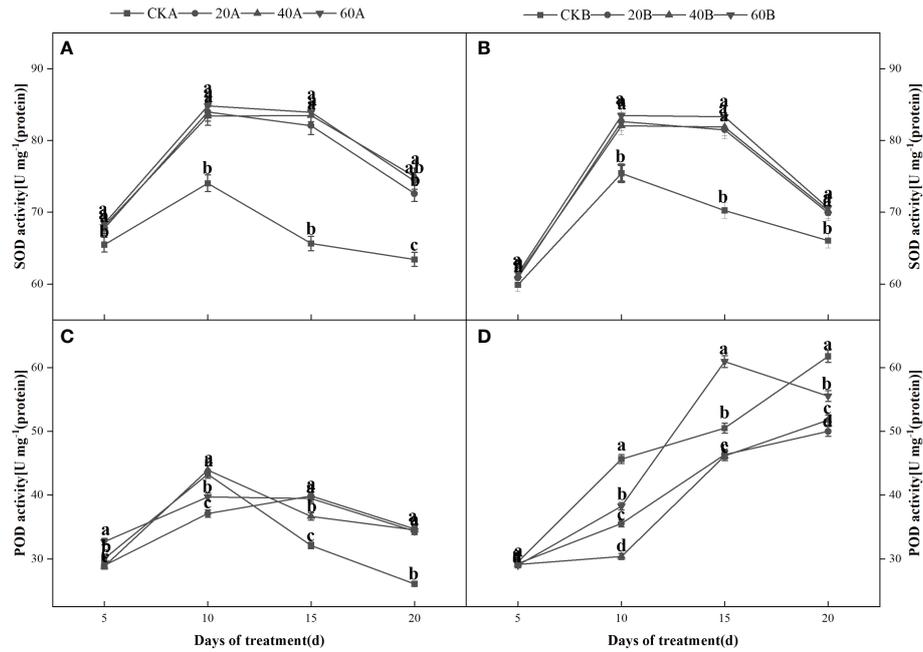
FIGURE 7
Effects of GA$_3$ on antioxidant enzymes contents in different light-sensitive inbred maize lines after different periods under low light stress. In the figure panels, 20A, 40A, and 60A denote SN98A sprayed with 20 mg L^{-1}, 40 mg L^{-1}, and 60 mg L^{-1} GA$_3$, respectively, and 20B, 40B, and 60B denote SN98B sprayed with 20 mg L^{-1}, 40 mg L^{-1}, and 60 mg L^{-1} GA$_3$. CKA denotes the SN98A control group sprayed with water and CKB denotes the SN98B control group sprayed with water. In the figure, **(A, C)** represent the changes of H$_2$O$_2$ and O$_2^-$ after SN98A is treated with GA$_3$. **(B, D)** are the changes of H$_2$O$_2$ and O$_2^-$ after SN98B is treated with GA$_3$. Values are expressed as mean $\pm$ SD of three replicates. Lower-case letters indicate the mean difference of different treatments in the same period, which is statistically significant (P<0.05).

stresses. The main limiting factors for photosynthesis are light and carbon dioxide (Smith, 1938). Under low light stress, photosynthesis is inhibited in crops and yields are reduced (Liu et al., 2020). In the present study, under low light stress, Pn, Tr, and Gs all decreased with time during shading, in the SN98A control group and the intercellular

carbon dioxide concentration increased. Applying GA$_3$ improved Pn, Tr, and Gs in SN98A and reduced the intercellular carbon dioxide concentration, where the effect of 60 mg L^{-1} GA$_3$ was most significant. Low light stress also reduced Pn, Tr, and Gs in the leaves in the SN98B control group, and increased the intercellular carbon dioxide concentration, but the normal physiological activities were generally maintained.
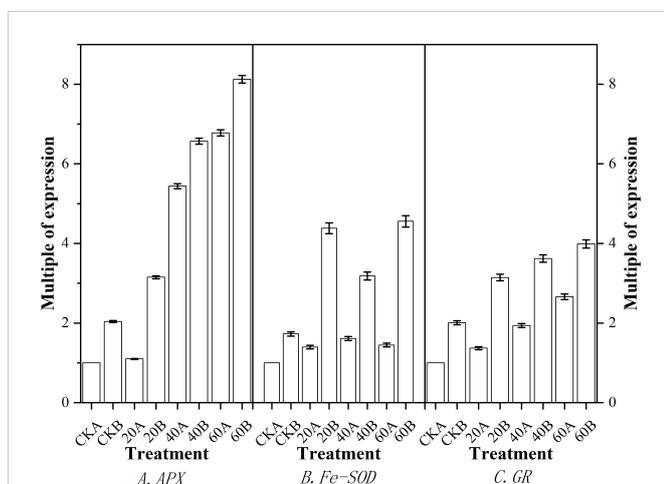
Conclusion

In the present study, maize inbred lines SN98A and SN98B with differences in their light sensitivity were subjected to shading in the maize tasseling stage (Figure 10). We found that low light treatment reduced the photosynthetic capacity of the maize leaves and inhibited the transport of photosynthetic products to other organs, thereby resulting in plant growth inhibition and leaf senescence. The adverse effects of shading were significantly greater in the weak light-sensitive inbred line SN98A than SN98B, mainly because SN98A had a significantly higher hollow stem rate than SN98B after shading. GA is an excellent antioxidant that can improve the tolerance of various biological and abiotic stresses in plants. These findings help us to understand the physiological mechanisms in maize inbred lines with differences in photosensitivity that mediate the response to low light stress under treatment with exogenous GA. The photosynthetic performance parameters of plants, i.e., Pn, Tr, Gs, photosynthetic pigment contents, (Fv/Fm), qP, and Φ_{PSII}, improved after applying GA$_3$ (20 mg L^{-1}, 40 mg L^{-1},

FIGURE 8
Effects of GA$_3$ application under low light stress on the expression levels of antioxidant-related genes in different light-sensitive inbred maize lines after shading for 15 days. **(A)** APX; **(B)** Fe-SOD; **(C)** GR. Values are expressed as mean $\pm$ SD of three replicates. Lower-case letters indicate the mean difference of different treatments in the same period, which is statistically significant (P<0.05).
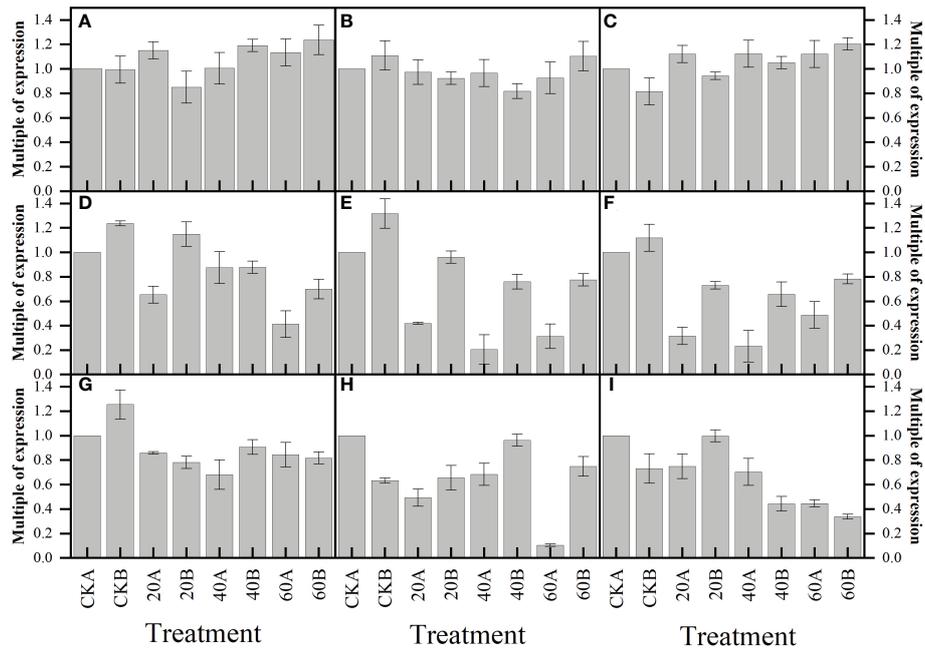
FIGURE 9
Effects of GA$_3$ application under low light stress on GA-related gene expression levels of different photosensitive inbred lines after shade for 15 days. **(A)** DELLA1; **(B)** DELLA2; **(C)** DELLA3; **(D)** GID1C1; **(E)** GID1C2; **(F)** GID1C3; **(G)** GA20ox2; **(H)** KAO1; **(I)**KAO2. Values are expressed as mean $\pm$ SD of three replicates.
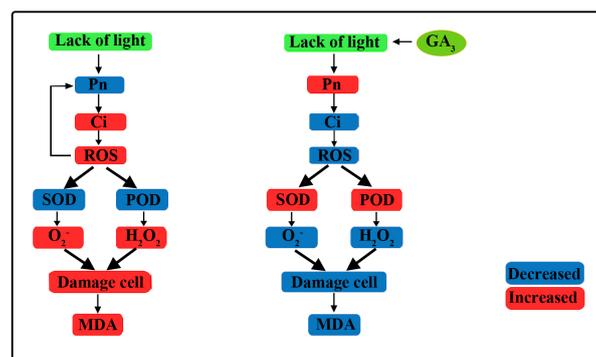

FIGURE 10
Overview of effects of exogenous GA$_3$ on plant photosynthetic physiology and reactive oxygen species (ROS) scavenging pathways. Under low light, the net photosynthetic rate (Pn) decreased, the intercellular carbon dioxide concentration increased, and the ROS content increased, which further affected Pn. Under low light, the activities of antioxidant enzymes decreased and the ROS scavenging rate decreased, thereby leading to cell damage and MDA was produced increase the degree of membrane lipid peroxidation. After the application of GA$_3$, Pn improved, the activities of antioxidant enzymes increased, ROS scavenging was enhanced, cell damage was reduced, and the MDA content decreased.

and 60 mg L^{-1}) to the leaves, including 60 mg L^{-1} GA$_3$ works best. Thus, the foliar application of GA$_3$ to SN98A and SN98B will be beneficial for their growth and development under lower light conditions.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

JF: investigation, data curation, validation, and writing—original draft; LL: review and editing; SW: data curation, methodology, formal analysis, and software; NY: formal analysis and editing; HS: investigation and formal analysis; ZS: resources and funding acquisition; FL: writing—review and editing; XZ: conceptualization, writing—review, editing and funding acquisition. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Author HS is employed by Liaoning Dongya Seed Co.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2023.1128780/full#supplementary-material

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