REVIEW

Photorespiration is complemented by cyclic electron flow and the alternative oxidase pathway to optimize photosynthesis and protect against abiotic stress

Bobba Sunil[1] · Deepak Saini[1] · Ramesh B. Bapatla[1] · Vetcha Aswani[1] · Agepati S. Raghavendra[1]

Abstract

Optimization of photosynthetic performance and protection against abiotic stress are essential to sustain plant growth. Photorespiratory metabolism can help plants to adapt to abiotic stress. The beneficial role of photorespiration under abiotic stress is further strengthened by cyclic electron flow (CEF) and alternative oxidase (AOX) pathways. We have attempted to critically assess the literature on the responses of these three phenomena—photorespiration, CEF and AOX, to different stress situations. We emphasize that photorespiration is the key player to protect photosynthesis and upregulates CEF as well as AOX. Then these three processes work in coordination to protect the plants against photoinhibition and maintain an optimal redox state in the cell, while providing ATP for metabolism and protein repair. H_2O_2 generated during photorespiratory metabolism seems to be an important signal to upregulate CEF or AOX. Further experiments are necessary to identify the signals originating from CEF or AOX to modulate photorespiration. The mutants deficient in CEF or AOX or both could be useful in this regard. The mutual interactions between CEF and AOX, so as to keep their complementarity, are also to be examined further.

Keywords Alternative oxidase · Chloroplasts · Glycine decarboxylase · Photoinhibition · Reactive oxygen species · Redox homeostasis

Introduction

Plants are sessile and often exposed to stressful environments due to suboptimal or supraoptimal conditions like drought, high or low CO_2, high or low light, high or low temperature, limiting N/P/K and heavy metal stress. The abiotic stress causes alterations in metabolism, nutrient uptake, growth and development. Severe stress results in damage and cell death (Wang et al. 2008; Verslues et al. 2006). The basal factor during most of the stresses is the excess production of reactive oxygen species (ROS) much more than its removal by scavenging (Miller et al. 2010; Suzuki et al. 2012). The ROS include radicals such as singlet oxygen, superoxide, hydrogen peroxide and hydroxyl radicals. Besides the accumulation of ROS, abiotic stress frequently causes an imbalance in the supply/demand of ATP/NADPH, changes in membrane structure and additional damage due to lipid peroxidation products (Mignolet-Spruyt et al. 2016). The production of ROS and the energy/redox imbalance occurs among different compartments of cell.

Plants have the ability to respond and acclimate to these adverse conditions. In order to protect themselves, plants employ adaptive mechanisms mainly to scavenge the excess ROS using antioxidants (e.g. ascorbate, glutathione, carotenoids, flavonoids) and/or antioxidant enzymes (e.g. catalase, superoxide dismutase) (Gratao et al. 2005; Scandalios 2005; Racchi 2013; Acosta-Motos et al. 2017). Additional protective mechanisms attempt to achieve an energy balance (ATP/NADPH). There are excellent reviews on the adaptive responses of plants to various stresses (to cite a few: Miller et al. 2010; Baxter et al. 2014; Golldack et al. 2014; Mignolet-Spruyt et al. 2016; Acosta-Motos et al. 2017; Szymanska et al. 2017; Zarattini and Forlani 2017).

✉ Agepati S. Raghavendra
  as_raghavendra@yahoo.com; asrsl@uohyd.ernet.in

[1] Department of Plant Sciences, School of Life Sciences, University of Hyderabad, Hyderabad 500046, India

Adaptations of photosynthesis to abiotic stress

Photosynthesis is one of the major metabolic pathways affected markedly by changing environmental conditions (Foyer et al. 2012). The abiotic stress slows down not only the biochemical reactions of carbon assimilation but also photochemical activities. Among the thylakoid components, PSII has a higher turnover rate in response to stress, while PSI is relatively stable except under cold stress. Under severe stress, all the components including the membranes get disrupted. Any disturbance of the balance between the production and utilization of ATP/NADPH can lead to the accumulation of ROS and subsequent photoinhibition or photodamage of photosystems (Walker et al. 2014). PSII photodamage and the inhibition of repair can be alleviated by different photoprotection mechanisms (Takahashi and Badger 2011).

Under fluctuating light, plants can adapt their photosynthetic characteristics by changing their photosynthetic apparatus (Kono et al. 2014). These adaptations can be for several hours and extend to even a few weeks. There are several authoritative reviews on the protection of photosynthesis against abiotic stress (Rumeau et al. 2007; Foyer and Noctor 2009; Takahashi and Badger 2011; Dall'Osto et al. 2012; Foyer et al. 2012; Goh et al. 2012; Erickson et al. 2015; Feller 2016; Yamori and Shikanai 2016; Suo et al. 2017). Besides antioxidant-based systems, plants use additional mechanisms to protect the photosystems from over-excitation. These are as follows: chlororespiration, water–water cycle (WWC), non-photochemical quenching and cyclic electron flow (CEF). Even mitochondrial metabolism, particularly oxidative electron transport, alternative oxidase (AOX) pathway and mitochondrial reactions of photorespiration can help to optimize and protect photosynthesis (Raghavendra and Padmasree 2003). Among these, activities of photorespiration, CEF and AOX appear to be quite crucial.

Photorespiration is one of the high-flux metabolic pathways associated with photosynthesis hosted in chloroplasts, peroxisomes, mitochondria and cytosol (Hodges et al. 2016). The process of photorespiration can dissipate excess ROS and energy either directly or indirectly (Voss et al. 2013). The reactions of photorespiration serve as direct sinks for photosynthetically generated ATP, NADPH and reduced ferredoxin. The peroxisomal catalase can directly scavenge H_2O_2. The indirect ways are the optimization of linear and CEF, promotion of AOX pathway and even the release of CO_2 from glycine decarboxylation for intracellular recycling. Furthermore, glycine from photorespiratory metabolism is a source for glutathione, a major antioxidant in plant cells. A detailed description of the components of photorespiration, their regulation and the protective role can be found in some recent reviews (Kangasjarvi et al. 2012; Sorhagen et al. 2013; Voss et al. 2013; Araujo et al. 2014; Hodges et al. 2016; Zhang and Peng 2016).

The photochemical electron transport in chloroplasts operates in two modes, linear and cyclic. The linear electron transport leads to the generation of ATP as well as NADPH while the CEF, mediated by PSI accomplishes only the synthesis of ATP, but not NADPH. The equilibrium between ATP/NADPH production and their consumption gets disturbed and leads to photoinhibition or photodamage under conditions of abiotic stress. The balance can be adjusted back to equilibrium, by upregulation of CEF, which dissipates the excess energy in thylakoids via an enhanced energy-dependent non-photochemical quenching (qE-type NPQ). A few recent reviews summarize the extensive work on CEF (Chaux et al. 2015; Suorsa 2015; Ishikawa et al. 2016; Yamori and Shikanai 2016; Alric and Johnson 2017; Shikanai and Yamamoto 2017; Murata and Nishiyama 2018). The phenomenon of CEF is referred also as cyclic electron transport (CET) but we used the term CEF throughout this manuscript.

The AOX, localized in mitochondria, catalyses cyanide insensitive respiration. AOX is an important component of the members of mitochondrial energy dissipation pathway (MEDP), along with uncoupling proteins. The MEDPs play crucial roles in adaptation of plants to stresses. Regulation of MEDP members can occur at transcriptional, translational, post-translational and metabolic levels (Pu et al. 2015). AOX branches off from the cytochrome pathway of mitochondria at the level of ubiquinone (UQ). AOX bypasses complex III and IV of the cytochrome pathway, without ATP generation and hence the energy is dissipated as heat. AOX can limit excessive ROS/RNS generation in plants and helps in maintaining redox balance. The activity and levels of AOX increase under a variety of stresses (Moore et al. 2013; Wang et al. 2018). As a consequence, AOX optimizes photosynthesis under stress by modulating NADPH/ATP ratio, ATP/ADP ratio and carbon use efficiency. Further information on the AOX can be found in some recent reviews (Feng et al. 2013; Moore et al. 2013; Vanlerberghe 2013, Pu et al. 2015; Saha et al. 2016; Vanlerberghe et al. 2016; Wang et al. 2018).

Scope of present mini-review

One of our research interests has been the beneficial role of photorespiration and mitochondrial oxidative metabolism for photosynthetic carbon assimilation (Voss et al. 2013; Raghavendra and Padmasree 2003). We therefore focused this mini-review on the modulation by abiotic stress of

photorespiratory components and associated phenomena of CEF and AOX. We describe how the three components of photorespiration, CEF and AOX exhibit adaptive responses to different stresses. In view of the large number of articles on this subject, we limited our discussion to a few selected stresses: drought, low CO_2, high light, low N, low temperature and heavy metal stress. Our review attempts to high light the cross-talk between photorespiration, CEF and AOX. We propose that photorespiration is not only a major driving force but also upregulates CEF as well as AOX to provide additional protection of photosynthesis. A scheme is proposed to emphasize how photorespiration, CEF and AOX pathways act in tandem to protect plants under stress. Thus, the protective role of photorespiration is well complemented by CEF as well as AOX.

Modulation of photorespiration by abiotic stress

Upregulation of photorespiration is an important factor in optimizing photosynthesis and protecting against oxidative damage under high light or other abiotic stresses, such as drought, salinity and even heavy metals (Raghavendra and Padmasree 2003; Voss et al. 2013; Dellero et al. 2016; Hagemann et al. 2016; Hodges et al. 2016). Most of these studies were conducted with leaves of higher plants and some examples are presented and described below (Table 1).

It is not necessary that photorespiration always gets upregulated under drought or dissipates excess energy. The absolute rate of photorespiration can vary depending on the plant species and the intensity of drought itself. Noctor et al. (2002) provided evidence for an increase in the photorespiratory flux in leaves of two C_3 plants: wheat and barley, at lower than ambient CO_2 and drought. However, the contribution of photorespiration towards the oxidative load was minimal during severe stress in *Pancratium maritimum* (Abogadallah 2011). Similarly, photorespiration may not be the only energy sink and other processes of energy dissipation may be important to protect photosynthesis against photoinhibition under water stress (Guan and Gu 2009). Under conditions of extreme water deficit, the marked decrease in overall metabolism decreases photorespiration too. Under such conditions, metabolic components such as mitochondrial respiration and resultant ATP might become more important than photorespiration (Lawlor and Tezara 2009).

Drought and low CO_2

Drought stress causes stomatal closure, creates low internal CO_2 and increases the ROS levels in plant tissues. In leaves of *Jatropha curcas* and *Ricinus communis*, water deficit reduced the rates of photosynthesis, while photorespiration rate was increased by twofold (Neto et al. 2017). When exposed to drought, there was a sharp increase in the activities of several photorespiratory enzymes in tomato leaves e.g. phosphoglycolate phosphatase (PLGP), glycolate oxidase (GOX), catalase (CAT) and glycine decarboxylase (GDC) confirming the role of photorespiration in the adaptation to drought stress (Yuan et al. 2016). Under water stress, the rate of photorespiration increased in leaves of Holm oak

Table 1 Modulation of photorespiration and its components in leaves by different stresses

Factor	Plant	Increase in photorespiratory component	References
Drought	*Ricinus communis*	Rate by twofold and GO activity by 2.5-fold	Neto et al. (2017)
	Solanum lycopersicum	Photorespiratory enzyme activities (PLGP, GOX, CAT, HPR, GDC and GLYK) by threefold to fourfold	Yuan et al. (2016)
	Populus sp.	Serine and glycine by fourfold to fivefold	Molina-Rueda and Kirby (2015)
	Quercus ilex	Rate by twofold	Tsonev et al. (2014)
	Jatropha curcas	Rate by 25% and GO activity by twofold	Silva et al. (2015)
	Nicotiana tabacum	CO_2 compensation point by ~60% and GK by 4-fold	Rivero et al. (2009)
Low CO_2	*Arabidopsis thaliana*	Increased pools of photorespiratory metabolites (Glycolate, glycine, serine and glycerate)	Eisenhut et al. (2017)
High light	*Coffeea arabica*	Rate by twofold to fourfold	Martins et al. (2014)
	Nicotiana tabacum	Rate by twofold	Huang et al. (2016a)
Low N	*Lactuca sativa* and *Brassica oleracea*	Rate by 85% and GO/GGAT activities by 1.6 to threefold	Navarro-Leon et al. (2016)
	Arabidopsis thaliana	Glycine content by fivefold	Jiang et al. (2013)
Low temperature	*Quercus guyavitolia*	Rate by about 50%	Huang et al. (2016b)
Heavy metal—Cadmium	*Brassica juncea*	Fivefold to tenfold increase in phosphoglycolate levels	D'Alessandro et al. (2013)

The observations were made on either rate of photorespiration, activities or transcripts of photorespiratory enzymes and photorespiratory metabolite levels. Selected examples are listed. Further details can be found in cited references

(*Quercus ilex*) and *J. curcas* (Tsonev et al. 2014; Silva et al. 2015).

Overproduction of cytokinin in transgenic tobacco plants induced photorespiration to sustain photosynthetic processes (Rivero et al. 2009). When leaves of GS-overexpressing transgenic poplar were exposed to water stress, photorespiration was enhanced and the levels of serine and glycine increased, suggesting a key role of photorespiration during drought (Molina-Rueda and Kirby 2015). During acclimation to short-term ambient CO_2, photorespiratory mutants of Arabidopsis exhibited an increase in pools of key metabolites e.g. glycolate, glycine, serine and glycerate. Thus, photorespiratory metabolite flux may protect photosynthesis during acclimation to low CO_2 (Eisenhut et al. 2017).

High light and low N

When coffee leaves were exposed to high light, the rate of photorespiration increased significantly along with marked increase in the antioxidant systems, indicating the ability of photorespiration to consume excess reductants (Martins et al. 2014). In tobacco plants, photorespiration increased by twofold under high light, along with activation of WWC in tobacco plants (Huang et al. 2016a). Thus, photorespiration along with WWC played an important role in energy balancing when plants are exposed to high light.

Photorespiration helps to maintain adequate N levels in plants by promoting NH_4^+ production and assimilation (Bloom 2015). The photorespiratory rate, along with glycine levels, was enhanced and the activities of GO and GGAT increased markedly in *Lactuca sativa* and *Brassica oleracea* under Zn deficiency, indicating a need for photorespiration for NH_4^+ assimilation (Narvarro-Leon et al. 2016).

Low temperature and heavy metal stress

Low temperature limits photosynthesis due to reduction in stomatal conductance and enhanced uptake of O_2, reflecting an increase in photorespiration (Flexas et al. 1999). When *Quercus guyavifolia* leaves were exposed to low temperature and high light, the rate of photorespiration increased by 50%, so as to protect the photosynthetic apparatus against photodamage (Huang et al. 2016b).

Exposure of plants to high concentrations of heavy metal results in the accumulation of ROS eliciting changes in the antioxidant components of cells (Gratão et al. 2005). Exposure of *Brassica juncea* to Cd stress, leads to reduction in stomatal conductance and decrease in internal CO_2 concentration. The Cd stress increased phosphoglycolate levels, indicating that photorespiration could act as an electron sink to prevent over-reduction of photosynthetic components and photoinhibition (D'Alessandro et al. 2013).

Modulation of CEF by abiotic stress

Some of the stresses, known to affect CEF, are drought, low CO_2, high light, low N, low temperature and heavy metal stress. The factor of elevated or high CO_2 is unique that it can upregulate CEF (Satoh et al. 2002; Levitan et al. 2010), while not favouring photorespiration. Under severe stress, PSII becomes more sensitive to damage than PSI. The operation of CEF is crucial for protecting PSI by alleviating the over-reduction of the acceptor side of PSI and ATP production (Munekage et al. 2004). The PSI-dependent CEF is mediated by either proton gradient regulation 5 (PGR5) or PGRL1 (PGR5 like photosynthetic phenotype) proteins or a chloroplast NADH dehydrogenase-like (NDH) complex (Yamori and Shikanai 2016). The CEF is invariably upregulated under these conditions (Table 2).

Drought and low CO_2

Water deficit triggers stomatal closure and results in low CO_2 within leaves. As a result, drought stress inhibits photosynthetic carbon fixation due to both stomatal and non-stomatal limitation (Golding and Johnson 2003; Jia et al. 2008). Upregulation of CEF ensures survival under high light or drought stress (Lehtimaki et al. 2010). In resurrection plants of *Parobea rufescens*, CEF was stimulated by twofold not only under high light but also under low light in leaves subjected to drought (Huang et al. 2012). The ratio of CEF to ETR was stimulated up to twofold in two ferns: *Microsorum punctatum and Paraleptochillus decurrens* (Wang et al. 2013a). When *J. curcas* was exposed to drought, the dissipation of excess energy increased along with a threefold increase in CEF (Neto et al. 2017). Such associated increases in NPQ, photorespiration and CEF appear to be important to mitigate the effects of excess light, while preventing cellular damage, and maintain photochemical efficiency under limiting CO_2.

In algal cells, a CO_2 concentrating mechanism (CCM) is activated under low CO_2 conditions. The CCM, involving a complex series of carbonic anhydrases and transporters, requires energy (Raven 2010; Wang et al. 2011). CEF can provide sufficient energy in the form of ATP to power the CCM. Under low CO_2 conditions, CEF is activated and provides ATP for cellular needs as well as CCM in *Chlamydomonas reinhardtii* and *Synechocystis* PCC6803 (Deng et al. 2003). The rates of CEF increased up to fivefold in *C. reinhardtii* cells under severe depletion of inorganic carbon (Lucker and Kramer 2013). In higher plants, low CO_2 availability induces higher photorespiratory flux. A similar situation of 2.5-fold increase

Table 2 Modulation of photosynthetic CEF in photosynthetic tissues by conditions favourable for photorespiration

Factor	Plant	Increase in CEF	References
Drought	*Paraboea rufescens*[a]	Twofold	Huang et al. (2012)
	Microsorum punctatum and *Paraleptochillus decurrens*[a]	Onefold to twofold	Wang et al. (2013a)
	Jatropha curcas[a]	Threefold	Neto et al. (2017)
Low CO_2	*Synechocystis* PCC 6803[b]	Twofold	Deng et al. (2003)
	Chlamydomonas reinhardtii[b]	Threefold to fivefold	Lucker and Kramer (2013)
	Helianthus annuus[a]	2.5-fold	Takagi et al. (2016)
High light	*Synechococcus* sp. PCC 7942[b]	Fourfold	Herbert et al. (1995)
	Nicotiana tabacum[a]	Fivefold	Miyake et al. (2005)
Low N	*Chlamydomonas reinhardtii*[b]	Twofold	Saroussi et al. (2016)
	Dunaliella salina[b]	Twofold	Einali et al. (2013)
Low temperature	*Gossypium hirsutum*[a]	Fivefold	Fei et al. (2017)
	Calotropis gigantea[a]	Tenfold	Huang et al. (2017)
Heavy metal (Sb) + HL	*Microcystis aeruginosa*[b]	Twofold	Wang et al. (2015)

The extent of CEF was measured by monitoring either ΔpH or P700 reduction state or Chl fluorescence yield of PSI and PSII. Selected examples are given. Further details can be found in cited references

[a]Leaves

[b]Cells

was found in sunflower under photorespiratory conditions i.e. low CO_2 and high O_2 (Takagi et al. 2016).

High light and low N

Under high light conditions, the CEF is stimulated, proton gradient is dissipated and the non-photochemical quenching (NPQ) is increased. The upregulation of the thylakoidal NDH-complex seems to be the basis for such rise in CEF in Oat plant under photoinhibitory conditions (Quiles and Lopez 2004). The PSI-mediated CEF increased to almost fourfold in *Synechococcus* sp. PCC 7942 under high light (Herbert et al. 1995). Similarly, tobacco plants grown in high light had a fivefold higher activity of CEF compared with low light grown plants (Miyake et al. 2005).

The effect of high light is exerted even under limiting nitrogen. The CEF increased by twofold in *Dunaliella salina* under N deficiency and under high light, likely as the result of improved PSI quantum yields (Einali et al. 2013). Nitrogen limitation forces photosynthetic cells to readjust the balance between ATP/NADPH generation and their use for cellular metabolism. In *C. reinhardtii*, N deprivation led to the stimulation of type II NADPH dehydrogenase (NDA2)-dependent CEF by twofold, with little contribution from PGR5/PGRL1-dependent CEF. The H^+ gradient which is generated by CEF was essential to sustain NPQ and ATP production for cell growth (Saroussi et al. 2016).

Low temperature and heavy metal stress

At low temperature, plants slow down their metabolism and create excess excitation energy, leading to ROS production and photoinhibition of PSII/PSI (Zhang and Scheller 2004). Furthermore, low-temperature stress decreases the levels of intracellular ATP and limits the repair of PSII and PSI (Murata et al. 2007). When cotton (*Gossypium hirsutum* L. var. Xinluzao 45) was grown under low temperature, there was a fivefold stimulation of CEF to prevent photoinhibition of photosynthesis (Fei et al. 2017). Similarly, low-temperature exposure increased CEF by tenfold in leaves of chilling sensitive *Calotropis gigantea* (Huang et al. 2017).

Heavy metals create oxidative stress by elevating ROS levels. The presence of heavy metals promotes CEF and helps in photoprotection of PSI while decreasing PSII-dependent electron flow. Generally, PSII is more sensitive than PSI to heavy metals (Atal et al. 1991; Siedlecka and Krupa 1996; Wang et al. 2013b). For e.g. when *Microcystis aeruginosa*, a cyanobacterial species was exposed to Sb(V), the CEF increased twofold (Wang et al. 2015).

Modulation of AOX by abiotic stress

The operation of AOX helps in maintaining a redox balance as well as metabolic homeostasis in plants (Vanlerberghe et al. 2016). Further, AOX is an important factor to switch between anabolic and catabolic modes of respiration and to maintain carbon, energy and redox

balance in plant cells (Rasmusson et al. 2009; Vanlerberghe 2013). An increase in the capacity and activity of AOX is common during the response of plants to abiotic stress (Saha et al. 2016).

AOX is encoded by small family of nuclear genes, belonging to two types: *AOX1* and *AOX2*. Among these genes, *AOX1a* is well studied and most responsive to variety of stress (drought, chilling, high light, high salt and low nitrogen) conditions. The over-expression of AOX1A in Arabidopsis plants conferred tolerance to different abiotic stresses (Feng et al. 2013; Wang et al. 2018). A few examples of stress modulated AOX components are given in Table 3.

Drought and low (ambient) CO_2

In many monocot and dicot leaves, drought stress leads to an increase in the components of AOX: transcription of AOX gene(s), capacity and activity. For e.g. under drought conditions, 12-fold increase in AOX protein and 1.6-fold increase in AOX activity occurred in tobacco (Dahal and Vanlerberghe 2017; Vanlerberghe et al. 2016). Similarly, the expression of AOX increased fivefold under drought in barley (Wanniarachchi et al. 2018). Low CO_2 or high O_2 favours the photorespiratory pathway. Very few reports are available on the effect of low CO_2 on respiration. In *C. reinhardtii*, slight decrease in AOX capacity was observed under ambient CO_2 grown algae (Goyal and Tolbert 1989).

High light and low N

Under high light conditions, AOX protects chloroplasts from over-reduction, thereby decreasing photoinhibition (Xu et al. 2011; Florez-Sarasa et al. 2016a). This is because AOX is an effective sink for excess reducing equivalents generated in chloroplasts. The capacity as well as expression of AOX increases under high light conditions in several plants, including *Arabidopsis thaliana* and *Cucumis sativus* (Florez-Sarasa et al. 2016a; Zhang et al. 2017). Strong correlations between respiration rates and leaf N contents were found in various plant species. When the N is low, the respiration in leaves consumes more starch and the mitochondrial AOX capacity increases (Noguchi and Terashima 2006). The capacity and protein levels of AOX increased in tobacco cells cultured in a low-N medium (Watanabe et al. 2010).

Low temperature and heavy metals

The AOX pathway dissipates energy in the form of heat and this is quite crucial for plant adaptation to chilling. The protein abundance and the activity of AOX are low in plants under normal conditions, but are enhanced at low-temperature (Feng et al. 2008). Similarly, more than twofold increase in AOX capacity and expression of AOX under chilling conditions was reported in *A. thaliana* (Wang et al. 2012).

Exposure of plants to heavy metals leads to an increase in ROS. When exposed to Cd, Cr and Al, the AOX pathway is activated at both transcriptional and translational levels in *A. thaliana* (Keunen et al. 2015), *Salvinia minima* (Prado et al. 2010) and tobacco plants (Panda et al. 2013).

Table 3 Modulation of AOX pathway and its components in leaves by conditions favourable for photorespiration

Factor	Plant	Increase in AOX components	References
Drought	Barley	Fivefold increase in expression	Wanniarachchi et al. (2018)
	Tobacco	> 1.5-fold increase in activity	Vanlerberghe et al. (2016)
	Tobacco	12-fold increase in protein	Dahal and Vanlerberghe (2017)
Ambient (low) CO_2	*Chlamydomonas reinhardtii*	Slight decrease in capacity	Goyal and Tolbert (1989)
High light	*Arabidopsis thaliana*	2.5-fold increase in protein and 30% increase in capacity	Florez-Sarasa et al. (2016a, b)
	Cucumis sativus	2.5-fold increase in capacity	Zhang et al. (2017)
Low nitrogen	*Arabidopsis thaliana*	Fivefold increase in expression and 6.5-fold increase in capacity	Watanabe et al. (2010)
	Spinach	Up to fourfold increase in capacity	Noguchi and Terashima (2006)
Low temperature	*Arabidopsis thaliana*	Up to threefold increase in capacity/expression	Wang et al. (2012) and Watanabe et al. (2008)
	Barley	> 1.5-fold increase in capacity/protein levels	Szal et al. (2009)
Heavy metals			
Cadium	*Arabidopsis thaliana*	15-fold increase in expression	Keunen et al. (2015)
Chromium	*Salvinia minima*	Increased capacity	Prado et al. (2010)
Aluminium	Tobacco	1.2-fold increase in capacity	Panda et al. (2013)

The increase was found in either gene expression, activity or protein content. Selected examples are listed. Further details can be found in cited references

Interactions of photorespiration with CEF and AOX during abiotic stress

Photorespiration, CEF and mitochondrial AOX pathway are all important components of adaptations to abiotic stress of leaves. These three phenomena help in dissipating the excess reducing equivalents generated in the cell and protect against photoinhibition (Raghavendra and Padmasree 2003; Foyer et al. 2012). There are convincing reports that the elevated photorespiratory metabolism under stress can in turn stimulate both CEF and AOX.

The contribution of photorespiration or CEF in maintaining the redox poise of the chloroplast stroma was studied in several plants, such as sunflower, Arabidopsis, tobacco, rice, cotton, cyanobateria and even microalgae (Kramer and Evans 2011; Alric 2014; Kono et al. 2014; Huang et al. 2015; Takagi et al. 2016; Yamori and Shikanai 2016; Yi et al. 2018; Wada et al. 2018). The importance of AOX pathway in energy balance, involving photosynthesis and photorespiration, has been demonstrated using plants of Arabidopsis and tobacco with altered levels of either *AOX1a* (Vanlerberghe et al. 2016; Watanabe et al. 2016), or GDC (Igamberdiev et al. 2001; Bykova et al. 2005, 2014). There

Table 4 Association of enhanced photorespiratory activity with CEF in maintaining redox poise of leaves

Factor/genetic manipulation	Plant	Observation	References
Low CO_2	Sunflower	Photorespiration promotes CEF turnover, to oxidize P700	Takagi et al. (2016)
Low CO_2 (transfer from high)	*Arabidopsis thaliana*	Photorespiration increased expression of NDH-dependent CEF pathway genes	Foyer et al. (2012)
Low CO_2 and high light	Rice (with altered levels of Rubisco)	Photorespiration is essential for P700 oxidation under excess light	Wada et al. (2018)
Varying O_2 and CO_2	*Zantedeschia aethiopica*[a]	Increased CEF may provide additional ATP required for enhanced photorespiratory activity	Yiotis and Manetas (2010)
High light	*Arabidopsis thaliana*	Increased CEF under photorespiratory conditions during high light	Walker et al. (2014)
Sub-saturating light (transfer from HL)	Tobacco	CEF contributes ATP required for photorespiration	Huang et al. (2015)
H_2O_2 production by GO in plastids	*Arabidopsis thaliana* (transgenic and mutants of CEF)	H_2O_2 from chloroplasts as a signal to increase CEF	Strand et al. (2015)

Selected examples are given. Further details can be found in cited references

[a]Petioles and pedicels

Table 5 Association of photorespiratory activity with AOX pathway in maintaining redox poise of leaves

Factor	Plant[a]/mutant	Observation	References
High light	Wild-type	Increased expression of *AOX1a* gene, photorespiratory activity, and glycine levels	Florez-Sarasa et al. (2012)
High light	AOX and CEF mutants	Impaired photorespiratory metabolism and enhanced CEF activity	Yoshida et al. (2011)
High light	CEF mutants	Inactivation of AOX and impaired photorespiration	Florez-Sarasa et al. (2016b)
High light	*aox1a* mutant	Decreased photorespiration and increased photoinhibition	Watanabe et al. (2016)
High light	*aox1a* mutant	Decreased photorespiration	Zhang et al. (2017)
High light and antimycin A	*aox1a* mutant	Upregulated expression of GDC-P protein in presence of antimycin A, a COX inhibitor	Strodtkötter et al. (2009)
Varying CO_2	Barley—GDC mutant	Reduced glycine decarboxylation, AOX activity and photorespiration	Igamberdiev et al. (2001)
Ambient air and light	Potato—GDC mutant	Reduced glycine decarboxylation, AOX capacity and photorespiration	Bykova et al. (2005)

The decrease in photorespiratory activity reduces the operation of AOX and vice versa. Selected examples are listed. Further details can be found in cited references

[a]*Arabidopsis thaliana*, unless otherwise mentioned

are several studies made on the modulation of either photorespiration (Table 1) or CEF (Table 2) or AOX (Table 3) in photosynthetic tissues under abiotic stress. However, only a few studies have monitored the modulation of CEF and/or AOX, in relation to photorespiration under a given stress (Tables 4, 5).

Photorespiration upregulates CEF

High light and low CO_2 conditions increase the photosynthetic linear electron flow, causing an over-reduction of the electron transport chain and high ROS accumulation. Under such stressful conditions, plants increase the oxidation of P700 through CEF to suppress ROS production at PSI. The importance of photorespiration in maintaining the oxidation of P700 through CEF under limiting CO_2 conditions was shown in sunflower leaves and transgenic rice with manipulated Rubisco content (Takagi et al. 2016; Wada et al. 2018). When Arabidopsis plants grown under high CO_2 are transferred to ambient air, plants trigger photorespiratory responses due to the decreased CO_2 availability. The enhanced expression of NDH-dependent CEF genes (*NDF4* and *NDF6*) under such conditions suggests the activation of CEF to meet the increased ATP/NADPH demand of photorespiration (Foyer et al. 2012). In petioles of Calla lily (*Zantedeschia aethiopica*), high CEF around PS I was always accompanied by higher photorespiratory rates. In the absence of O_2, the electron transport rate decreased dramatically in petioles and pedicels indicating the need for high photorespiration rates (Yiotis and Manetas 2010).

In Arabidopsis plants, the contribution of CEF to energy balance was quite significant during high light under photorespiratory conditions (high O_2 and low CO_2) (Walker et al. 2014). Under high light, the rate of photorespiration is expected to be high, and can afford additional ATP synthesis. Tobacco leaves acclimated to high light exhibited high rates of CEF (Miyake et al. 2005; Huang et al. 2015). The attenuated response of Gly/Ser ratio to high light in Arabidopsis CEF mutants—single (*pgr5*) and double (*pgr5 crr4-3*)—suggests an impairment in photorespiration, denoting a tight link between CEF and photorespiration (Florez-Sarasa et al. 2016b).

It has long been suggested that H_2O_2 generated as a result of over-reduction of the electron transport chain in chloroplasts can promote CEF (Livingston et al. 2010). Strand et al. (2015) checked the possibility of CEF regulation by H_2O_2 using transgenic Arabidopsis plants that express glycolate oxidase (GO) in chloroplasts. When chloroplast GO expressing plants were shifted from non-photorespiratory conditions of high CO_2 to ambient air (photorespiratory conditions), rapid increase in CEF was observed within 20 min. Even an external supply of H_2O_2

induced higher levels of NDH proteins, facilitating the activation of CEF (Strand et al. 2015).

Photorespiration upregulates AOX

There is a positive correlation between photorespiratory glycine decarboxylation and activity of the AOX pathway. Oxidation of glycine by GDC results in the increased concentrations of NADPH in mitochondria activating AOX (Vanlerberghe et al. 1995; Bykova et al. 2014). AOX pathway favours photorespiration and can alleviate photoinhibition by maintaining a functional photorespiratory pathway, by effective utilization of NADH from glycine oxidation under high light conditions (Watanabe et al. 2016).

Most of the work on the relation between AOX and photorespiration is done with *aox1a* mutants. There were only two studies on mutants with decreased photorespiratory activity, as the photorespiration-deficient mutants cannot grow in normal air. Suppression of GDC, one of the rate limiting steps of photorespiration, in a barley mutant resulted in significant changes in redox state, leading to over-reduction of the cellular components. Then compensatory mechanisms like increased mitochondrial respiration by either AOX or cytochrome oxidase (COX) were initiated (Igamberdiev et al. 2001). In fact, under conditions favourable for photorespiration such as drought, the enhanced AOX activity may protect even COX (Dahal and Vanlerberghe 2017). In transgenic potato plants with antisense reduction in P-protein of GDC, decrease in photorespiratory decarboxylation is compensated by an increase in respiratory decarboxylation (Bykova et al. 2005).

The Arabidopsis mutant lacking AOX (*aox1a*) showed decreased photosynthetic efficiency, expected to be due to disturbed photorespiratory metabolism (Yoshida et al. 2011). Similarly, under severe light stress (chronic photoinhibition) the inactivation of AOX in the CEF double mutants (*pgr5 crr4-3*) resulted in impairment of photorespiration as evidenced by small or no response of Gly/Ser ratio (Florez-Sarasa et al. 2016b).

Watanabe et al. (2016) showed that under high light conditions, AOX pathway alleviates photo inhibition by maintaining a functional photorespiratory pathway, when the cytochrome pathway was suppressed. Disruption or inhibition of AOX pathway (by inhibitors or the use of mutants) significantly decreased the photorespiration in Arabidopsis and *C. sativus* (Zhang et al. 2017). Suppression of AOX1A does not affect plant metabolism in normal light, but under high light results in the activation of photorespiratory components. The *aox1a* mutants increased their capacity for photorespiration compared to wildtype plants when the cytochrome pathway was inhibited (Strodtkotter et al. 2009).

CEF and AOX can compensate each other

From our understanding of the current literature, it appears that both CEF in chloroplasts and AOX in mitochondria are upregulated by photorespiration (Tables 4, 5) and perform the same function of dissipating excess reducing equivalents and protecting photosynthesis against stress.

Tobacco, with the knockdown of AOX showed enhanced CEF, whereas the overexpressed lines showed decreased CEF, when compared to wildtype, particularly during drought and light stress (Vanlerberghe et al. 2016). The AOX deficiency in tobacco resulted in highly reduced PSI, highly reduced NAD(P)H pool in the stroma and enhanced CEF. When overexpressed, AOX maintained an oxidized stromal NAD(P)H pool and lowered CEF in tobacco plants (Dahal et al. 2014, 2015).

Similarly, the Arabidopsis *aox1a* mutant showed a decrease in operating efficiency of photosystem II and enhanced CEF, indicating the importance of AOX in preventing the over-reduction of photosynthetic electron transport in chloroplasts under light stress (Yoshida et al. 2011). The Arabidopsis double mutant with lowered levels of both *aox1a* and *pgr5* showed growth impairment and severe photoinhibition under even moderate light conditions, suggesting the co-operative nature of CEF and AOX in plant growth under high light (Yoshida et al. 2011). Florez-Sarasa et al. (2016b) found that the chronic photoinhibition in double mutant of CEF (*pgr5 crr4-3*) resulted in inactivation of AOX, while upregulating cytochrome pathway as sink for excess electrons from chloroplasts.
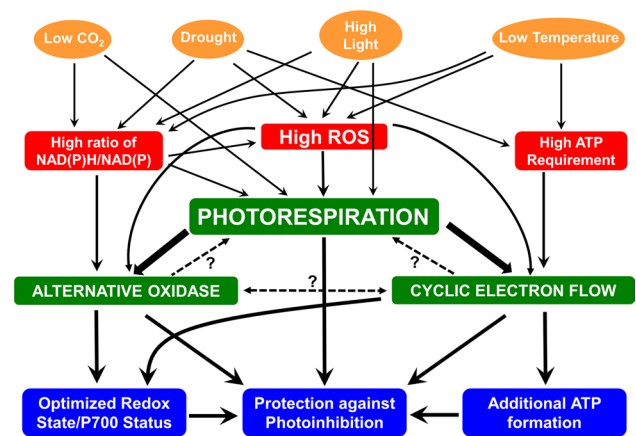

Fig. 1 A schematic diagram of the beneficial role of photorespiration and its complementation by CEF and AOX to protect plants against abiotic stress. Any abiotic stress increases the level of ROS. Parallely, due to the disturbance in metabolism, the cellular compartments become over-reduced and thylakoids over-excited. The cells would then need more ATP for metabolism as well as repair processes. Under abiotic stress, the photorespiratory pathway is activated. In turn, photorespiration upregulates CEF and AOX. All three phenomena of photorespiration, CEF and AOX work together to optimize redox state of the cell, protect against photoinhibition and supply ATP for repair mechanisms. While the stimulation of CEF and AOX by photorespiration is well established, it is not clear, if there is a feedback modulation. Similarly, the extent of cross-talk between CEF and AOX is also not completely known. Solid arrows represent information available in the literature. The dotted arrows represent suggestions, which need to be verified experimentally

Concluding remarks

The available reports indicate the stimulation of CEF as well as AOX by photorespiratory conditions (e.g. sub-optimal CO_2 or high O_2 or fluctuating light). In turn, the operation of CEF and/or AOX seems to favour photorespiration. Once upregulated, photorespiration, CEF and AOX act in tandem, to achieve the same goal of protection and optimization of photosynthetic machinery (Fig. 1). Although these three processes are upregulated by a variety of stresses, we consider photorespiration as the major player, while CEF and AOX can be considered as priming factors that pre-condition plant tissues to be ready for exposure and adaptability to abiotic stresses. We also emphasize that photorespiration is upregulated under conditions favourable for CEF or AOX. Further, CEF or AOX appear to be capable of compensating the deficiency of the other, so as to keep photorespiration operational.

Photorespiratory H_2O_2 can be a powerful signal to stimulate CEF (Strand et al. 2015) or AOX (Sewelam et al.

2014). It would be interesting to check if CEF or AOX can generate any signal to stimulate photorespiration directly. This can be done by using mutants lacking key components of photorespiration, but this is quite challenging as most of the photorespiratory mutants are hard to grow in ambient air. However, the heterozygous barley mutants with partially reduced GDC (Wingler et al. 2000), which can grow in normal air, seem to provide an excellent window for such experiments.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Abogadallah GM (2011) Differential regulation of photorespiratory gene expression by moderate and severe salt and drought stress in relation to oxidative stress. Plant Sci 180:540–547

Acosta-Motos JR, Ortuno MF, Bernal-Vicente A, Diaz-Vivancos P, Sanchez-Blanco MJ, Hernandez JA (2017) Plant responses to salt stress: adaptive mechanisms. Agronomy 7:18

Alric J (2014) Redox and ATP control of photosynthetic cyclic electron flow in *Chlamydomonas reinhardtii*: II. Involvement of the PGR5-PGRL1 pathway under anaerobic conditions. Biochim Biophys Acta 1837:825–834

Alric J, Johnson X (2017) Alternative electron transport pathways in photosynthesis: a confluence of regulation. Curr Opin Plant Biol 37:78–86

Araujo WL, Nunes-Nesi A, Fernie AR (2014) On the role of plant mitochondrial metabolism and its impact on photosynthesis in both optimal and sub-optimal growth conditions. Photosynth Res 119:141–156

Atal N, Saradhi PP, Mohanty P (1991) Inhibition of the chloroplast photochemical reactions by treatment of wheat seedlings with low concentrations of cadmium: analysis of electron transport activities and changes in fluorescence yield. Plant Cell Physiol 32:943–951

Baxter A, Mittler R, Suzuki N (2014) ROS as key players in plant stress signaling. J Exp Bot 65:1229–1240

Bloom AJ (2015) Photorespiration and nitrate assimilation: a major intersection between plant carbon and nitrogen. Photosynth Res 123:117–128

Bykova NV, Keerberg O, Parnik T, Bauwe H, Gardestrom P (2005) Interaction between photorespiration and respiration in transgenic potato plants with antisense reduction in glycine decarboxylase. Planta 222:130–140

Bykova NV, Moller IM, Gardestrom P, Igamberdiev AU (2014) The function of glycine decarboxylase complex is optimized to maintain high photorespiratory flux via buffering of its reaction products. Mitochondrion 19:357–364

Chaux F, Peltier G, Johnson X (2015) A security network in PSI photoprotection: regulation of photosynthetic control, NPQ and O_2 photoreduction by cyclic electron flow. Front Plant Sci 6:875

D'Alessandro A, Taamalli M, Gevi F, Timperio AM, Zolla L, Ghnaya T (2013) Cadmium stress responses in *Brassica juncea*: hints from proteomics and metabolomics. J Proteome Res 12:4979–4997

Dahal K, Vanlerberghe GC (2017) Alternative oxidase respiration maintains both mitochondrial and chloroplast function during drought. New Phytol 213:560–571

Dahal K, Wang J, Martyn GD, Rahimy F, Vanlerberghe GC (2014) Mitochondrial alternative oxidase maintains respiration and preserves photosynthetic capacity during moderate drought in *Nicotiana tabacum*. Plant Physiol 166:1560–1574

Dahal K, Martyn GD, Vanlerberghe GC (2015) Improved photosynthetic performance during severe drought in *Nicotiana tabacum* overexpressing a nonenergy conserving respiratory electron sink. New Phytol 208:382–395

Dall'Osto L, Holt NE, Kaligotla S, Fuciman M, Cazzaniga S, Carbonera D, Frank HA, Alric J, Bassi R (2012) Zeaxanthin protects plant photosynthesis by modulating chlorophyll triplet yield in specific light-harvesting antenna subunits. J Biol Chem 287:41820–41834

Dellero Y, Jossier M, Schmitz J, Maurino VG, Hodges M (2016) Photorespiratory glycolate-glyoxylate metabolism. J Exp Bot 67:3041–3052

Deng Y, Ye J, Mi H (2003) Effects of low CO_2 on NAD(P)H dehydrogenase, a mediator of cyclic electron transport around photosystem I in the cyanobacterium *Synechocystis* PCC 6803. Plant Cell Physiol 44:534–540

Einali A, Shariati M, Sato F, Endo T (2013) Cyclic electron transport around photosystem I and its relationship to non-photochemical quenching in the unicellular green alga *Dunaliella salina* under nitrogen deficiency. J Plant Res 126:179–186

Eisenhut M, Bräutigam A, Timm S, Florian A, Tohge T, Fernie AR, Bauwe H, Weber APM (2017) Photorespiration is crucial for dynamic response of photosynthetic metabolism and stomatal movement to altered CO_2 availability. Mol Plant 10:47–61

Erickson E, Wakao S, Niyogi KK (2015) Light stress and photoprotection in *Chlamydomonas reinhardtii*. Plant J 82:449–465

Fei X, Long YY, Ting WY, Hui MA, Feng ZW (2017) Effects of low temperature on PSI and PSII photoinhibition in cotton leaf at boll stage. Acta Agron Sin 43:1401–1409

Feller U (2016) Drought stress and carbon assimilation in a warming climate: reversible and irreversible impacts. J Plant Physiol 203:84–94

Feng HQ, Li X, Duan JG, Li HY, Liang HG (2008) Chilling tolerance of wheat seedlings is related to an enhanced alternative respiratory pathway. Crop Sci 48:2381–2388

Feng H, Guan D, Sun K, Wang Y, Zhang T, Wang R (2013) Expression and signal regulation of the alternative oxidase genes under abiotic stresses. Acta Biochim Biophys 45:985–994

Flexas J, Badger M, Chow WS, Medrano H, Osmond CB (1999) Analysis of the relative increase in photosynthetic O_2 uptake when photosynthesis in grapevine leaves is inhibited following low night temperatures and/or water stress. Plant Physiol 121:675–684

Florez-Sarasa I, Araújo WL, Wallström SV, Rasmusson AG, Fernie AR, Ribas-Carbo M (2012) Light-responsive metabolite and transcript levels are maintained following a dark-adaptation period in leaves of *Arabidopsis thaliana*. New Phytol 195:136–148

Florez-Sarasa I, Ribas-Carbo M, Del-Saz NF, Schwahn K, Nikoloski Z, Fernie AR, Flexas J (2016a) Unravelling the in vivo regulation and metabolic role of the alternative oxidase pathway in C3 species under photoinhibitory conditions. New Phytol 212:66–79

Florez-Sarasa I, Noguchi K, Araujo WL, Garcia-Nogales A, Fernie AR, Flexas J, Ribas-Carbo M (2016b) Impaired cyclic electron flow around photosystem I disturbs high-light respiratory metabolism. Plant Physiol 172:2176–2189

Foyer CH, Noctor G (2009) Redox regulation in photosynthetic organisms: signaling, acclimation, and practical implications. Antioxid Redox Signal 11:861–905

Foyer CH, Neukermans J, Queval G, Noctor G, Harbinson J (2012) Photosynthetic control of electron transport and the regulation of gene expression. J Exp Bot 63:1637–1661

Goh CH, Ko SM, Koh S, Kim YJ, Bae HJ (2012) Photosynthesis and environments: photoinhibition and repair mechanisms in plants. J Plant Biol 55:93–101

Golding AJ, Johnson GN (2003) Down-regulation of linear and activation of cyclic electron transport during drought. Planta 218:107–114

Golldack D, Li C, Mohan H, Probst N (2014) Tolerance to drought and salt stress in plants: unraveling the signaling networks. Front Plant Sci 5:151

Goyal A, Tolbert NE (1989) Variations in the alternative oxidase in *Chlamydomonas* grown in air or high CO_2. Plant Physiol 89:958–962

Gratao PL, Polle A, Lea PJ, Azevedo RA (2005) Making the life of heavy metal-stressed plants a little easier. Funct Plant Biol 32:481–494

Guan X, Gu S (2009) Photorespiration and photoprotection of grapevine (*Vitis vinifera* L. cv. Cabernet Sauvignon) under water stress. Photosynthetica 47:437–444

Hagemann M, Weber APM, Eisenhut M (2016) Photorespiration: origins and metabolic integration in interacting compartments. J Exp Bot 67:2915–2918

Herbert SK, Martin RE, Fork DC (1995) Light adaptation of cyclic electron transport through photosystem I in the cyanobacterium *Synechococcus* sp. PCC 7942. Photosynth Res 46:277–285

Hodges M, Dellero Y, Keech O, Betti M, Raghavendra AS, Sage R, Zhu XG, Allen DK, Weber APM (2016) Perspectives for a better understanding of the metabolic integration of photorespiration within a complex plant primary metabolism network. J Exp Bot 67:3015–3026

Huang W, Yang SJ, Zhang SB, Zhang JL, Cao KF (2012) Cyclic electron flow plays an important role in photoprotection for the resurrection plant *Paraboea rufescens* under drought stress. Planta 235:819–828

Huang W, Yang YJ, Hu H, Zhang SB (2015) Different roles of cyclic electron flow around photosystem I under sub-saturating and saturating light intensities in tobacco leaves. Front Plant Sci 6:923

Huang W, Yang YJ, Hu H, Zhang SB (2016a) Response of the water-water cycle to the change in photorespiration in tobacco. J Photochem Photobiol B 157:97–104

Huang W, Hu H, Zhang SB (2016b) Photosynthesis and photosynthetic electron flow in the alpine evergreen species *Quercus guyavifolia* in winter. Front Plant Sci 7:1511

Huang W, Zhang SB, Xu JC, Liu T (2017) Plasticity in roles of cyclic electron flow around photosystem I at contrasting temperatures in the chilling-sensitive plant *Calotropis gigantea*. Environ Exp Bot 141:145–153

Igamberdiev AU, Bykova NV, Lea PJ, Gardestrom P (2001) The role of photorespiration in redox and energy balance of photosynthetic plant cells: a study with a barley mutant deficient in glycine decarboxylase. Physiol Plant 111:427–438

Ishikawa N, Takabayashi A, Sato F, Endo T (2016) Accumulation of the components of cyclic electron flow around photosystem I in C4 plants, with respect to the requirements for ATP. Photosynth Res 129:261–277

Jia H, Oguchi R, Hope AB, Barber J, Chow WS (2008) Differential effects of severe water stress on linear and cyclic electron fluxes through photosystem I in spinach leaf discs in CO_2-enriched air. Planta 228:803–812

Jiang L, Liu Y, Sun H, Han Y, Li J, Li C, Guo W, Meng H, Li S, Fan Y, Zhang C (2013) The mitochondrial folylpolyglutamate synthetase gene is required for nitrogen utilization during early seedling development in Arabidopsis. Plant Physiol 161:971–989

Kangasjarvi S, Neukermans J, Li SC, Aro EM, Noctor G (2012) Photosynthesis, photorespiration, and light signalling in defence responses. J Exp Bot 63:1619–1636

Keunen E, Schellingen K, Van Der Straeten D, Remans T, Colpaert J, Vangronsveld J, Cuypers A (2015) ALTERNATIVE OXIDASE1a modulates the oxidative challenge during moderate Cd exposure in *Arabidopsis thaliana* leaves. J Exp Bot 66:2967–2977

Kono M, Noguchi K, Terashima I (2014) Roles of the cyclic electron flow around PSI (CEF-PSI) and O_2-dependent alternative pathways in regulation of the photosynthetic electron flow in short-term fluctuating light in *Arabidopsis thaliana*. Plant Cell Physiol 55:990–1004

Kramer DM, Evans JR (2011) The importance of energy balance in improving photosynthetic productivity. Plant Physiol 155:70–78

Lawlor DW, Tezara W (2009) Causes of decreased photosynthetic rate and metabolic capacity in water-deficient leaf cells: a critical evaluation of mechanisms and integration of processes. Ann Bot 103:561–579

Lehtimaki N, Lintala M, Allahverdiyeva Y, Aro EM, Mulo P (2010) Drought stress-induced upregulation of components involved in ferredoxin-dependent cyclic electron transfer. J Plant Physiol 167:1018–1022

Levitan O, Kranz SA, Spungin D, Prášil O, Rost B, Berman-Frank O (2010) Combined effects of CO_2 and light on the N_2 fixing cyanobacterium *Trichodesmium* IMS101: a mechanistic view. Plant Physiol 154:346–356

Livingston AK, Cruz JA, Kohzuma K, Dhingra A, Kramer DM (2010) An Arabidopsis mutant with high cyclic electron flow around photosystem I (hcef) involving the NADPH dehydrogenase complex. Plant Cell 22:221–233

Lucker B, Kramer DM (2013) Regulation of cyclic electron flow in *Chlamydomonas reinhardtii* under fluctuating carbon availability. Photosynth Res 117:449–459

Martins SCV, Araújo WL, Tohge T, Fernie AR, DaMatta FM (2014) In high-light-acclimated coffee plants the metabolic machinery is adjusted to avoid oxidative stress rather than to benefit from extra light enhancement in photosynthetic yield. PLoS ONE 9:e94862

Mignolet-Spruyt L, Xu E, Idänheimo N, Hoeberichts FA, Mühlenbock P, Brosche M, Van Breusegem F, Kangasjärvi J (2016) Spreading the news: subcellular and organellar reactive oxygen species production and signaling. J Exp Bot 67:3831–3844

Miller G, Suzuki N, Ciftci-Yilmaz S, Mittler R (2010) Reactive oxygen species homeostasis and signalling during drought and salinity stresses. Plant Cell Environ 33:453–467

Miyake C, Horiguchi S, Makino A, Shinzaki Y, Yamamoto H, Tomizawa K (2005) Effects of light intensity on cyclic electron flow around PSI and its relationship to non-photochemical quenching of chl fluorescence in tobacco leaves. Plant Cell Physiol 46:1819–1830

Molina-Rueda JJ, Kirby EG (2015) Transgenic poplar expressing the pine GS1a show alterations in nitrogen homeostasis during drought. Plant Physiol Biochem 94:181–190

Moore AL, Shiba T, Young L, Harada S, Kita K, Ito K (2013) Unraveling the heater: new insights into the structure of the alternative oxidase. Annu Rev Plant Biol 64:637–663

Munekage Y, Hashimoto M, Miyake C, Tomizawa KI, Endo T, Tasaka M, Shikanai T (2004) Cyclic electron flow around photosystem I is essential for photosynthesis. Nature 429:579–582

Murata N, Nishiyama Y (2018) ATP is a driving force in the repair of photosystem II during photoinhibition. Plant Cell Environ 41:285–299

Murata N, Takahashi S, Nishiyama Y, Allakhverdiev SI (2007) Photoinhibition of photosystem II under environmental stress. Biochim Biophys Acta 1767:414–421

Navarro-León E, Barrameda-Medina Y, Lentini M, Esposito S, Ruiz JM, Blasco B (2016) Comparative study of Zn deficiency in *L. sativa* and *B. oleracea* plants: NH_4^+ assimilation and nitrogen derived protective compounds. Plant Sci 248:8–16

Neto MCL, Cerqueira JVA, da Cunha JR, Ribeiro RV, Silveira JAG (2017) Cyclic electron flow, NPQ and photorespiration are crucial for the establishment of young plants of *Ricinus communis* and *Jatropha curcas* exposed to drought. Plant Biol (Stuttg) 19:650–659

Noctor G, Veljovic-Jovanovic S, Driscoll S, Novitskaya L, Foyer CH (2002) Drought and oxidative load in wheat leaves: a predominant role for photorespiration? Ann Bot 89:841–850

Noguchi K, Terashima I (2006) Responses of spinach leaf mitochondria to low N availability. Plant Cell Environ 29:710–719

Panda SK, Sahoo L, Katsuhara M, Matsumoto H (2013) Overexpression of alternative oxidase gene confers aluminum tolerance by altering the respiratory capacity and the response to oxidative stress in tobacco cells. Mol Biotechnol 54:551–563

Prado C, Rodriguez-Montelongo L, Gonzalez JA, Pagano EA, Hilal M, Prado FE (2010) Uptake of chromium by *Salvinia minima*: effect on plant growth, leaf respiration and carbohydrate metabolism. J Hazard Mater 177:546–553

Pu X, Lv X, Tan T, Fu F, Qin G, Lin H (2015) Roles of mitochondrial energy dissipation systems in plant development and acclimation to stress. Ann Bot 116:583–600

Quiles MJ, López NI (2004) Photoinhibition of photosystems I and II induced by exposure to high light intensity during oat plant growth effects on the chloroplast NADH dehydrogenase complex. Plant Sci 166:815–823

Racchi ML (2013) Antioxidant defences in plants with attention to Prunus and Citrus spp. Antioxidants 2:340–369

Raghavendra AS, Padmasree K (2003) Beneficial interactions of mitochondrial metabolism with photosynthetic carbon assimilation. Trends Plant Sci 8:546–553

Rasmusson AG, Fernie AR, van Dongan JT (2009) Alternative oxidase: a defence against metabolic fluctuations? Physiol Plant 137:371–382

Raven JA (2010) Inorganic carbon acquisition by eukaryotic algae: four current questions. Photosynth Res 106:123–134

Rivero RM, Shulaev V, Blumwald E (2009) Cytokinin-dependent photorespiration and the protection of photosynthesis during water deficit. Plant Physiol 150:1530–1540

Rumeau D, Peltier G, Cournac L (2007) Chlororespiration and cyclic electron flow around PSI during photosynthesis and plant stress response. Plant Cell Environ 30:1041–1051

Saha B, Borovskii G, Panda SK (2016) Alternative oxidase and plant stress tolerance. Plant Signal Behav 12:e1256530

Saroussi SI, Wittkopp TM, Grossman AR (2016) The type II NADPH dehydrogenase facilitates cyclic electron flow, energy-dependent quenching, and chlororespiratory metabolism during acclimation of *Chlamydomonas reinhardtii* to nitrogen deprivation. Plant Physiol 170:1975–1988

Satoh A, Kurano N, Senger H, Miyachi S (2002) Regulation of energy balance in photosystems in response to changes in CO_2 concentrations and light intensities during growth in extremely-high-CO_2-tolerant green microalgae. Plant Cell Physiol 43:440–451

Scandalios JG (2005) Oxidative stress: molecular perception and transduction of signals triggering antioxidant gene defenses. Braz J Med Biol Res 38:995–1014

Sewelam N, Jaspert N, Van Der Kelen K, Tognetti VB, Schmitz J, Frerigmann H, Stahl E, Zeier J, Van Breusegem F, Maurino VG (2014) Spatial H_2O_2 signaling specificity: H_2O_2 from chloroplasts and peroxisomes modulates the plant transcriptome differentially. Mol Plant 7:1191–1210

Shikanai T, Yamamoto H (2017) Contribution of cyclic and pseudo-cyclic electron transport to the formation of proton motive force in chloroplasts. Mol Plant 10:20–29

Siedlecka A, Krupa Z (1996) Interaction between cadmium and iron and its effects on photosynthetic capacity of primary leaves of *Phaseolus vulgaris*. Plant Physiol Biochem 34:833–841

Silva EN, Silveira JAG, Ribeiro RV, Vieira SA (2015) Photoprotective function of energy dissipation by thermal processes and photorespiratory mechanisms in *Jatropha curcas* plants during different intensities of drought and after recovery. Environ Exp Bot 110:36–45

Sorhagen K, Laxa M, Peterhansel C, Reumann S (2013) The emerging role of photorespiration and non-photorespiratory peroxisomal metabolism in pathogen defence. Plant Biol 15:723–736

Strand DD, Livingston AK, Satoh-Cruz M, Froehlich JE, Maurino VG, Kramer DM (2015) Activation of cyclic electron flow by hydrogen peroxide in vivo. Proc Natl Acad Sci USA 112:5539–5544

Strodtkotter I, Padmasree K, Dinakar C, Speth B, Niazi PS, Wojtera J, Voss I, Do PT, Nunes-Nesi A, Fernie AR, Linke V, Raghavendra AS, Scheibe R (2009) Induction of the AOX1D isoform of alternative oxidase in *A. thaliana* T-DNA insertion lines lacking isoform AOX1A is insufficient to optimize photosynthesis when treated with antimycin A. Mol Plant 2:284–297

Suo J, Zhao Q, David L, Chen S, Dai S (2017) Salinity response in chloroplasts: Insights from gene characterization. Intl J Mol Sci 18:1011

Suorsa M (2015) Cyclic electron flow provides acclimatory plasticity for the photosynthetic machinery under various environmental conditions and developmental stages. Front Plant Sci 6:800

Suzuki N, Koussevitzky S, Mittler R, Miller G (2012) ROS and redox signaling in the response of plants to abiotic stress. Plant Cell Environ 35:259–270

Szal B, Lukawska K, Zdolinska I, Rychter AM (2009) Chilling stress and mitochondrial genome rearrangement in the MSC16 cucumber mutant affect the alternative oxidase and antioxidant defense system to a similar extent. Physiol Plant 137:435–445

Szymanska R, Slesak I, Orzechowska A, Kruk J (2017) Physiological and biochemical responses to high light and temperature stress in plants. Environ Exp Bot 139:165–177

Takagi D, Hashiguchi M, Sejima T, Makino A, Miyake C (2016) Photorespiration provides the chance of cyclic electron flow to operate for the redox-regulation of P700 in photosynthetic electron transport system of sunflower leaves. Photosynth Res 129:279–290

Takahashi S, Badger MR (2011) Photoprotection in plants: a new light on photosystem II damage. Trends Plant Sci 16:53–60

Tsonev T, Wahbi S, Sun P, Sorrentino G, Centritto M (2014) Gas exchange, water relations and their relationships with photochemical reflectance index in *Quercus ilex* plants during water stress and recovery. Int J Agr Biol 16:335–341

Vanlerberghe GC (2013) Alternative oxidase: a mitochondrial respiratory pathway to maintain metabolic and signaling homeostasis during abiotic and biotic stress in plants. Int J Mol Sci 14:6805–6847

Vanlerberghe GC, Day DA, Wiskich JT, Vanlerberghe AE, McIntosh L (1995) Alternative oxidase activity in tobacco leaf mitochondria (dependence on tricarboxylic-acid cycle-mediated redox regulation and pyruvate activation). Plant Physiol 109:353–361

Vanlerberghe GC, Martyn GD, Dahal K (2016) Alternative oxidase: a respiratory electron transport chain pathway essential for maintaining photosynthetic performance during drought stress. Physiol Plant 157:322–337

Verslues PE, Agarwal M, Katiyar-Agarwal S, Zhu J, Zhu JK (2006) Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. Plant J 45:523–539

Voss I, Sunil B, Scheibe R, Raghavendra AS (2013) Emerging concept for the role of photorespiration as an important part of abiotic stress response. Plant Biol 15:713–722

Wada S, Suzuki Y, Takagi D, Miyake C, Makino A (2018) Effects of genetic manipulation of the activity of photorespiration on the redox state of photosystem I and its robustness against excess light stress under CO_2-limited conditions in rice. Photosynth Res. https://doi.org/10.1007/s11120-018-0515-y

Walker BJ, Strand DD, Kramer DM, Cousins AB (2014) The response of cyclic electron flow around photosystem I to changes in photorespiration and nitrate assimilation. Plant Physiol 165:453–462

Wang R, Chen S, Zhou X, Shen X, Deng L, Zhu H, Shao J, Shi Y, Dai S, Fritz E, Huttermann A, Polle A (2008) Ionic homeostasis and reactive oxygen species control in leaves and xylem sap of two poplars subjected to NaCl stress. Tree Physiol 28:947–957

Wang Y, Duanmu D, Spalding MH (2011) Carbon dioxide concentrating mechanism in *Chlamydomonas reinhardtii*: inorganic carbon transport and CO_2 recapture. Photosynth Res 109:115–122

Wang H, Huang J, Liang X, Bi Y (2012) Involvement of hydrogen peroxide, calcium, and ethylene in the induction of the alternative pathway in chilling-stressed Arabidopsis callus. Planta 235:53–67

Wang JH, Li SC, Sun M, Huang W, Cao H, Xu F, Zhou NN, Zhang SB (2013a) Differences in the stimulation of cyclic electron flow in two tropical ferns under water stress are related to leaf anatomy. Physiol Plant 147:283–295

Wang S, Chen F, Mu S, Zhang D, Pan X, Lee D-J (2013b) Simultaneous analysis of photosystem responses of *Microcystis aeruginoga* under chromium stress. Ecotoxicol Environ Saf 88:163–168

Wang S, Pan X, Zhang D (2015) PSI showed higher tolerance to Sb(V) than PSII due to stimulation of cyclic electron flow around PSI. Curr Microbiol 70:27–34

Wang Y, Berkowitz O, Selinski J, Xu Y, Hartmann A, Whelan J (2018) Stress responsive mitochondrial proteins in Arabidopsis thaliana. Free Radic Biol Med. https://doi.org/10.1016/j.freeradbiomed.2018.03.031

Wanniarachchi VR, Dametto L, Sweetman C, Shavrukov Y, Day DA, Jenkins CLD, Soole KL (2018) Alternative respiratory pathway component genes (AOX and ND) in Rice and Barley and their response to stress. Int J Mol Sci 19:915

Watanabe CK, Hachiya T, Terashima I, Noguchi K (2008) The lack of alternative oxidase at low temperature leads to a disruption of the balance in carbon and nitrogen metabolism, and to an up-regulation of antioxidant defence systems in *Arabidopsis thaliana* leaves. Plant Cell Environ 31:1190–1202

Watanabe CK, Hachiya T, Takahara K, Kawai-Yamada M, Uchimiya H, Uesono Y, Terashima I, Noguchi K (2010) Effects of AOX1a deficiency on plant growth, gene expression of respiratory components and metabolic profile under low-nitrogen stress in *Arabidopsis thaliana*. Plant Cell Physiol 51:810–822

Watanabe CK, Yamori W, Takahashi S, Terashima I, Noguchi K (2016) Mitochondrial alternative pathway-associated photoprotection of photosystem II is related to the photorespiratory pathway. Plant Cell Physiol 57:1426–1431

Wingler A, Lea PJ, Quick WP, Leegood RC (2000) Photorespiration: metabolic pathways and their role in stress protection. Philos Trans R Soc B 355:1517–1529

Xu F, Yuan S, Lin H (2011) Response of mitochondrial alternative oxidase (AOX) to light signals. Plant Signal Behav 6:55–58

Yamori W, Shikanai T (2016) Physiological functions of cyclic electron transport around photosystem I in sustaining photosynthesis and plant growth. Annu Rev Plant Biol 67:81–106

Yi XP, Zhang YL, Yao HS, Han JM, Chow WS, Fan DY, Zhang WF (2018) Changes in activities of both photosystems and the regulatory effect of cyclic electron flow in field-grown cotton (*Gossypium hirsutum* L.) under water deficit. J Plant Physiol 220:74–82

Yiotis C, Manetas Y (2010) Sinks for photosynthetic electron flow in green petioles and pedicels of *Zantedeschia aethiopica*: evidence for innately high photorespiration and cyclic electron flow rates. Planta 232:523–531

Yoshida K, Watanabe CK, Terashima I, Noguchi K (2011) Physiological impact of mitochondrial alternative oxidase on photosynthesis and growth in *Arabidopsis thaliana*. Plant Cell Environ 34:1890–1899

Yuan H, Cheung CY, Poolman MG, Hilbers PA, van Riel NAW (2016) A genome-scale metabolic network reconstruction of tomato (*Solanum lycopersicum* L.) and its application to photorespiratory metabolism. Plant J 85:289–304

Zarattini M, Forlani G (2017) Toward unveiling the mechanisms for transcriptional regulation of proline biosynthesis in the plant cell response to biotic and abiotic stress conditions. Front Plant Sci 8:927

Zhang ZS, Peng XX (2016) Multifunctional roles of photorespiration and its regulation for the balance. Plant Physiol 52:1692–1702

Zhang SP, Scheller HV (2004) Photoinhibition of photosystem I at chilling temperature and subsequent recovery in Arabidopsis. Plant Cell Physiol 45:1595–1602

Zhang ZS, Liu MJ, Scheibe R, Selinski J, Zhang LT, Yang C, Meng XL, Gao HY (2017) Contribution of the alternative respiratory pathway to PSII photoprotection in C3 and C4 plants. Mol Plant 10:131–142