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RESEARCH ARTICLE

Suppression of photorespiratory metabolism by low O_2 and presence of aminooxyacetic acid induces oxidative stress in *Arabidopsis thaliana* leaves

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Abstract
Photorespiration, an essential component of plant metabolism, was upregulated under abiotic stress conditions, such as high light or drought. One of the signals for such upregulation was the rise in reactive oxygen species (ROS). Photorespiration was expected to mitigate oxidative stress by reducing ROS levels. However, it was unclear if ROS levels would increase when photorespiration was lowered. Our goal was to examine the redox status in leaves when photorespiratory metabolism was restricted under low O_2 (medium flushed with N_2 gas) or by adding aminooxyacetic acid (AOA), a photorespiratory inhibitor. We examined the impact of low O_2 and AOA in leaves of *Arabidopsis thaliana* under dark, moderate, or high light. Down-regulation of typical photorespiratory enzymes, including catalase (CAT), glycolate oxidase (GO), and phosphoglycolate phosphatase (PGLP) under low O_2 or with AOA confirmed the lowering of photorespiratory metabolism. A marked increase in ROS levels (superoxide and H_2O_2) indicated the induction of oxidative stress. Thus, our results demonstrated for the first time that restricted photorespiratory conditions increased the extent of oxidative stress. We propose that photorespiration is essential to sustain normal ROS levels and optimize metabolism in cellular compartments of *Arabidopsis* leaves.

Keywords Reactive oxygen species · High light · Photorespiration · Aminooxyacetic acid · Low oxygen · Anoxia

Introduction

Abiotic or biotic stress often modulates metabolic components, including photorespiration, by raising reactive oxygen species (ROS) levels. Exposure to such stress can harm the photosynthetic machinery over time, especially photosystem II, leading to photoinhibition (Gururani et al. 2015; Szymańska et al. 2017; Gunell et al. 2023). Although it is a significant source of ROS by itself, photorespiration could help to restrict ROS levels (Voss et al. 2013; Sunil et al. 2019). Photorespiration utilized ATP/NADPH/reduced ferredoxin, thus forming a sink for excess energy. Strong photorespiratory flux helped avoid excessive reduction and photoinhibition of the chloroplastic electron transport chain (Saji et al. 2017; Huang et al. 2019). Thus, it was clear that photorespiratory metabolism was upregulated in response to elevated ROS levels under oxidative or photo-oxidative stress (Sunil et al. 2019; Bapatla et al. 2021). Though it implied that any restriction of photorespiration should increase the cellular ROS levels, there were no studies to prove or disprove such a possibility. We, therefore, attempted to examine the consequences of restricted photorespiration in ROS levels of leaves. In contrast to the extensive literature on the minimization of ROS/oxidative stress by photorespiration, very few attempts were made to assess the consequences of reduced photorespiration on the redox status of plant leaves.

Several methods were employed to restrict photorespiration. These included photorespiratory mutants, high CO_2, low O_2, and photorespiratory inhibitors. Each strategy has its advantages as well as drawbacks. Exposure to elevated CO_2 required a sealed growing chamber with CO_2 levels of at least 3000 μL/L (Queval et al. 2007). The oxygen content of the medium could be reduced by nitrogen purging, low-pressure boiling, and sonication (Butler et al. 1994). Purging the solution for 20 to 30 min with N_2 gas was the quickest and most efficient technique to reduce the amount of O_2 in

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the solution (Riazunnisa et al. 2006; Ershova et al. 2011; Vergara et al. 2012).

Photorespiration was limited by inhibitors that interfered with the enzymes or transporters in particular organelles. Examples are isonicotinyl hydrazide (INH), glycine hydroxamate (GHA), aminoacetonitrile (AAN), aminooxyacetic acid (AOA), α-hydroxy-2-pyridinemethansulfonic acid (HPMS), and sodium fluoride (NaF). Among these, AAN, GHA, and INH interfered with glycine conversion to serine (Riazunnisa et al. 2006; Kleczkowski et al. 1987; Kang et al. 2018). NaF inhibited PGLP activity, whereas HPMS interfered with the glycolate oxidase (Hewitt et al. 1990). AOA blocked glycine oxidation to inhibit the photorespiratory pathway (Kleczkowski et al. 1987; Han et al. 2018).

Photorespiratory mutants lacking essential genes were another approach for studying photorespiration (Timm and Bauwe 2013; Eisenhut et al. 2019). Most of these photorespiratory mutants could not grow in regular air, except *hpr1* (Wang et al. 2022). As a result, the photorespiratory mutants needed to be raised at high CO_2. When these plants were moved from high CO_2 to normal air, they manifested stress symptoms, including chlorotic and bleached leaves (Timm et al. 2012).

After evaluating available techniques reported in the literature, we employed lowered O_2 and treatment with a photorespiratory inhibitor. There were no attempts to examine the status of photorespiration in lowered O_2/anoxia. A few reports showed the effect of photorespiratory inhibitors on photosynthesis, but none of them checked the ROS levels under such suppressed photorespiratory conditions (Riazunnisa et al. 2006; Kang et al. 2018). Ours is the first attempt to assess the redox status of leaves when the photorespiratory metabolism was interrupted by AOA or low O_2. We are also the first to demonstrate photorespiration's inverse relationship with leaf ROS levels. The status of key photorespiratory enzymes and ROS levels were evaluated in *Arabidopsis* leaves on treatment with low O_2 and AOA and exposing leaves to dark, ML, and HL. The photorespiratory enzymes in different organelles, such as CAT, GO, and PGLP, were downregulated. A marked increase in ROS levels (superoxide and H_2O_2) was noticed, reflecting the induction of severe oxidative stress. Our results emphasize that photorespiration helps to minimize ROS levels, while restricted photorespiration leads to an increase in ROS and oxidative stress.

Materials and methods

Plant growth

Seeds of *Arabidopsis thaliana* wild type (Columbia) (from *Arabidopsis* Biological Resource Centre, Ohio State University, Columbus, Ohio) were sown in a mixture of vermiculite, perlite, and soilrite (1:1:1) in plastic disposable pots and kept at 4˚C in the dark for 48 h. The seedings were transferred to the pots, and the plants were grown. After 30 days of germination, individual plants were transferred into the disposable pots containing soil mixture and raised under a photoperiod of 8 h light/16 h dark and a temperature of 20–22˚C. The nutrient solution was applied twice a week, as suggested by Somerville (1982). Seven to eight-week-old plants provided the leaves for the experiments.

For treatment at low $O_{2,}$ the Petri dishes were sealed with parafilm, and the incubation medium (2 mM potassium phosphate buffer pH 6.5, 1 mM KCl, and 1 mM $CaCl_2$) was purged with N_2 gas for 30 min. In the case of AOA, leaves were incubated in dark or moderate light (ML, 150 µmol m^{-2} s^{-1}) or high light (HL, 600 µmol m^{-2} s^{-1}) for 3 h. At the end of treatment, leaves were frozen, stored in liquid $N_{2,}$ and to be used later.

Chemicals/Antibodies/Primers

AOA and premix-BCIP/NBT solutions were from Sigma Aldrich (USA). Antibodies and primers of photorespiratory enzymes were from Agrisera AB (Sweden) and Allied Scientific Products (India), respectively. Others were of analytical grade from India.

Levels of ROS (H_2O_2 and superoxide)

Nitroblue tetrazolium chloride (NBT) and 3,3'-diaminobenzidine (DAB) were used to monitor the accumulation of superoxide or H_2O_2, respectively. Superoxide or H_2O_2 levels were quantified as described (Kwon et al. 2013; Bapatla et al. 2021). Standard curves generated with known amounts of H_2O_2/NBT were used for calculations.

Assays of photorespiratory enzymes

The extraction from leaves (100 mg) and enzyme assays were as described (Bapatla et al. 2021). The principles were: GO – glycolate oxidation to glyoxylate (Yamaguchi and Nishimura 2000); catalase - consumption of H_2O_2 monitored at A_{240nm} (Patterson et al. 1984) and PGLP – hydrolysis of phosphoglycolate releasing Pi (Somerville and Ogren 1979).

Glycolate oxidase (GO) activity

100 mg of leaves were homogenized in extraction buffer containing 100 mM HEPES-KOH (pH 7.2), 1 mM EDTA, and 10 mM 2-mercaptoethanol. After centrifugation at 10,000 *g* for 10 min at 4˚C, the supernatant was collected and used for enzyme assay. The reaction mixture contains 100 mM triethanolamine (pH 7.8), 0.75 mM oxidized GSSH, 4 mM phenylhydrazine, 3 mM EDTA, 2.3 mM sodium glycolate,

and supernatant equivalent to 12.5 µg chlorophyll. The reaction was monitored for the increase in absorbance for five minutes at $A_{324\ nm}$. The phenylhydrazine extinction coefficient (16.8 $mM^{-1}\ cm^{-1}$) was used to calculate the enzyme activity (Yamaguchi and Nishimura 2000).

Catalase (CAT) activity

100 mg of leaves were homogenized in an extraction buffer containing 50 mM phosphate buffer (pH 7.0). After centrifugation at 10,000 *g* for 10 min at 4˚C, the supernatant was collected and used for enzyme assay. The reaction mixture contains 50 mM phosphate buffer (pH 7.0), 20 mM H_2O_2, and a supernatant equivalent to 25 µg chlorophyll. The reaction was monitored for the decrease in absorbance for three minutes at $A_{240\ nm}$. The molar extinction coefficient of H_2O_2 (43.6 $M^{-1}\ cm^{-1}$) was used to calculate the enzyme activity (Patterson et al. 1984).

Phosphoglycolate phosphatase (PGLP) activity

100 mg of leaves were homogenized in extraction buffer containing 10 mM HEPES (pH 7.0) at 4˚C. After centrifugation at 20,000 *g* for 10 min at 4˚C, the supernatant was collected and used for enzyme assay. The reaction mixture contains 40 mM sodium cacodylate (pH 6.3), 5 mM HEPES, 0.5 mM EDTA, 5 mM $ZnSO_4$ and a supernatant equivalent to 12.5 µg chlorophyll. The reaction was started by adding 2 mM phosphoglycolate. After five minutes at 25˚C, the reaction was stopped by adding acid molybdate reagent [1:6 mixture of 10% (w/v) ascorbate and 0.42% (w/v) ammonium molybdenum in 1 N sulfuric acid]. The samples were incubated at 45˚C for 20 min, and the released phosphate was measured at A820 nm. A standard curve with known phosphate concentrations was used to determine the enzyme activity (Somerville and Ogren 1979).

Chlorophyll and protein estimation

Chlorophyll was determined by extraction into 80% (v/v) acetone (Arnon 1949). Protein was estimated by the Bradford assay. A standard curve with a known concentration of BSA was used to calculate the protein concentration (Bradford 1976).

Protein and transcript levels

The protein levels of photorespiratory enzymes were studied by Western blotting. The quantification of protein band intensities was done by Image J software. Ponceau-stained gels of Rubisco large subunit were used for normalization (Bapatla et al. 2021).

The extraction of RNA, cDNA synthesis, and sqRT-PCR using primer sequences (Supplementary Table 1) were described earlier (Bapatla et al. 2021). We optimized the number of cycles required for amplification of photorespiratory genes (CAT1, CAT2, GOX1, GOX2, and PGLP1) and actin-8 genes. We did not get much amplification of photorespiratory genes and actin 8 on 32, 34, or 36 cycles. However, the amplification was good at 40 cycles. Image J was used to quantify the transcript level, normalized with actin 8.

Replication and significance

The presented data were averages ± SE from at least three experiments conducted on different days. ANOVA was used to derive *P* values. A *P* value of less than 0.05 was considered significant.

Results

Changes in typical photorespiratory enzymes: activities and protein levels

Among the enzymes studied, PGLP was chloroplastic, while GO and CAT were in peroxisomes. The activities of CAT and PGLP were lowered with AOA (photorespiratory inhibitor) treatment or low O_2, compared to control. The activity of GO was either marginally enhanced or decreased under low O_2, or by AOA (Fig. 1).

To validate the enzyme assay data, we checked the protein levels of GO and CAT under restricted photorespiration. The protein level of PGLP was not checked due to the non-availability of antibodies. Treatment with AOA decreased the GO and CAT proteins, particularly under ML and HL, compared to that of the respective control (Fig. 2). Similarly, the protein levels of CAT were decreased in ML on exposure to low O_2. However, the GO protein levels were marginally increased under HL (Fig. 3).

Transcripts of photorespiratory enzymes

To further validate the enzyme and protein data, we have checked the transcript levels of *CAT1*, *CAT2*, *GOX1*, *GOX2*, and *PGLP1* under restricted photorespiratory conditions. The transcripts of *CAT2*, *GOX1*, and *GOX2* decreased when treated with AOA compared to the control. The downregulation of these transcripts was pronounced under HL. Similarly, the transcripts of *CAT1* and *PGLP1* were also downregulated by AOA under HL (Fig. 4). When treated with low O_2, the transcripts of *CAT1*, *CAT2*, and *PGLP1* were downregulated under ML and HL conditions. In contrast, transcripts of *GOX1*/*GOX2* were upregulated

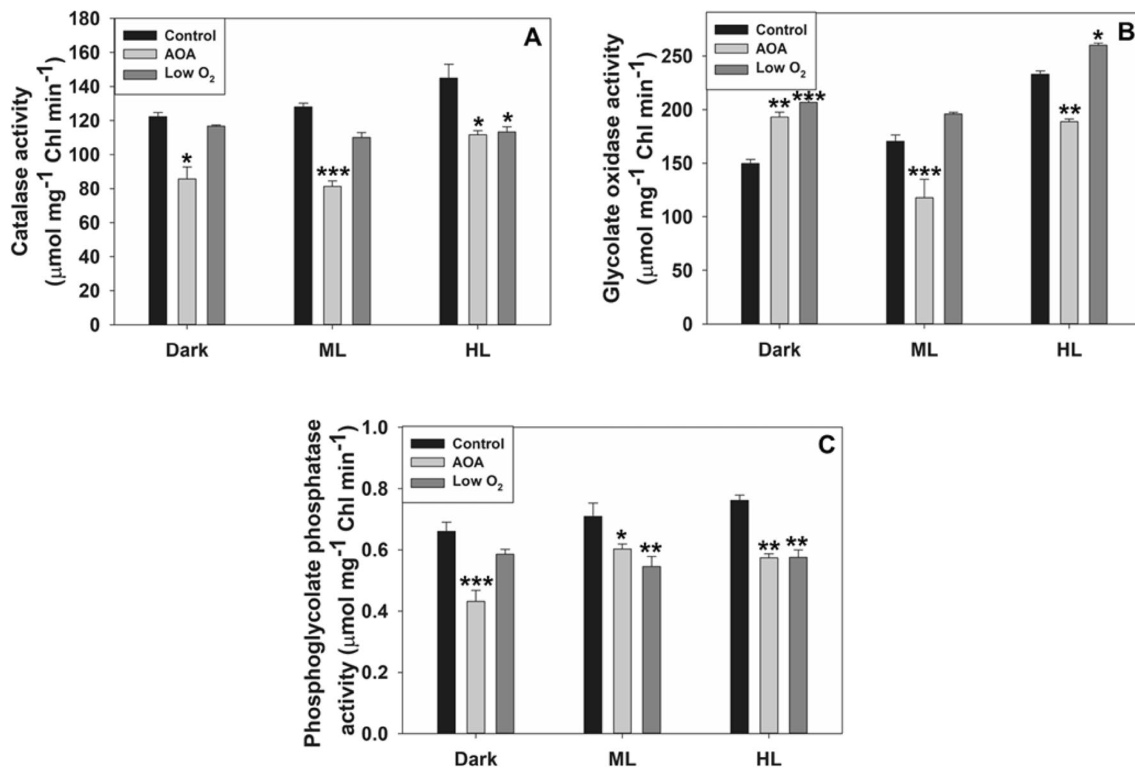

Fig. 1 The activities of key photorespiratory enzymes, peroxisomal CAT/ glycolate oxidase (GO) **A/B**, chloroplastic phosphoglycolate phosphatase (PGLP) **C,** in leaves on treatment with aminooxyacetic acid (AOA) or low O_2 for 3 h under dark, moderate light (ML, 150 µmol m^{-2} s^{-1}), or high light (HL, 600 µmol m^{-2} s^{-1}). Data were averages ± SE of three independent experiments. Wherever relevant, the significance of AOA or low O_2 effects compared to control are indicated. *$P<0.05$; **$P<0.01$, ***$P<0.001$

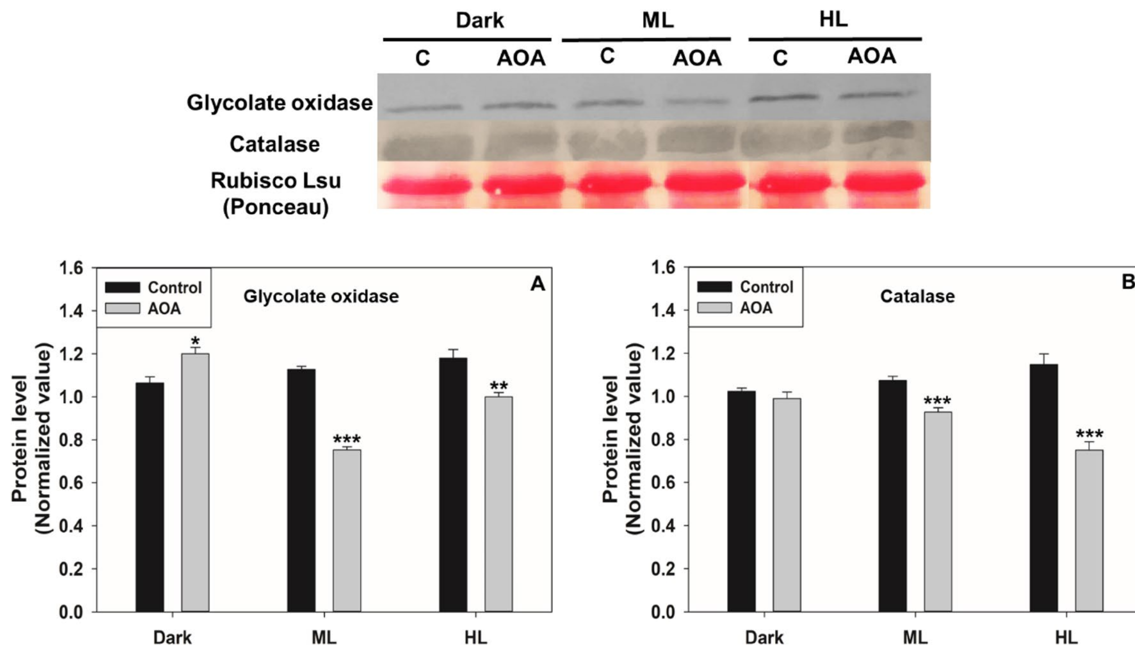

Fig. 2 The protein levels of GO and CAT on exposure to AOA. Ponceau staining was done to show equal loading (Top Panel). The proteins levels were normalized using Rubisco large subunit and quantified by Image J (Bottom Panel). Other details, including the significance were as in Fig. 1 and Materials and Methods

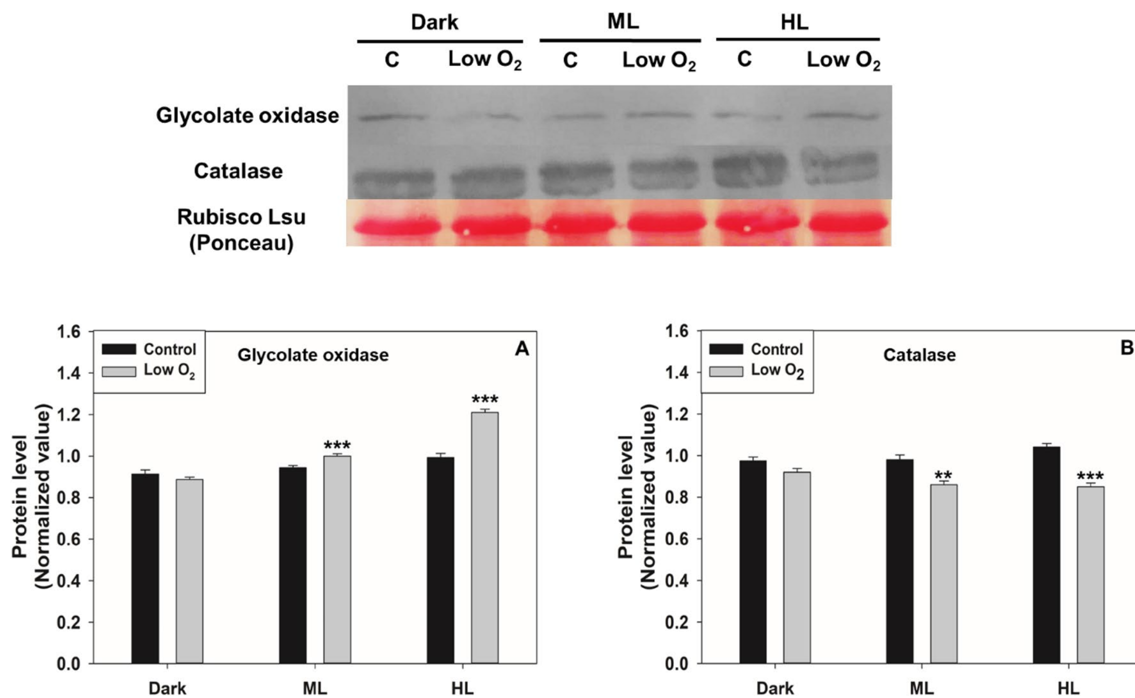

Fig. 3 The protein levels of GO and CAT on exposure to low O_2. Ponceau staining was done to show equal loading (Top Panel). The proteins levels were normalized using Rubisco large subunit and quantified by Image J (Bottom Panel). Other details, including the significance were as in Fig. 1 and Materials and Methods

(Fig. 5). The fold-change of the transcripts was calculated after normalization with reference to actin 8.

ROS accumulation in leaves

Superoxide and H_2O_2 levels increased markedly in ML and HL, as indicated by NBT or DAB staining (Fig. 6). Superoxide content of leaves rose by 2 to 3-fold with AOA or low O_2 (Fig. 7A). Similar to this, DAB staining revealed that the H_2O_2 level in *Arabidopsis* leaves was also enhanced by 2 to 3-fold when treated with AOA or low O_2 under HL (Fig. 7B). The levels of superoxide were far higher than those of H_2O_2 in *Arabidopsis* leaves.

Discussion

Upregulation of photorespiration under abiotic or biotic stress was well established. It was envisaged that such upregulation could adapt to the oxidative stress challenge (Voss et al. 2013; Sunil et al. 2019). However, whether photorespiration can modulate leaf redox in return was unclear. The present article is the first attempt to assess the redox status of leaves when the photorespiratory metabolism is interrupted.

Evidence of suppression of selected photorespiratory enzyme components

Two approaches to limit photorespiration were employed, namely low O_2 and incubation with AOA. Low O_2 levels were caused by purging with N_2 gas that slowed the activity of RuBP oxygenase. On the other hand, AOA blocked the glycine oxidation to ammonia, a critical step in the photorespiratory pathway. We focussed on CAT/GO in peroxisomes and PGLP in chloroplasts. Marked suppression of enzyme components related to GO, CAT, and PGLP confirmed that the photorespiratory metabolism was restricted under low O_2 (Figs. 1, 3 and 5). Similarly, the use of AOA too ensured the down-regulation of photorespiration (Figs. 1, 2 and 4).

The existing literature on the pattern of GO activity under low O_2 or hypoxia was ambiguous. There was a marked upregulation of GO gene expression in *Arabidopsis* under hypoxia (Engqvist et al. 2015). When roots were flooded, creating anoxia, there was a decrease in the GO activity in barley and common bean plants (Yordanova et al. 2003; Posso et al. 2018). Since these studies on the responses to low O_2 (anoxia) focussed on roots, they may not all be relevant, as we studied leaves. Studies made with rice and *Hibiscus hamabo* seedlings observed a slight transient increase in GO activity, followed by a decrease (Igamberdiev et al. 1991; Wu et al. 2013). Our results demonstrated a downregulation of not only CAT but also PGLP under low O_2,

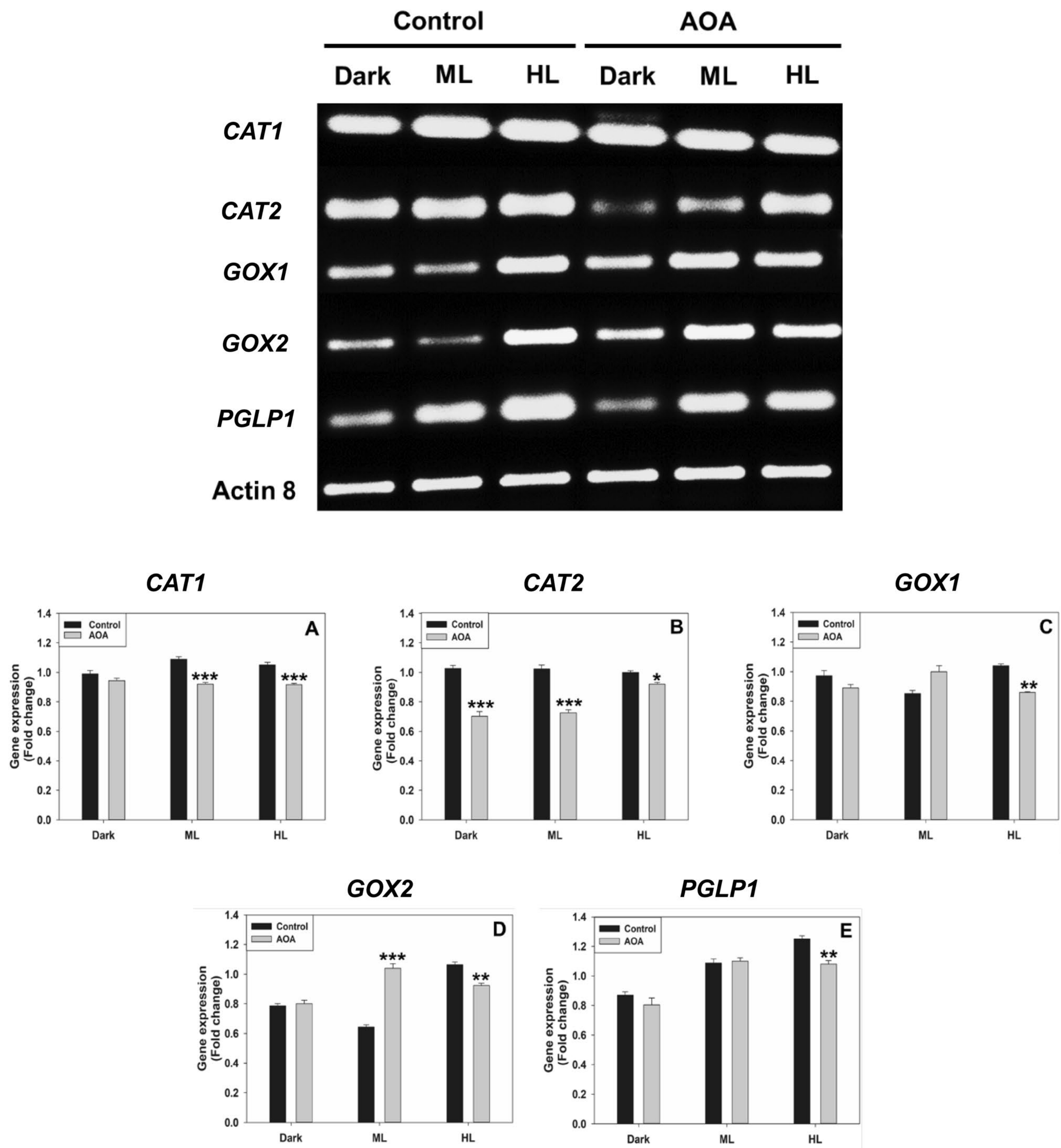

Fig. 4 The transcript levels of *CAT1*, *CAT2*, *GOX1*, *GOX2*, and *PGLP1* on exposure to AOA under dark, moderate, or high light (Top Panel). The fold-change was calculated after normalization with reference to actin 8 (Bottom Panel). Other details, including the significance were as in Fig. 1 and Materials and Methods

confirming that the use of low O_2 was effective in lowering photorespiratory metabolism in *Arabidopsis* leaves.

Similarly, there were attempts to restrict photorespiration using suitable inhibitors. For e.g., AOA and PPT treatment decreased photosynthesis and stomatal conductance/ transpiration while decreasing the CAT and Rubisco activity in *Zea mays*, *Amaranthus palmeri*, and *Chlamydomonas reinhardtii* (González-Moro et al. 1993, 1997; Coetzer and Al-Khatib 2001; Goyal 2002). Glycidate, an inhibitor of glycolate synthesis, restricted photorespiration and increased the photosynthetic rate in tobacco (Zelitch 1974). Our observations with AOA complement the earlier work that an appropriate compound can restrict photorespiration.

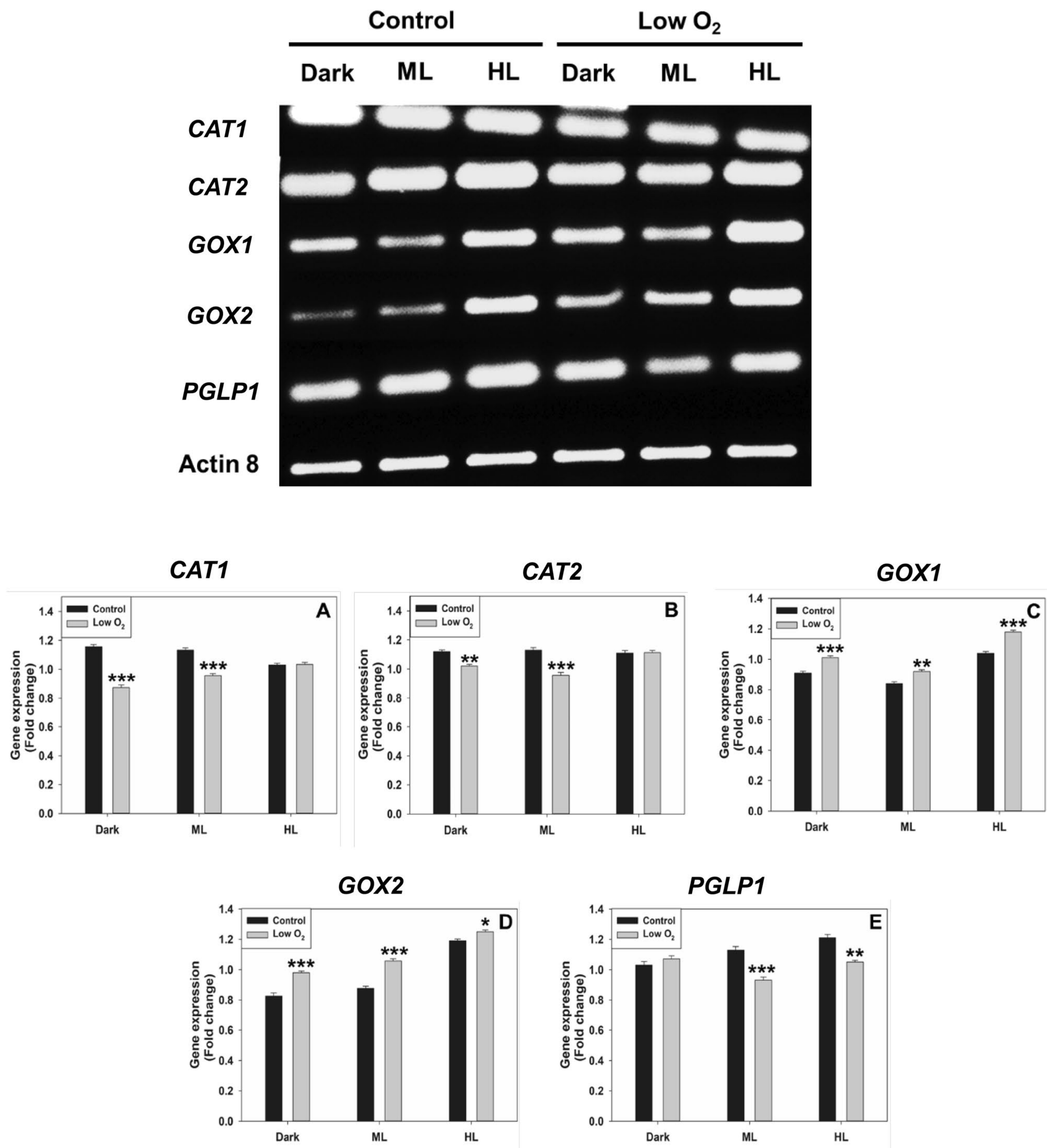

Fig. 5 The transcript levels of *CAT1*, *CAT2*, *GOX1*, *GOX2*, and *PGLP1* on exposure to low O_2 under dark, moderate, or high light (Top Panel). The fold-change was calculated after normalization with reference to Actin 8 (Bottom Panel). Other details, including the significance were as in Fig. 1 and Materials and Methods

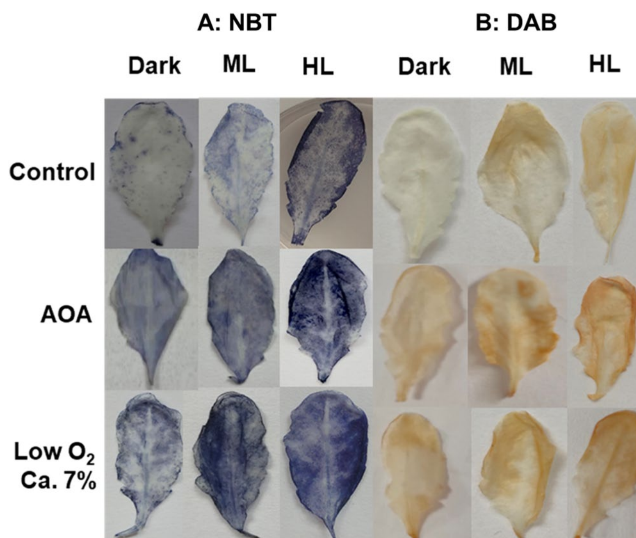

Fig. 6 The accumulation of superoxide and H_2O_2 in *Arabidopsis* leaves, visualized by NBT and DAB staining. The leaves were treated with AOA or low O_2 and exposed to moderate light (ML) or high light (HL). Other details were as in Fig. 1 and Materials and Methods

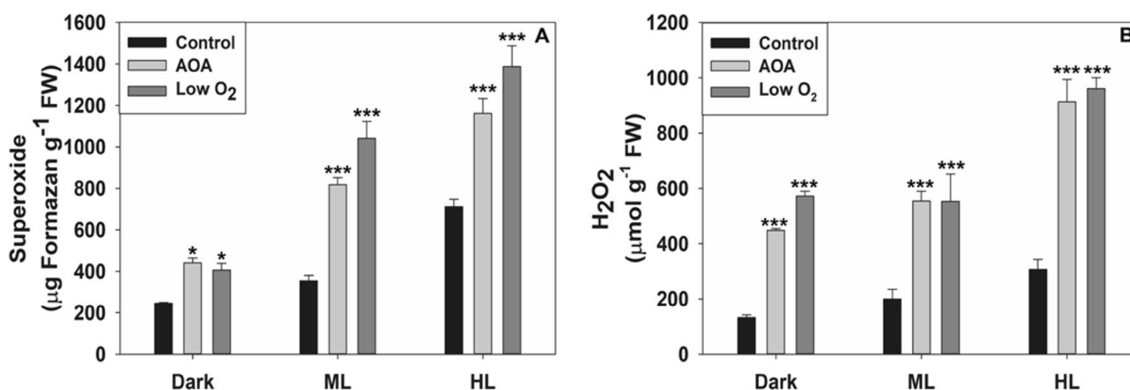

Fig. 7 Superoxide and H_2O_2 levels were quantified from NBT and DAB-stained leaves on exposure to AOA and low O_2. Other details including the significance were as in Fig. 1 and Materials and Methods

ROS accumulation under restricted photorespiration

Whether the incubation was in the dark or in the light, the levels of ROS (H_2O_2 and superoxide) increased considerably when photorespiration was restricted by low O_2 or AOA (Figs. 6 and 7). The majority of the reports typically indicated an increase in ROS under hypoxia in several plants: pea, soybean, *Arabidopsis thaliana*, rice, and tobacco (Ershova et al. 2011; Kamal and Komatsu 2015; Paradiso et al. 2016; Liu et al. 2017; Yamauchi et al. 2017; Jayawardhane et al. 2020; Liu et al. 2023).

One of the reasons for elevated ROS under flood and hypoxia was the decrease in the CAT activity, as in lentil, rice, and lettuce (Tang et al. 2015; Bharadwaj et al. 2023; Liu et al. 2023). Glufosinate treatment in *Amaranthus palmeri* led to the accumulation of superoxide and H_2O_2 (ROS) and downregulated the photosynthetic rate (Takano et al. 2019, 2020). Photorespiratory mutants, like *hpr1*, accumulated ROS, which was detrimental to metabolism and growth, under high light (Wang et al. 2022).

Under ambient air, photorespiration occurs, but it is reduced under high CO_2 conditions (Wujeska-Klause et al. 2019; Celebi-Ergin et al. 2022). Photorespiration could be minimal once photosynthesis is saturated at high CO_2 (Lenka et al. 2019; Marçal et al. 2021). However, the advantages of elevated CO_2 depend on the nitrogen and phosphate status of leaves (Tcherkez et al. 2020). The benefits would not be available if elevated CO_2 were not well-supplemented with nitrogen and phosphorus. In an analogy to our approach, a question arises about the consequences of exposing plants to high CO_2. Since RuBP oxygenase is still functional even under high CO_2, photorespiratory metabolism continues to be necessary to ensure the conversion of 2-PG to 3-PGA with the help of enzymes located in peroxisomes, mitochondria and chloroplasts (Timm and Bauwe 2013; Timm and Hagemann 2020).

There are contrasting claims about the effect of elevated CO_2 on oxidative stress. Oxidative stress was increased at high CO_2, as indicated by increased protein carbonylation and ROS accumulation in *Arabidopsis*, soybean and pea (Qiu et al. 2008; Ershova et al. 2011). In contrast, increased CO_2 reduced oxidative damage in plants, particularly under abiotic stress conditions, such as heat, salt, and drought (Pérez-López et al. 2009; Mishra and Agrawal 2014; Zinta et al. 2014). We suggest that under elevated CO_2 if sufficient nitrogen is unavailable, and if plants are not under abiotic stress, photorespiration is likely to be restricted. As a result, the cellular ROS levels would increase.

Based on our findings, we emphasize that ROS generation increased under various situations of restricted photorespiratory metabolism. The increased ROS would harm physiological functions like photosynthesis and respiration (Mittler 2002, 2017). In return, photorespiration helped to keep optimal ROS levels in leaves.

An inverse relationship between photorespiratory components and the leaf ROS levels

The process of photorespiration had an inverse relationship with the redox status of leaves. Abiotic stress, e.g., drought or high light, elevated the photorespiratory enzyme activities (like GO, CAT, or HPR) in plants (Yuan et al. 2016; Cui et al. 2016; Bapatla et al. 2021). Photorespiration protected photosynthesis from stress-induced oxidative damage (Voss et al. 2013; Sunil et al. 2019). The present study emphasized that photorespiration and increased ROS/ oxidative stress in leaves exhibited an inverse relationship. Thus, photorespiration and cellular ROS levels were well coordinated in leaves.

Conclusion

The ROS (both superoxide and H_2O_2) levels were elevated under restricted photorespiratory conditions, confirming the hypothesis that photorespiration could minimize the levels of ROS and reduce oxidative stress. Photorespiration could complement the antioxidant enzyme systems to sustain low ROS levels in leaves. Further experiments are necessary to understand if photorespiration could be complemented with other components such as cyclic electron flow (CEF) or alternative oxidase (AOX) pathway during plant adaptation to abiotic stress.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12298-023-01388-4.

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Author contributions ASR planned the investigation. DS conducted several experiments, while PB and SG helped in some. ASR and DS drafted the manuscript. All the authors helped to edit and approved the final manuscript.

Declarations

Conflict of interest The authors declare that they have no conflict of interest regarding the publication of this paper.

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