Physiological Mechanisms of Grain Yield Loss Under Combined Drought and Shading Stress at the Post-silking Stage in Maize

10 authors, including:

ORIGINAL PAPER

Physiological Mechanisms of Grain Yield Loss Under Combined Drought and Shading Stress at the Post-silking Stage in Maize

Muhammad Asad Naseer[1,2] · Zhang Nengyan[1,2] · Irsa Ejaz[3] · Sadam Hussain[1,2] · Muhammad Ahsan Asghar[4] · Muhammad Farooq[5] ⓘ · Qian Rui[1,2] · Abd Ullah[6] · Chen Xiaoli[1,2] · Ren Xiaolong[1,2]

Abstract

Decreased light conditions due to cloud cover and smog pollution severely limit crop cultivation and production. Reduced light interception coupled with irregular rainfall caused damage to major crops' yield at their critical growth stages, especially at the post-silking stage in maize (*Zea mays* L.). This study was conducted in underground soil columns containing a moveable shed (to apply shade and avoid rainfall) to investigate the combined effect of drought and shading stress at the post-silking stage of maize. Plants were exposed to five shading treatments (a control without shading (SD0), shading for 3 (SD3), 6 (SD6), 9 (SD9), and 12 days (SD12)) and four drought levels (100, 75, 50, and 25% of irrigation) after silking in maize. A split-plot design was used. The combined stresses caused oxidative damage to maize leaves, which caused a significant reduction in the photosynthetic efficacy, grain yield, and grain quality. The combination of SD12 and 25% irrigation caused a 24% reduction in photosynthetic activity and grain yield compared with the respective control. Under interactive drought and shading conditions, SD12 combined with 25, 50, and 75% irrigation caused an upsurge in grain protein by 3.94, 8.06, and 6.70%, respectively. The combined drought and shading stress during the post-silking stage in maize caused a significant reduction in rain yield by altering antioxidant potential and photosynthetic efficiency. An increase in antioxidant defense was observed under combined stresses; however, this increase was insufficient to combat the oxidative damage caused by stress.

Keywords Low light · Water deficit · Reproductive stage · Morpho-physiology · Grain yield

1 Introduction

Crop production has recently become more susceptible to extreme weather events due to the high dependency of crop yield and productivity on climatic conditions (Naumann et al. 2018). The frequency of extreme weather events has snowballed in recent years (Huang et al. 2014). Drought stress is expected to affect more than 50% of arable land worldwide in 2050 (Gupta et al. 2020). For instance, the most recent reports on model-based climatic projections indicated that

✉ Muhammad Farooq
farooqcp@squ.edu.om

✉ Chen Xiaoli
cxlrxl@aliyun.com

✉ Ren Xiaolong
rxlcxl@aliyun.com

1 College of Agronomy, Key Laboratory of Crop Physio-Ecology and Tillage in Northwestern Loess Plateau, Ministry of Agriculture, Northwest A&F University, Yangling, Shaanxi, China

2 Key Laboratory of Agricultural Soil and Water Engineering in Arid and Semi-Arid Area, Ministry of Education/Institute of Water Saving Agriculture in Arid Areas of China, Northwest A&F University, Yangling, Shaanxi, China

3 College of Agronomy and Biotechnology, China Agricultural University, Beijing, China

4 Agricultural Institute, Centre for Agricultural Research, ELKH, Martonvásár, Hungary

5 Department of Plant Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University, Al-Khoud 123, Muscat, Oman

6 Xinjiang Key Laboratory of Desert Plant Root Ecology and Vegetation Restoration, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China

variable rainfall patterns might reduce freshwater resources by up to 50% and increase drought stress incidence (Allan et al. 2021). This is one of the most pervasive abiotic stresses causing significant crop yield reduction, thereby threatening global food security (Lesk et al. 2016). In addition, a substantial decline in global irradiation has also been observed due to an increase in aerosols, cloud cover, and urbanization, reducing the yield of major crops (Stanhill and Cohen 2001). The combined occurrence of drought and shade stress may have a more devastating effect on plant growth, development, and yield formation (Asghar et al. 2020).

In addition to water shortage, light is one of the most crucial environmental factors that affect agricultural plants' cultivation and production. A diminution in light intensity and quality (shade) during different growth phases may alter the photosynthetic efficiency of plant leaves and affect the quality of grains (Setter et al. 2001). Reduced photosynthetic rates due to the shading effect caused a severe reduction in photosynthetic product and plant biomass accumulation (Yao et al. 2017a, b; Yao et al. 2017a, b). Plants under shade or low light usually exhibited lower intercellular CO_2 assimilation rates, photosynthetic photon flux density (PPFD), and electron transfer carriers than unshaded or normal light conditions (Zhang et al. 2004; Jiang et al. 2011).

Water deficit conditions cause many plant disorders at physiological and biochemical levels and reduce the leaf's relative water contents. Severe water deficit conditions cause stomatal closure owing to alter the CO_2 concentrations, reduce the synthesis of ATP, limit the activity of the rubisco, and cease the regeneration of RuBP, which in turn lead to attenuated photosynthetic activity and yield losses (Farooq et al. 2011; Shokat et al. 2021). Drought stress also affected the chlorophyll fluorescence (CF) and photosystem-II (PSII) efficiency owing to a decrease in photosynthetic rates and, ultimately, grain yield (Albert et al. 2010; Tattini et al. 2015). Drought stress increases lipid peroxidation, produces malondialdehyde (MDA), and decreases antioxidant enzymatic activities (Ashraf and Harris 2013; Shokat et al. 2020). Plants can respond to drought stress by altering their growth and physiological events, i.e., through modification in root architecture and stomatal closure (An and Liang 2012).

The combined impact of drought and shading stress on plant growth is more complex than the individual existence of these determinants (Shabbir et al. 2022). Environmentalists and plant physiologists have been baffled by how plants respond to drought and shadow stress for many years. Under dry conditions, shading typically improves plant growth and survival (Holmgren 2000). Shading prevents overheating by lowering the air and leaf temperatures (Franco and Nobel 1989) and reducing transpiration demands (Pospisilova 2003). Similar to previous studies on combined stresses, the unavailability of sufficient light and soil water may lessen photosynthesis and carbon gain, negatively affecting plants' water use efficiency

(Aranda et al. 2007). The co-existence of drought and shade stress causes plants to cope with a trade-off between drought and shade tolerance. Consequently, plants may weaken their tolerance to shade under drought conditions or vice versa (Smith and Huston 1990). However, the mitigation or synergistic response of shading to drought stress varies for plant species, crop stage, and stress conditions (Holmgren et al. 2012).

Maize, a typical example of the C4 class, is more sensitive to shade stress, which severely damages growth and productivity. Several studies have discussed that shade stress also causes a decline in maize yield and the nutritional status of grains (Zhang et al. 2006; Gao et al. 2017; Gao et al. 2020). However, studies are also available in which low light conditions did not affect photosynthesis and even increased photosynthesis, for example, in wheat (Mu et al. 2010) and soybean (Asghar et al. 2020). The increase in photosynthetic characteristics of different plants is due to morphological modifications, such as an increase in plant height observed in wheat plants (Naseer et al. 2021) and the efficient light-capturing ability of the plants. Shading during the reproductive stage also influences the quality of maize grains by decreasing the activity of starch synthase enzymes (Zhang et al. 2008; Shifang et al. 2010). Shading after pollination can diminish the starch content and kernel weight and increase the fat and protein contents (Jia et al. 2011). Several studies have assessed the individual effect of shading or drought on maize crops owing to reducing photosynthesis and decreasing yield (Gao et al. 2017; Gao et al. 2020; Song et al. 2021). However, it is essential to check the combined influence of the reduced light conditions and limited water supply at the critical growth stage of maize.

Our recent study evaluated the combined effects of drought and shading stress at the grain-filling stage on photosynthetic activity and grain yield in wheat (Naseer et al. 2021). However, studies on the influence of combined drought and shading stress at the post-silking stage of maize are lacking. Therefore, in this work, we hypothesized that combined drought and shading stresses at post-silking could cause a significant decline in the photosynthetic activity, grain yield, and quality of maize. This study is aimed at evaluating the response of maize under individual and combining drought and shading stresses at the post-silking stage in maize.

## 2 Materials and Methods

2.1 Experimental Site

In 2020, an experiment was carried out at the Northwest Agriculture & Forestry University's Institute of Water Saving Agriculture Experimental Station in Yangling

(34° 20′ N, 108° 24′ E), People's Republic of China. A blend of farmed soil and compost (2:1 w/w) was used to fill subterranean soil columns (with a diameter of 45 cm and a length of 3 m) under rainproof shelters (with an interior size of 3 m height, 15 m width, and 16 m length) (Fig. 1). The moveable shelter was used to manage natural precipitation. Irrigation treatments were adjusted considering previous weather data (precipitation (mm) and average monthly temperature (°C)) from 2011 to 2020 as shown in Fig. 2.

2.2 Treatments and Experimental Design

Maize (*Zea mays* L.) cultivar, Zhengdan 958 (obtained from Jun Hun seed company, China) was used for this experiment. Three seeds were sown in each underground soil column on July 01, 2020. Nitrogen (225 mg kg^{-1} soil, from urea) and phosphorus (75 mg kg^{-1} soil, from diammonium phosphate) were applied at the time of sowing. Pipes coming from drums were used to supplement irrigation, and specific amounts of water were given to each soil column. The design

Fig. 1 Drought and shading treatments imposed at post silking stage of maize at Water-Saving Agriculture Experimental Station of Northwest A & F University, Yangling, China

Fig. 2 Average monthly temperature, precipitation, and monthly temperature of 10 years (2011–2020) at the Water-Saving Agriculture Experimental Station of Northwest A & F University, Yangling, China
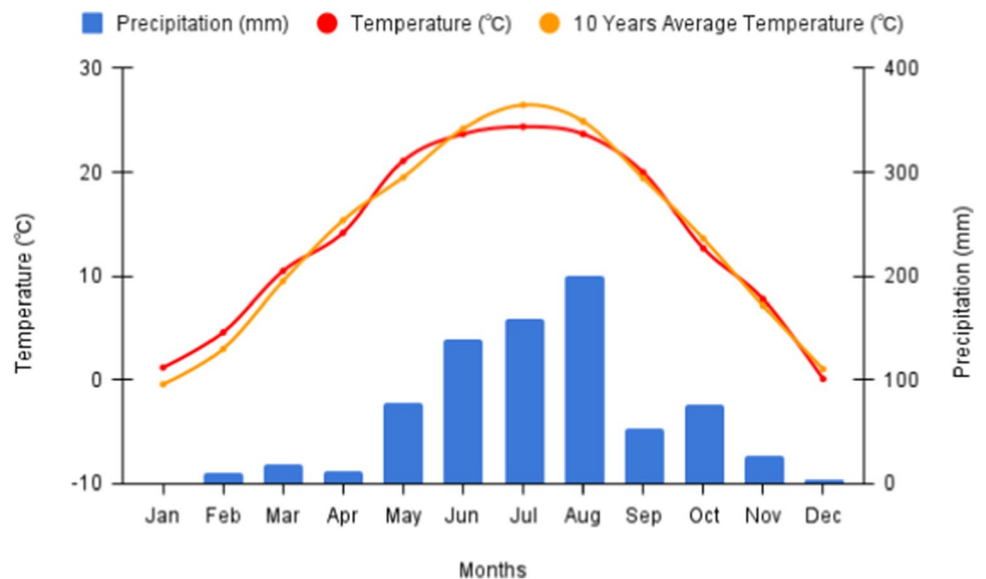
used in the experiment was a split-plot design with three replications. This experimental design was used because of fixed soil columns and shading applied in one direction.

Five shading treatments were maintained for this study, including non-shaded plants (SD0) and shading for 3 (SD3), 6 (SD6), 9 (SD9), and 12 (SD12) days. Shading treatments were started at the silk emergence stage at 68, 71, 74, and 77 days after sowing for SD12, SD9, SD6, and SD3 treatments, respectively. During the experiment, the photosynthetic photon flux density (PPFD) for normal light treatment was about 150 ± 10 and red/far red (R:FR) ratio of 1.2. For the shading conditions, the PPFD was 75 ± 10 µmol photons $m^{-2} s^{-1}$ and R:FR ratio of 0.4 ~ 0.6. A detachable shed (3.5 m × 12 m × 7 m, height × length × width) was built using scaffolding and black polypropylene fabric. The cloth was 2 m longer at the edges to block the oblique sunlight. Different water deficit (drought) treatments, including 100% (CK; 18.24 L), 75% (12.16 L), 50% (6.08 L), and 25% (3.04 L) irrigation, were imposed during shading of 68–80 DAS. The drought treatments were applied through a natural gradual drought imposed by withholding water from 25 to 100%. For 60 DAS, the soil moisture in fixed underground columns was kept at 85–90% FC, and three maize plants with identical growth patterns were sustained in each column.

2.3 Sampling and Measurements

2.3.1 Leaf Relative Water Contents

The fresh leaf sample was taken to assess the relative water content of maize leaves after the drought and shading treatments (80 DAS), and then, the fresh weight (FW) of each leaf sample was recorded (Su et al. 2019). The samples were then submerged in distilled water. After 24 h, fully turgid leaf weight (TW) was recorded. The leaf samples were then dried in an oven for 72 h at 75 °C to determine the dry weight (DW). The following formula was used to determine the RWC (%) of maize leaves:

$$RWC = \frac{FW - DW}{TW - DW} \times 100$$

2.3.2 Gas Exchange Parameters

Net photosynthetic rate (P_n), intracellular CO_2 concentration (C_i), stomatal conductance (gs), and transpiration rate (Tr) were determined at 80 DAS by considering the first leaf above the node of the primary ear insertion. The observations were taken from 9:00 to 11:00 am. The portable photosynthesis system LI-6400XT (LI-COR, Biosciences, Lincoln, NE, USA) was employed to compute the photosynthetic indicators.

The leaf chamber CO_2 concentrations and photosynthesis active radiation were fixed at 380 µmol mol^{-1} and 1100 µmol $m^{-2} s^{-1}$, respectively.

2.3.3 Malondialdehyde Contents and Anti-oxidant Enzyme Activities

Lead malondialdehyde (MDA) contents, as an index of lipid peroxidation, were determined by the method as described by (Cakmak and Marschner 1992) with slight modifications. The 500 mL of supernatant from the MDA reaction mixture (which contained 0.65% (w/v) thiobarbituric acid in 20% trichloroacetic acid) was heated for 30 min before being quickly chilled to halt the reaction. After that, the mixture was centrifuged at 10,000 g for 10 min. At 532 nm, the mixture's absorbance was quantified. The absorbance data was subtracted from the non-specific absorption at 600 nm.

For the determination of activities of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), 0.2 g frozen leaf tissues were ground in 5 mL of 0.1 mol L^{-1} Tris–HCl buffer (pH 7.8) containing 1% polyvinyl pyrrolidone, 1 mmol L^{-1} EDTA, and 1 mmol L^{-1} dithiothreitol. Then, the homogenate was centrifuged at 18,000 g for 20 min at 4 °C. The supernatant was then used for the measurement of enzyme activities.

For the determination of SOD activity, the reaction mixture contained 0.2 mL of the enzyme solution mixed with 50 mM phosphate buffer (pH 7.6), 13 mM methionine, 750 mM NBT, 4 mM riboflavin, and 0.1 mM EDTA. The photochemical reduction of NBT was measured following the procedure of Lei et al. (2006). Catalase activity was assayed by mixing the reaction mixture containing 50 mM phosphate buffer (pH 7.0) and 12.5 mM H_2O_2 with enzyme extract following (Djanaguiraman et al. 2009). To estimate POD, 50 mM phosphate buffer (pH 7.0), 16 mM guaiacol, enzyme extract, and 10 mM H_2O_2 were added to the reaction mixture and the POD activity was determined as described by Cakmak and Marschner (1992).

2.3.4 Dry Matter per Plant, Grain Yield, and Harvest Index

The crop was harvested at maturity on October 06, 2020. Three plants from each column were harvested, and the total biomass was calculated before separating grains. Dry matter per plant was recorded, oven drying the plants until constant weight. The cobs were removed from each plant, and grains were separated to calculate grain yield. The grains with a moisture content of 14% were considered the standard yield. The harvest index was calculated as a ratio of grain yield and biological yield.

2.3.5 Grain-Quality Traits

Grain-quality parameters were determined using a near-infrared spectrophotometer (NIR) (Başlar and Ertugay 2011). For that, 10 g of intact maize grain samples was separated and examined for protein, starch, lipids, and fiber contents (NIR) (AACC Method 39–25.01 Near-Infrared Reflectance Method for Protein Content in Whole-Grain Wheat). A cup-shaped accessory was used with the bottom made of glass to pass the radiation. The cup was filled with 100 g of grains and adjusted over the NIR spectrometer. In-built computerized functions were used to run the machine and to calculate the final grain quality parameters.

2.4 Statistical Analysis

Data were analyzed by applying analysis of variance (two-way ANOVA) between drought and shading treatments using R-software (Version; 4.1.0) with the support of agricolae package (Version 1.3–5) to confirm its variability (RStudio Team 2021). The Tukey HSD test was used to quantify the differences between the treatments at a 5% probability level. Data representation and illustration were done in R-software (Version; 4.1.0) using ggplot2, graphics, and dplyer packages (RStudio Team 2021). Pearson correlation analysis was done using the corrplot package to examine the relationship among the studied parameters.

3 Results

3.1 Relative Water Contents

Shading (SD), irrigation regimes (IR), and their interaction (SD × IR) significantly influenced the leaf relative water content. Drought stress significantly reduced the relative water contents of maize, where the lowest values were observed under 25% irrigation while the highest was for 100% irrigation. Generally, SD12 had higher relative water contents compared to other shading treatments. Plants under no shading had 10.97, 5.78, and 1.97% lower relative water contents at 25, 50, and 75% irrigation, respectively, compared with 100% irrigation treatment. While under SD12, the relative water content declined by 9.06, 5.17, and 3.44% under 25, 50, and 75% irrigation when compared with 100% irrigation, respectively. Under 100% irrigation, the increase in relative water contents for SD3, SD6, SD9, and SD12 treatments was 0.11, 0.66, 1.32, and 2.37%, respectively. While under 25% irrigation, the increment in relative water contents for SD3, SD6, SD9, and SD12 was 1.22, 3.22, 4.45, and 4.57%, respectively. Collectively, the shading caused an increase in the relative water contents of maize under drought stress (Fig. 3).

3.2 Lipid Peroxidation and Anti-oxidant Activities

Significant variations were observed in MDA content under shading, drought, and their cumulative effects. As an

Fig. 3 Effect of shading treatments (days) on relative water content (RWC, %) of maize under different irrigation conditions (100, 75, 50, and 25% irrigation). The values represent the mean ± standard error. Similar letters indicate non-significant differences at $P < 0.05$
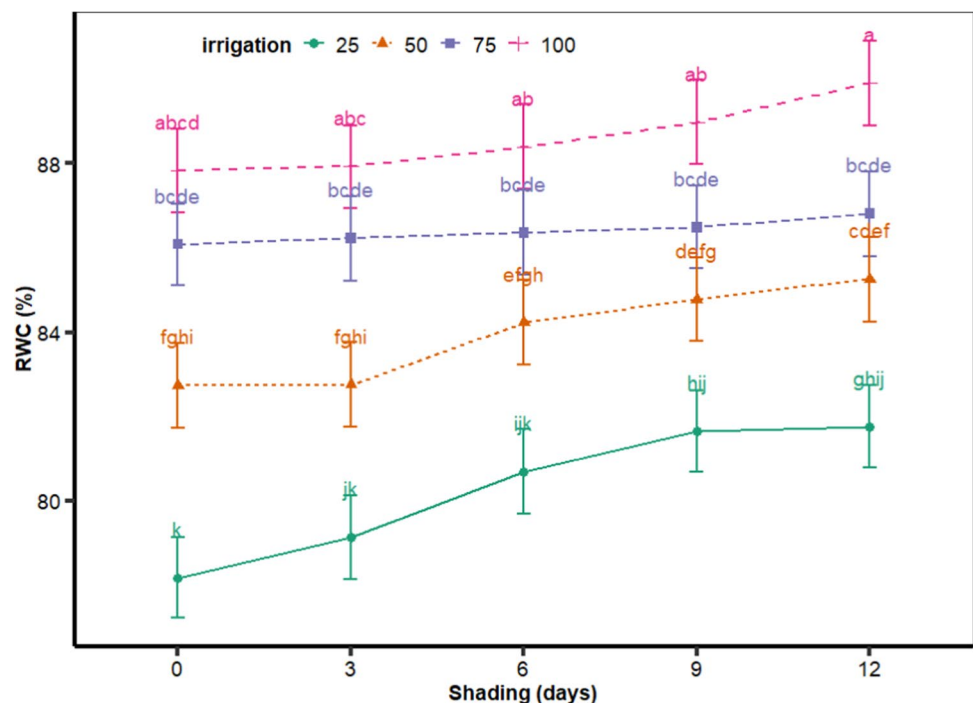
individual effect, shading for 3, 6, 9, and 12 days increased MDA content by 18.28, 27.69, 34.37, and 43.60%, respectively, when compared with no shading. Under individual drought stress, an increase of 21.29, 5.58, and 13.53% was observed for 25, 50, and 75% irrigation conditions compared to control, respectively. Whereas, compared to individual shading and drought, SD3, SD6, SD9, and SD12 combined with 25% irrigation increased MDA contents by 14.90, 33.90, 43.20, and 63.40%, respectively. SD12 combined with 25, 50, and 75% irrigation conditions produced an amplification of MDA contents by 38.01, 17.62, and 4.78%, respectively.

The SOD and POD activities were also affected significantly by drought, shading, and their interactive effects (SD × IR) (Fig. 4). Plants under individual drought recorded a decreasing tendency in SOD activity with decreasing irrigation amount. Under individual shading of SD3, SD6, SD9, and SD12, SOD activity was increased by 6.55, 7.04, 12.89, and 19.23%, respectively, compared to the control. Under individual drought, plants depicted 26.16, 14.36, and 13.15% reduction in SOD activity for 25, 50, and 75% reduction in irrigation, respectively, relative to control. However, under combined shading and 25%

IR, shading treatments showed an increase in SOD activity, except for SD12, which decreased the values by 40.59, 18.42, and 5.85% under 25, 50, and 75% irrigation reduction, respectively. A significant and maximum decline in SOD activity was observed under combined drought (25% IR) and shading (SD12) treatments (Fig. 4c).

Under individual shading, SD3 decreased the POD activity by 12.13%, while SD6, SD9, and SD12 increased the POD activity by 33.23, 26.10, and 45.23%, respectively, compared to the control (Fig. 4d). SD12 combined with 25, 50, and 75% IR decreased the POD activity compared to control by 60.68, 46.77, and 37.65%, respectively.

Similarly, CAT activity increased under individual shading effects while decreasing significantly under combined drought and shading stress. Under individual shading stress, SD3 and SD6 increased the CAT activity by 2.27 and 12.31%, while SD9 and SD12 decreased the CAT activity by 2.80 and 2.21, respectively, over control. Under individual drought, 25, 50, and 75% reduction in irrigation decreased the CAT activity by 10.76, 7.84, and 9.92%, respectively, compared to full irrigation (100IR). SD12 combined with 25, 50, and 75% IR increased the CAT activity by 16.09, 19.48, and 11.0%, respectively, compared to the control.
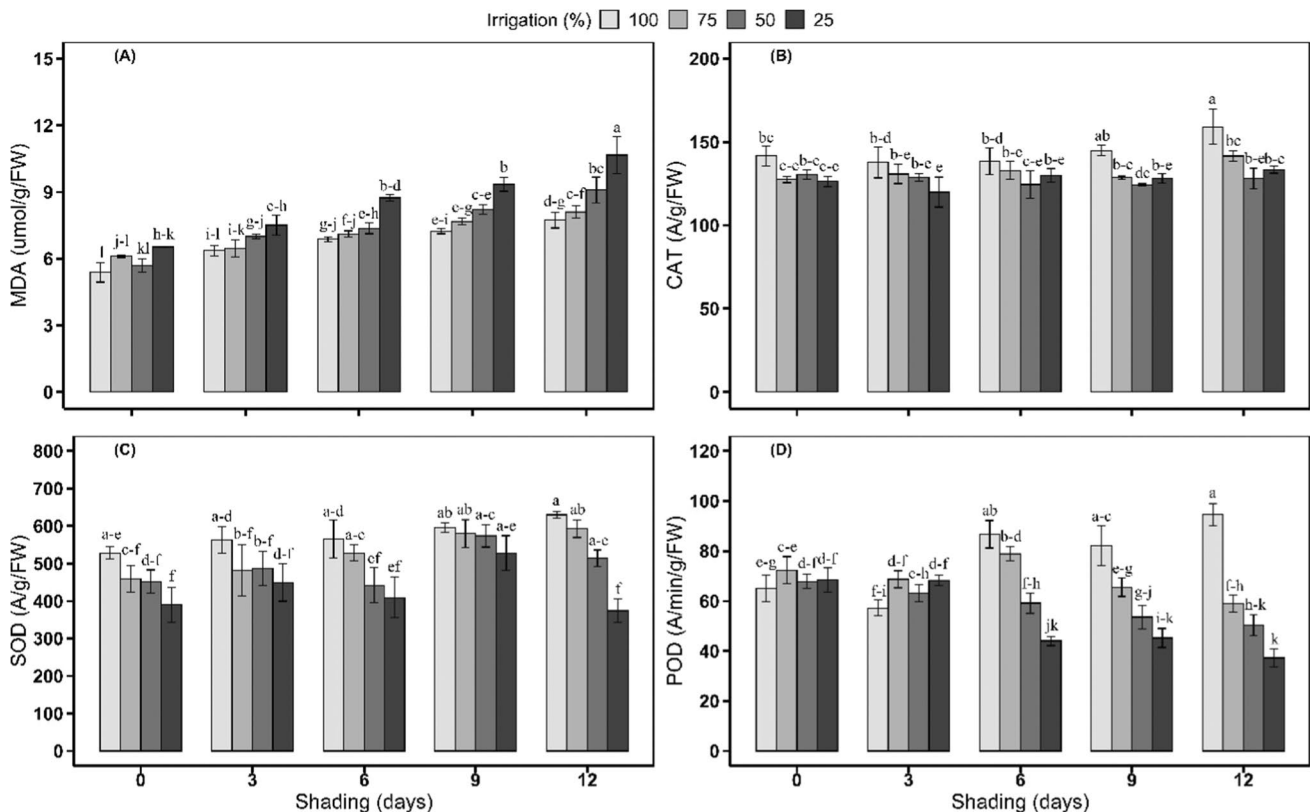

Fig. 4 Effect of shading on (**a**) malondialdehyde (MDA), (**b**) catalase (CAT), (**c**) superoxide dismutase (SOD), and (**d**) peroxidase (POD) of maize under different irrigation conditions (100, 75, 50, and 25% irrigation). The values represent the mean ± standard error, and bars sharing the similar letters for a parameter indicate non-significant ($P < 0.05$) differences

For CAT activity, the lowest value was recorded in plants exposed to 12 days of shading and a 25% reduction in irrigation (Fig. 4b). Taken together, it is indicated that the combined occurrence of drought (25% irrigation) and shading (12 days) negatively impacted the antioxidant enzyme activity more severely than their sole effect (Fig. 4).

3.3 Effect of Drought and Shading on Gas Exchange Parameters in Maize

Photosynthetic activity in terms of *Pn*, *gs*, *Ci*, and *Tr* exhibited a significant response under individual and combined drought and shading stress treatments (Fig. 5). The highest *Pn* was recorded under individual shading of 9 days, whereas the highest decline in *Pn* was observed in plants subjected to 25% irrigation reduction. Under no shading, plants undergo drought stress and displayed 4.23, 2.68, and 19.76% reduction in *Pn* for 75, 50, and 25% irrigation conditions, compared to 100% irrigated plants. For SD12, this reduction was -5.13, -3.52, and 23.59%, respectively. At 100% irrigation, plants with SD3, SD6, SD9, and SD12 depicted an increase of 20.45, 18.34, 23.97, and 13.67%, when compared with SD0, respectively. It implied that

combined drought and shading significantly reduced the *Pn*. However, individual shading increased the photosynthesis of maize plants (Fig. 5a).

The highest *Tr* was recorded in plants exposed to individual shading stress for 9 days. In comparison, the lowest *Tr* was observed in plants supplemented with 25% irrigation and SD12. Under SD0, the plants under 25, 50, and 75% irrigation displayed a 25.57, 11.27, and 3.05% decrease in *Tr*, compared to 100% irrigation conditions. Interestingly, the plants exposed to SD12 showed a 4.07, 4.59, and 20.84% decrease in *Tr* under 75, 50, and 25% irrigation compared to 100%. Under 100% irrigation, relative to SD0, the maize plants under SD3, SD6, and SD12 presented a downregulation of 0.92, 1.67, and 10.64%, respectively, while upregulation in SD9 by 17.35%. The overall influence of shading under full irrigation was statistically the same ($P < 0.05$; Fig. 5b). The *gs* also showed a similar trend as *Pn* and *Tr* since its highest value (0.096 μmol H_2O m^{-2} s^{-1}) was recorded in plants subjected to shading for 9 days under fully irrigated plants. Under fully irrigated conditions, an increase of 23.65, 37.60, and 7.26% in *gs* was recorded in maize plants exposed to 6, 9, and 12 days of shading, as compared with no shading, respectively. Under
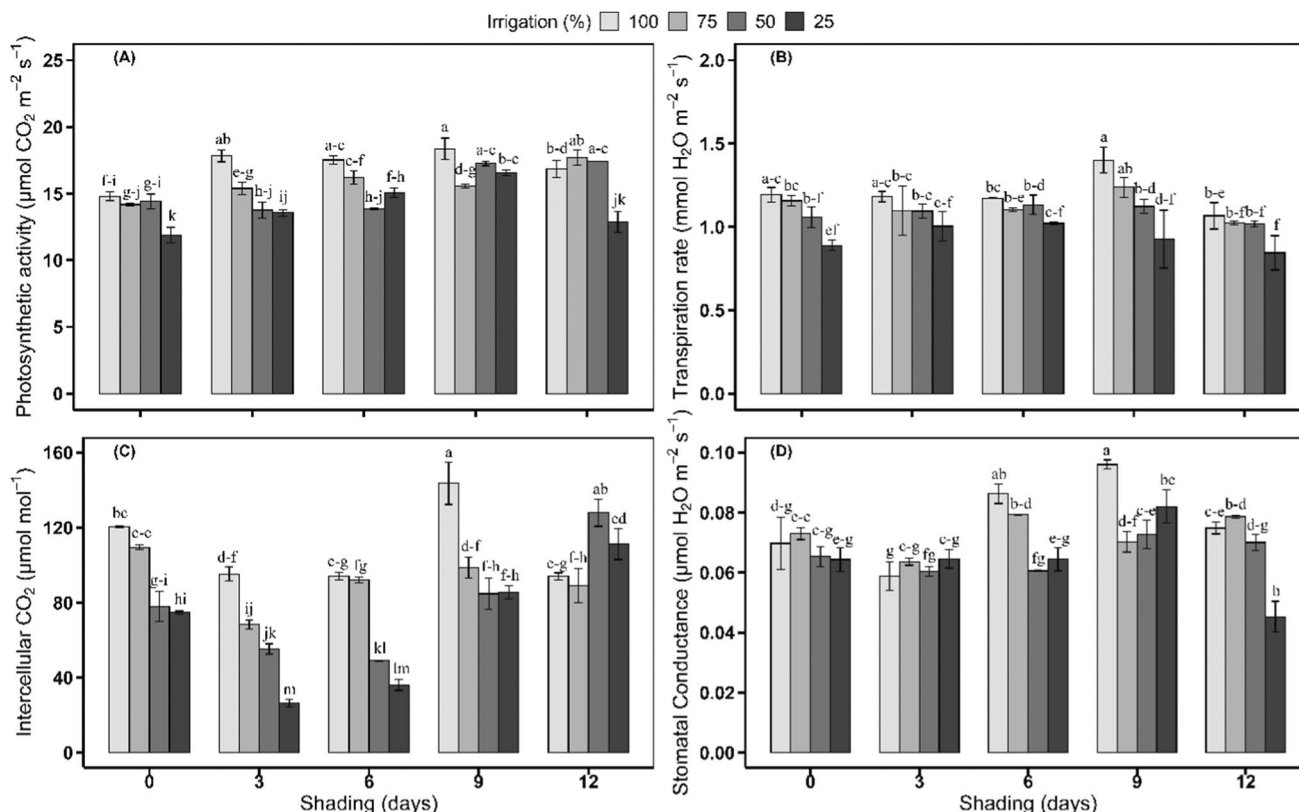

Fig. 5 Effect of shading on (**a**) rate of photosynthesis, (**b**) transpiration rate, (**c**) intracellular CO_2 concentration, and (**d**) stomatal conductance of maize under different irrigation conditions (100, 75, 50, and 25% irrigation). The values represent the mean ± standard error, and bars sharing the similar letters for a parameter indicate non-significant ($P < 0.05$) differences

SD0, irrigation reductions of 25, 50, and 75% resulted in a decrease of -7.73, 6.30, and 4.64% in *gs*, over control. Under SD12, *gs* showed a decreasing trend as a reduction of 39.48 and 6.36% was recorded under 25 and 50% irrigated plants, respectively (Fig. 5d).

Likewise, the maximum *Ci* (143.63 µmol mol^{-1}) was observed in fully irrigated plants when exposed to 9 days of shading (SD9). While the lowest value (26.37 µmol mol^{-1}) was noted under 25% irrigation conditions and shading for 3 days, overall, it is noted that the co-occurrence of shading and drought substantially reduced the photosynthetic efficiency of maize plants (Fig. 5c).

3.4 Grain Yield, Dry Matter, and Harvest Index

Grain yield, dry matter production, and harvest index were estimated as final yield parameters, which were significantly ($P < 0.05$) affected by shading, irrigation regimes, and their interactive effects (Table 1). It was noticed that the grain yield was inhibited with the prolongation of the shading period. Under fully irrigated

conditions, the plants under SD3, SD6, SD9, and SD12 displayed a reduction of 21.35, 26.67, 34.26.90, and 41.61% in grain yield when compared with SD0, respectively. For drought stress, a maximum reduction in grain yield was observed under 25% irrigation. Moreover, as an individual effect, 75, 50, and 25% irrigation decreased grain yield by 15.37, 25.36, and 22.44%, respectively, over control. Under SD9, in contrast to full irrigation, plants under 25, 50, and 75% irrigation depicted a decline of 20.78, 27.69, and 38.46% in grain yield, respectively. Collectively, it is recorded that the co-occurrence of drought and shading stress was more effective in declining grain yield than their individual effects.

Under full irrigation, the dry matter production declined by 7.62, 18.28, 33.23, and 18.76% under shading of 3, 6, 9, and 12 days, respectively. As the individual effect, 50 and 25% irrigation treatments decreased dry matter production by 11.21 and 25.78%, respectively when compared to fully irrigated plants (Table 1). A similar trend was recorded for HI for the individual effect of these treatments. Under the interactive effect of drought and shading, the minimum

Table 1 Effect of shading (SD) on dry matter, 100 grain wright, grain yield, and harvest index of maize under different irrigation regimes (IR, %)

IR (%)	SD	Dry matter (g/plant)	100-grain weight (g)	Grain yield (g/plant)	Harvest index
100	12	107.97 ± 10.39 abc	14.92 ± 1.45a	38.49 ± 1.52fghi	0.35 ± 0.04bcd
	09	88.73 ± 7.71 c	18.29 ± 1.64a	43.99 ± 3.54defg	0.50 ± 0.08a
	06	108.60 ± 3.38 abc	19.89 ± 0.59a	48.34 ± 1.12 cd	0.44 ± 0.01ab
	03	122.77 ± 5.11 ab	18.91 ± 4.12a	51.81 ± 2.63bc	0.42 ± 0.03abc
	0	132.90 ± 13.45 a	18.00 ± 1.06a	65.93 ± 3.48a	0.50 ± 0.07a
75	12	110.63 ± 5.86 abc	19.00 ± 1.41a	29.96 ± 1.97j	0.27 ± 0.00d
	09	121.80 ± 8.40 ab	16.77 ± 0.54a	39.06 ± 3.24efgh	0.32 ± 0.04bcd
	06	111.37 ± 4.30 abc	17.40 ± 2.43a	45.20 ± 2.59cdef	0.40 ± 0.01abc
	03	123.17 ± 9.63 ab	17.89 ± 3.59a	50.42 ± 1.90bcd	0.41 ± 0.04abc
	0	133.40 ± 13.49 a	17.45 ± 0.92a	55.79 ± 3.09b	0.41 ± 0.01abc
50	12	103.73 ± 16.95 abc	18.22 ± 2.06a	31.73 ± 1.40ij	0.31 ± 0.04 cd
	09	109.77 ± 9.41 abc	16.70 ± 1.94a	36.20 ± 1.44hij	0.33 ± 0.03bcd
	06	108.03 ± 12.82 abc	15.63 ± 1.08a	37.86 ± 0.57ghi	0.35 ± 0.03bcd
	03	113.07 ± 15.31 abc	17.22 ± 2.72a	45.29 ± 2.18cdef	0.40 ± 0.06abc
	0	118.40 ± 12.70 abc	16.27 ± 0.40a	49.21 ± 1.21bcd	0.41 ± 0.05abc
25	12	107.97 ± 4.95 abc	17.31 ± 0.09a	35.65 ± 1.45hij	0.33 ± 0.00bcd
	09	106.17 ± 8.63 abc	17.10 ± 2.93a	38.71 ± 0.66fgh	0.36 ± 0.02bcd
	06	97.00 ± 3.36 bc	16.22 ± 1.95a	40.9 ± 1.92efgh	0.42 ± 0.02abc
	03	114.50 ± 13.03 abc	16.10 ± 2.01a	45.66 ± 0.28cde	0.40 ± 0.04abc
	0	98.63 ± 5.25 bc	18.50 ± 1.54a	51.13 ± 3.60bc	0.51 ± 0.00a
		Analysis of variance			
LSD		DM	100-GW	Grain yield	HI
IR		0.02126 (*)	(ns)	9.75 × 10^{-14} (***)	3.34 × 10^{-6} (***)
SD		0.00059 (***)	(ns)	< 2 × 10^{-16} (***)	3.39 × 10^{-9} (***)
IR × SD		0.00254 (**)	(ns)	0.000188 (***)	0.0293 (*)

IR, irrigation regimes; *SD*, shading days; *100-GW*, hundred grain weight; *DM*, dry matter; *HI*, harvest index; (***), $P < 0.001$; (**), $P < 0.01$; (*), $P < 0.05$; *(ns)*, non-significant. Values represent means ± standard error. Means sharing the similar letters, for a parameter, indicate non-significant ($P < 0.05$) differences

average grain yield (29.96 g) was exhibited for plants exposed to shading of 9 days and 75% irrigation.

3.5 Shade and Drought-Induced Changes in Grain Quality of Maize

Shading, drought, and their interactions significantly ($P < 0.05$) affected the grain-quality traits, including protein, fat, and fiber contents (Fig. 6). The highest protein contents were recorded for SD9 under 50% of irrigation. However, the lowest protein contents were recorded in grains for individual shading of 3 days (Fig. 6a). Under 100% irrigation conditions, a 0.21, 2, 11.52, and 16.15% amplification in protein contents was seen in plants exposed to 3, 6, 9, and 12 days of shading, as compared with SD0, respectively. While under 25% irrigation, plants displayed a 0.98, 4.62, and 0.21% increase under 3, 9, and 12 days of shading, respectively. The increment in protein contents for normal light-treated plants of 17.15, 17.52, and 15.94% and SD12-treated plants of 3.94, 8.06, and 6.70% was observed under 25, 50, and 75% irrigation conditions, respectively.

Interestingly, starch contents showed a non-significant difference among different drought and shading treatments

and their interactions (Fig. 6b). Fat and fiber contents were influenced significantly by individual and interactive effects of drought and shading treatments (Fig. 6c). The highest fiber contents were recorded for individual SD12 under 100IR (Fig. 6d). Under 100IR, the fiber contents were continuously amplified as the prolongation of the shaded period as seen by its enhancement (8.21, 18.18, 13.34, and 32.99%) after the respective SD3, SD6, SD9, and SD12, compared to SD0 (individual shading effect). Plants under 25% irrigation showed a response of fiber contents as 3, 6, 9, and 12 days shading increased the fiber contents by -1.58, 0.39, 7.11, and 5.27%, respectively, compared to SD0. The combined effect of drought and shading on the fiber contents was drastic. Under fully irrigated conditions, a decrease of 18.05, 5.59, 9.65, and 24.70% in fat contents were depicted for shading of 3, 6, 9, and 12 days, respectively. The SD12-treated plants showed a reduction of 12.91, 31.04, and 28.25% under 25, 50, and 75% irrigation conditions, respectively. Taken altogether, the grain quality parameters were affected by combined drought and shading, but the effect was different for different indices of quality.
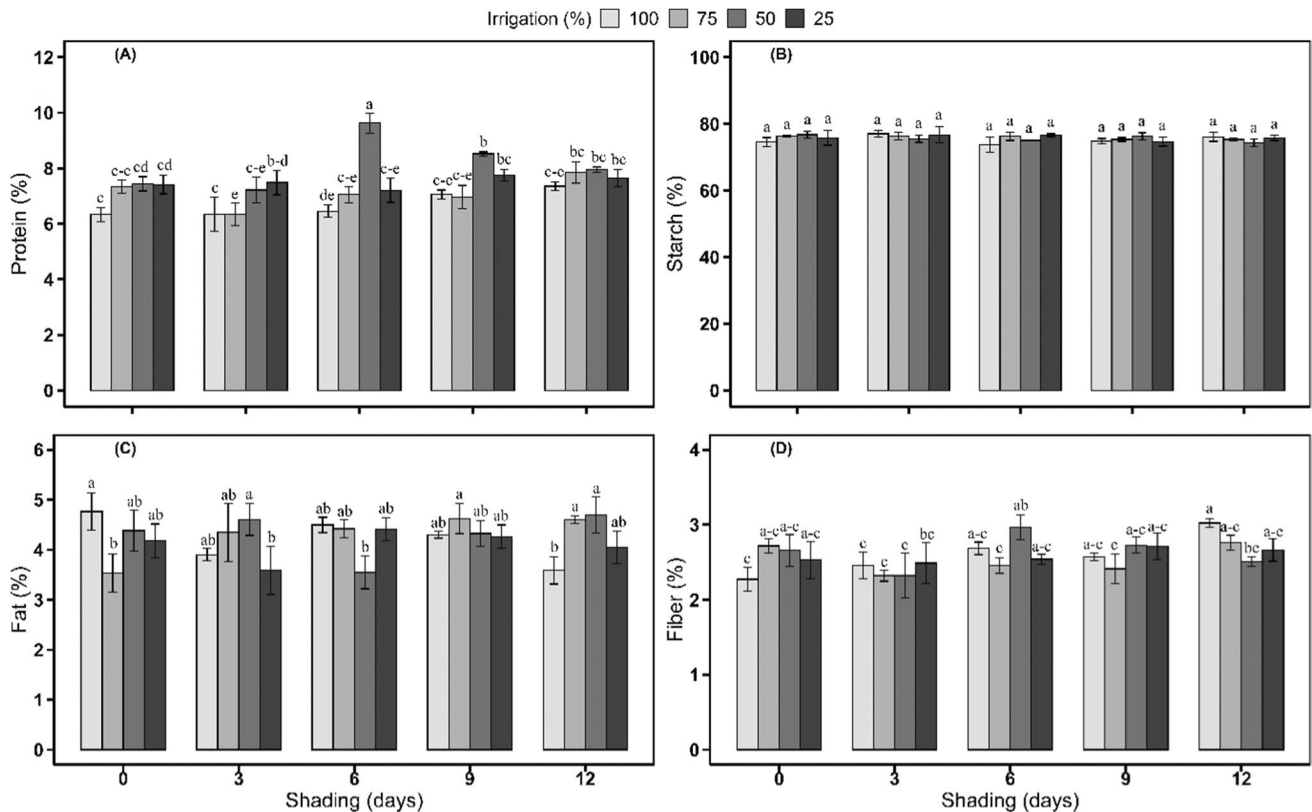

Fig. 6 Effect of shading on grain contents of (**a**) protein, (**b**) starch, (**c**) fat, and (**d**) fiber of maize under different irrigation conditions (100, 75, 50, and 25% irrigation). The values represent the mean ± standard error, and bars sharing the similar letters for a parameter indicate non-significant ($P < 0.05$) differences

3.6 Relationship Between the Observed Parameters

Pearson's correlation analysis revealed that the relative water contents significantly positively correlated with *Pn*, *Tr*, *Ci*, and *gs*. However, a significant negative correlation was observed with SOD, CAT, POD, and MDA contents (Fig. 7). A positive relationship was recorded for *Pn* with *Tr*, *Ci*, and *gs* and a negative correlation with SOD, POD, and CAT. Additionally, *Tr* showed a positive correlation between grain yield and dry matter. The SOD expressed a significant positive correlation ($P > 0.05$) with CAT and POD. The MDA showed a negative relation with relative water contents, photosynthetic parameters, and enzymatic activities.

4 Discussion

The combined drought and shading stresses significantly affected the grain yield and quality of maize by altering the photosynthetic activity. This supports our hypothesis that the combined occurrence of these stresses declined the photosynthetic activity along with grain yield and quality traits. Abiotic stresses in maize lead to a synergistic impact on the plant life cycle, affecting plant growth and development and hence reductions in yield and yield components

(Huang et al. 2014). In our observation, relative water contents showed a declining trend due to drought stress under all shading treatments. These findings contrast with a previous study by Li et al. (2011). Due to the impact of low temperatures on evapotranspiration, differences in relative water content between well-watered and drought treatments were presumably lessened under shading (Chhetri et al. 2022). The photosynthetic characteristics of maize plants under individual shading have been well observed previously (Cerrudo et al. 2013; Gao et al. 2019).

Shading influenced the leaf photosynthesis of maize and weakened the photosynthetic assimilation capacity, resulting in a reduction in grain yield (Ren et al. 2016). However, it is also observed previously that individual shading or low light conditions can enhance the photosynthetic activity of different plants at different growing stages. Asghar et al. (2020) reported that shading pretreatment could enhance photosynthesis at the vegetative stage of soybean. A recent study has found that heterogenic light conditions can enhance the photosynthesis of maize plants, but it depends on the cultivar (Sun et al. 2020). Our results suggest that shading of 9 days under full irrigation showed the highest photosynthetic activity (Fig. 5), which can be explained by the systematic regulation of plants under low light conditions. The morphological modifications also occurred, increasing

Fig. 7 Relationships among relative water content, net photosynthetic rate, antioxidant enzymes, lipid peroxidation, and grain yield. RWC, relative water content; Pn, photosynthetic activity; Tr, transpiration rate; Ci, intracellular CO_2 concentration; gs, stomatal conductance; SOD, superoxide dismutase; CAT, catalase; POD, peroxidase; MDA, malondialdehyde; GY, grain yield; DM, dry matter; HI, harvest index
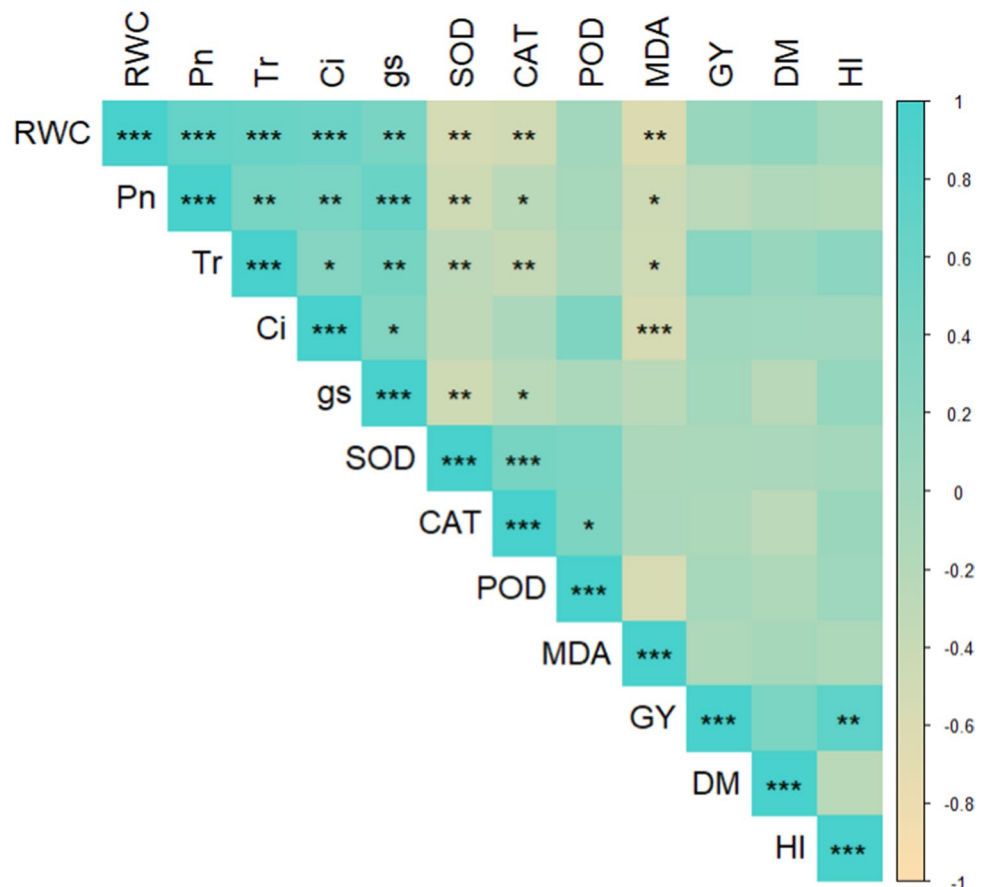
the photosynthesis of shaded plants. Our results indicated that the combined effect of drought and shading drastically influenced photosynthesis and related parameters. The reduction in photosynthesis in combined drought and shading stresses is due to oxidative damage (expressed as MDA contents). These results are in line with Li et al. (2011), in which *Cotinus coggygria* seedlings showed a reduction in net photosynthetic rate due to membrane damage due to lipid peroxidation and increased MDA contents under combined drought and shading stress conditions.

The MDA is considered a by-product of membrane lipid peroxidation (Masia 2003). In this experiment, the presence of drought substantially exacerbated MDA under various shading treatments, indicating oxidative membrane damage (Fazeli et al. 2007). Similar outcomes have also been found in prior studies (Huang et al. 2008). Plants have an efficient mechanism of stress tolerance in which different antioxidant enzymes are produced under stressful environments. The defensive mechanism for stress reduction consists of SOD, POD, and CAT enzymes (Yang et al. 2008). In this study, individual drought stress greatly decreased the activities of the above-mentioned enzymes (SOD, POD, and CAT). Contrastingly, these enzymes increased under individual shading stress (well-watered conditions), coping with the oxidative damages (reduction in MDA contents) and increasing photosynthetic activity. This could be a result of the elevated auxin level, which considerably raised the antioxidant enzyme activity in shaded plants (Shi et al. 2014) as it was principally engaged in the abolition of plants' ROS (Sun et al. 2009). Interestingly, it is found that enzymatic activities were ominously increased under combined drought and shading treatment. However, the increase was not sufficient to cope with the stress-induced oxidative damage and upsurge of MDA contents (Fig. 2).

Combined shading and drought increased the protein contents of maize. This is similar to the previous studies in which shading increased the protein contents of maize grains (Yang et al. 2016). Shifang et al. (2010) also observed that the contents of proteins and their fractions are increased by post-silking shading stress, and the increase was highest in the early grain-filling stage, which is similar to our results. Similarly, drought stress also influenced to increase in the protein contents of maize grains (Lu et al. 2015). Overall, a combination of drought and shading stress exacerbated the grain protein contents.

Changes in light conditions at any developmental stage can affect the normal growth of crop plants. In the current study, combined drought and shading decreased grain yield which is corroborative to previous studies which revealed that low light stress decreased the grain yield in maize (Wang et al. 2020a), wheat (Wang and Lu 2020; Naseer et al. 2021), and soybean (Wang et al. 2020b). Our results indicated that shading stress combined with severe drought (25%

irrigation) conditions decreased grain yield (Table 1), less than the yield reduction in fully irrigated plants. Our study observed increased dry matter production under non-shaded control plants compared to shaded ones. As discussed in a recent study, the increased dry matter in unshaded plants may be due to the increase in nitrogen contents (Huang et al. 2022). However, it is still unclear how the heterogenic light conditions can affect the normal distribution of assimilates and the growth of plants.

All the morpho-physiological parameters observed in this study were associated with estimating their relation and impact on yield components. A positive correlation of photosynthetic parameters (*Pn*, *gs*, and *Tr*) with yield components indicated that the photosynthetic efficiency decreased along with the decrease in yield under the coexistence of drought and shading stresses. We found a similar response; the correlation coefficient was drastically negative between the MDA contents and photosynthetic and relative water contents, which showed the negative correlation of enzymes with photosynthetic activity (Fig. 7). Further studies need to be done to evaluate the shared phenomenon of drought and shading stress which might be helpful for management strategies to cope with the combined drought and shading stresses.

5 Conclusion

An increase in anti-oxidant enzyme activities was noted under combined stresses; however, that was not sufficient to cope with the stress-induced oxidative damage. The oxidative damages (expressed by MDA) and reduction in photosynthetic attributes during the post-silking stage contributed to the grain yield reduction of maize. However, the individual shading stress under well-watered conditions increased the photosynthetic activity and abolition of reactive oxygen species by the antioxidant defense system. The combined drought and shading stress increased the protein contents of grains. Further studies are needed to study the original molecular mechanisms of the combined impact of drought and shading. Furthermore, the low light conditions in plant canopy under drought stress can affect the normal distribution of assimilates and systematic regulation of photosynthesis.

Data Availability The authors confirm that the data supporting the findings of this study are available from corresponding authors upon reasonable request.

Declarations

Conflict of Interest The authors declare no competing interests.

References

Albert RA, Waas NE, Langer S, Pavlons SC, Feldner JL, Rossello-Mora R, Busse HJ (2010) Labrys wisconsinensis sp nov, a budding bacterium isolated from Lake Michigan water, and emended description of the genus Labrys. Int J Syst Evol Microbiol 60:1570–1576

Allan RP, Hawkins E, Bellouin N, Collins B (2021) IPCC, 2021: summary for Policymakers

An YY, Liang ZS (2012) Staged strategy of plants in response to drought stress. J Appl Ecol 23:2907–2915

Aranda I, Pardos M, Puértolas J, Jiménez MD, Pardos JA (2007) Water-use efficiency in cork oak (Quercus suber) is modified by the interaction of water and light availabilities. Tree Physiol 27:671–677. https://doi.org/10.1093/treephys/27.5.671

Asghar MA, Du J, Jiang H, Li Y, Sun X, Shang J, Liu J, Liu W, Imran S, Iqbal N, Ahmad B, Hussain S, Yu L, Liu C, Yang W (2020) Shade pretreatment enhanced drought resistance of soybean. Environ Exp Bot 171:103952. https://doi.org/10.1016/j.envexpbot.2019.103952

Ashraf M, Harris PJC (2013) Photosynthesis under stressful environments: an overview. Photosynthetica 51:163–190. https://doi.org/10.1007/s11099-013-0021-6

Başlar M, Ertugay MF (2011) Determination of protein and gluten quality-related parameters of wheat flour using near-infrared reflectance spectroscopy (NIRS). Turk J Agirc for 35:139–144. https://doi.org/10.3906/tar-0912-507

Cakmak I, Marschner H (1992) Magnesium deficiency and high light intensity enhance activities of superoxide dismutase, ascorbate peroxidase, and glutathione reductase in bean leaves. Plant Physiol 98:1222–1227. https://doi.org/10.1104/pp.98.4.1222

Cerrudo A, Di Matteo J, Fernandez E, Robles M, Olmedo Pico L, Andrade F (2013) Yield components of maize as affected by short shading periods and thinning. Crop Pasture Sci 64:580. https://doi.org/10.1071/CP13201

Chhetri M, Fontanier C, Moss JQ, Wu Y (2022) Effects of combined shade and drought stress on turf-type bermudagrasses. Int Turfgrass Soc Res J 14:194–204. https://doi.org/10.1002/its2.68

Djanaguiraman M, Annie Sheeba J, Durga Devi D, Bangarusamy U (2009) Cotton leaf senescence can be delayed by nitrophenolate spray through enhanced antioxidant defence system. J Agron Crop Sci 195:213–224. https://doi.org/10.1111/j.1439-037X.2009.00360.x

Farooq M, Bramley H, Palta JA, Siddique KH (2011) Heat stress in wheat during reproductive and grain-filling phases. Crit Rev Plant Sci 30:491–507. https://doi.org/10.1080/07352689.2011.615687

Fazeli F, Ghorbanli M, Niknam V (2007) Effect of drought on biomass, protein content, lipid peroxidation and antioxidant enzymes in two sesame cultivars. Biol Plantarum 51:98–103. https://doi.org/10.1007/s10535-007-0020-1

Franco AC, Nobel PS (1989) Effect of nurse plants on the microhabitat and growth of cacti. J Ecol 77:870–886. https://doi.org/10.2307/2260991

Gao J, Shi J, Dong S, Liu P, Zhao B, Zhang J (2017) Grain yield and root characteristics of summer maize (Zea mays L.) under shade stress conditions. J Agron Crop Sci 203:562–573. https://doi.org/10.1111/jac.12210

Gao Z, Sun L, Ren J-H, Liang XG, Shen S, Lin S, Zhao X, Chen X-M, Zhou S-L (2019) Detasseling increases kernel number in maize under shade stress. Agric for Meteorol 280:107811. https://doi.org/10.1016/j.agrformet.2019.107811

Gao J, Liu Z, Zhao B, Dong ST, Liu P, Zhang JW (2020) Shade stress decreased maize grain yield, dry matter, and nitrogen accumulation. Agron J 112:2768–2776. https://doi.org/10.1002/agj2.20140

Gupta A, Rico-Medina A, Caño-Delgado AI (2020) The physiology of plant responses to drought. Science 368:266–269. https://doi.org/10.1126/science.aaz7614

Holmgren M (2000) Combined effects of shade and drought on tulip poplar seedlings: trade-off in tolerance or facilitation? Oikos 90:67–78. https://doi.org/10.1034/j.1600-0706.2000.900107.x

Holmgren M, Gómez-Aparicio L, Quero JL, Valladares F (2012) Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. Oecologia 169:293–305. https://doi.org/10.1007/s00442-011-2196-5

Huang X, Yin C, Duan B, Li C (2008) Interactions between drought and shade on growth and physiological traits in two Populus cathayana populations. Can J Forest Res 38:1877–1887. https://doi.org/10.1139/X08-040

Huang J-K, Jiang J, Wang J-X, Hou L-L (2014) Crop diversification in coping with extreme weather events in China. J Integra Agric 13:677–686. https://doi.org/10.1016/s2095-3119(13)60700-5

Huang S-R, Ai Y, Du J-B, Yu L, Wang X-C, Yang W-Y, Sun X (2022) Photosynthetic compensation of maize in heterogeneous light is impaired by restricted photosynthate export. Plant Physiol Biochem 192:50–56. https://doi.org/10.1016/j.plaphy.2022.09.026

Jia S-F, Li C-F, Dong S-T, Zhang J-W (2011) Effects of shading at different stages after anthesis on maize grain weight and quality at cytology level. Agric Sci China 10:58–69. https://doi.org/10.1016/S1671-2927(11)60307-6

Jiang C-D, Wang X, Gao H-Y, Shi L, Chow WS (2011) Systemic regulation of leaf anatomical structure, photosynthetic performance, and high-light tolerance in sorghum. Plant Physiol 155:1416–1424. https://doi.org/10.1104/pp.111.172213

Lei A, Hu Z, Wong Y, Tam NF (2006) Antioxidant responses of microalgal species to pyrene. J Appl Phycol 18:67–78. https://doi.org/10.1007/s10811-005-9016-4

Lesk C, Rowhani P, Ramankutty N (2016) Influence of extreme weather disasters on global crop production. Nature 529:84–87. https://doi.org/10.1038/nature16467

Li Y, Zhao H, Duan B, Korpelainen H, Li C (2011) Effect of drought and ABA on growth, photosynthesis and antioxidant system of Cotinus coggygria seedlings under two different light conditions. Enviro Exp Bot 71:107–113. https://doi.org/10.1016/j.envexpbot.2010.11.005

Lu D, Cai X, Zhao J, Shen X, Lu W (2015) Effects of drought after pollination on grain yield and quality of fresh waxy maize. J Sci Food Agric 95:210–215. https://doi.org/10.1002/jsfa.6709

Masia A (2003) Physiological effects of oxidative stress in relation to ethylene in postharvest produce. Postharvest oxidative stress in horticultural crops, pp 165–197

Mu H, Jiang D, Wollenweber B, Dai T, Jing Q, Cao W (2010) Long-term low radiation decreases leaf photosynthesis, photochemical efficiency and grain yield in winter wheat. J Agron Crop Sci 196:38–47. https://doi.org/10.1111/j.1439-037X.2009.00394.x

Naseer MA, Hussain S, Nengyan Z, Ejaz I, Ahmad S, Farooq M, Xiaolong R (2021) Shading under drought stress during grain filling attenuates photosynthesis, grain yield and quality of winter wheat in the Loess Plateau of China. J Agron Crop Sci 208:255–263. https://doi.org/10.1111/jac.12563

Naumann G, Alfieri L, Wyser K, Mentaschi L, Betts RA, Carrao H, Spinoni J, Vogt J, Feyen L (2018) Global changes in drought conditions under different levels of warming. Geophys Res Lett 45:3285–3296. https://doi.org/10.1002/2017GL076521

Pospisilova J (2003) Larcher, W.: Physiological plant ecology. Ecophysiology and Stress Physiology of Functional Groups. Fourth

Edition Biol Plant 46:500–500. https://doi.org/10.1023/B:BIOP.0000041119.93332.43

Ren B, Cui H, Camberato JJ, Dong S, Liu P, Zhao B, Zhang J (2016) Effects of shading on the photosynthetic characteristics and mesophyll cell ultrastructure of summer maize. Sci Nat 103:67. https://doi.org/10.1007/s00114-016-1392-x

RStudio Team (2020) RStudio: Integrated Development for R. RStudio, PBC, Boston. http://www.rstudio.com/

Setter TL, Flannigan BA, Melkonian J (2001) Loss of kernel set due to water deficit and shade in maize. Crop Sci 41:1530–1540. https://doi.org/10.2135/cropsci2001.4151530x

Shabbir R, Singhal RK, Mishra UN, Chauhan J, Javed T, Hussain S, Kumar S, Anuragi H, Lal D, Chen P (2022) Combined abiotic stresses: challenges and potential for crop improvement. Agronomy 12:2795. https://doi.org/10.3390/agronomy12112795

Shi H, Chen L, Ye T, Liu X, Ding K, Chan Z (2014) Modulation of auxin content in Arabidopsis confers improved drought stress resistance. Plant Phyisol Biochem 82:209–217. https://doi.org/10.1016/j.plaphy.2014.06.008

Shifang J, Shuting D, Kongjun W, Jiwang Z, Congfeng L (2010) Effect of shading on grain quality at different stages from flowering to maturity in maize. Euorpe PMC Plus. https://europepmc.org/article/cba/648106. Accessed 18 Sept 2022

Shokat S, Großkinsky DK, Roitsch T, Liu F (2020) Activities of leaf and spike carbohydrate-metabolic and antioxidant enzymes are linked with yield performance in three spring wheat genotypes grown under well-watered and drought conditions. BMC Plant Bio 20:400. https://doi.org/10.1186/s12870-020-02581-3

Shokat S, Novák O, Široká J, Singh S, Gill KS, Roitsch T, Großkinsky DK, Liu F (2021) Elevated CO2 modulates the effect of heat stress responses in Triticum aestivum by differential expression of an isoflavone reductase-like gene. J Exp Bot 72:7594–7609. https://doi.org/10.1093/jxb/erab247

Smith T, Huston M (1990) A theory of the spatial and temporal dynamics of plant communities Progress in theoretical vegetation science. Springer, pp 49–69

Song X, Zhou G, He Q (2021) Critical leaf water content for maize photosynthesis under drought stress and its response to rewatering. Sustainability 13:7218. https://doi.org/10.3390/su13137218

Stanhill G, Cohen S (2001) Global dimming: a review of the evidence for a widespread and significant reduction in global radiation with discussion of its probable causes and possible agricultural consequences. Agric for Meterol 107:255–278. https://doi.org/10.1016/S0168-1923(00)00241-0

Su X, Fan X, Shao R, Guo J, Wang Y, Yang J, Yang Q, Guo L (2019) Physiological and iTRAQ-based proteomic analyses reveal that melatonin alleviates oxidative damage in maize leaves exposed to drought stress. Plant Physiol Biochem 142:263–274. https://doi.org/10.1016/j.plaphy.2019.07.012

Sun YP, Zhang ZP, Wang LJ (2009) Promotion of 5-aminolevulinic acid treatment on leaf photosynthesis is related with increase of antioxidant enzyme activity in watermelon seedlings grown under shade condition. Photosynthetica 47:347. https://doi.org/10.1007/s11099-009-0055-y

Sun X, Huang S-R, Ai Y, Zhang E-Z, Wang X-C, Du J-B, Yang W-Y (2020) Comparative study on the different responses of maize photosynthesis to systemic regulation under light heterogeneity.

Plant Sci 301:110666. https://doi.org/10.1016/j.plantsci.2020.110666

Tattini M, Loreto F, Fini A, Guidi L, Brunetti C, Velikova V, Gori A, Ferrini F (2015) Isoprenoids and phenylpropanoids are part of the antioxidant defense orchestrated daily by drought-stressed Platanus × acerifolia plants during Mediterranean summers. New Phytol 207:613–626. https://doi.org/10.1111/nph.13380

Wang S, Lu Y (2020) Post-silking shading stress affects leaf nitrogen metabolism of spring maize in Southern China. Plants 9:210. https://doi.org/10.3390/plants9020210

Wang X, Wu X, Guohui D, Yang F, Yong T, Wang X, Yang W (2020) Analysis of grain yield differences among soybean cultivars under maize–soybean intercropping. Agronomy 10:110. https://doi.org/10.3390/agronomy10010110

Wang Y, Zhang Z, Liang Y, Han Y, Han Y, Tan J (2020) High potassium application rate increased grain yield of shading-stressed winter wheat by improving photosynthesis and photosynthate translocation. Front Plant Sci 11:134. https://doi.org/10.3389/fpls.2020.00134

Yang Y, Han C, Liu Q, Lin B, Wang J (2008) Effect of drought and low light on growth and enzymatic antioxidant system of Picea asperata seedlings. Acta Physiol Plant 30:433–440. https://doi.org/10.1007/s11738-008-0140-z

Yang H, Shi Y, Xu R, Lu D, Lu W (2016) Effects of shading after pollination on kernel filling and physicochemical quality traits of waxy maize. Crop J 4:235–245. https://doi.org/10.1016/j.cj.2015.12.004

Yao X, Li C, Li S, Zhu Q, Zhang H, Wang H, Yu C, Martin S, Xie F (2017) Effect of shade on leaf photosynthetic capacity, light-intercepting, electron transfer and energy distribution of soybeans. Plant Growth Regul 83(3):409–416. https://doi.org/10.1007/s10725-017-0307-y

Yao X, Zhou H, Zhu Q, Li C, Zhang H, Wu J-J, Xie F (2017) Photosynthetic response of soybean leaf to wide light-fluctuation in maize-soybean intercropping system. Front Plant Sci 8:1695. https://doi.org/10.3389/fpls.2017.01695

Zhang JZ, Shi L, Shi AP, Zhang QX (2004) Photosynthetic responses of four Hosta cultivars to shade treatments. Photosynthetica 42:213–218. https://doi.org/10.1023/B:PHOT.0000040592.10133.ee

Zhang J, Dong S, Wang K, Hu C, Liu P (2006) Effects of shading on the growth, development and grain yield of summer maize. J Appl Ecol 17:657–662

Zhang J-W, Dong S-T, Wang K-J, Hu C-H, Liu P (2008) Effects of shading in field on key enzymes involved in starch synthesis of summer maize. Acta Agron Sin 34:1470–1474. https://doi.org/10.3724/SP.J.1006.2008.01470