Review

Physiological roles of plastid terminal oxidase in plant stress responses

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The plastid terminal oxidase (PTOX) is a plastoquinol oxidase localized in the plastids of plants. It is able to transfer electrons from plastoquinone (PQ) to molecular oxygen with the formation of water. Recent studies have suggested that PTOX is beneficial for plants under environmental stresses, since it is involved in the synthesis of photoprotective carotenoids and chlororespiration, which could potentially protect the chloroplast electron transport chain (ETC) from over-reduction. The absence of PTOX in plants usually results in photo-bleached variegated leaves and impaired adaptation to environment alteration. Although PTOX level and activity has been found to increase under a wide range of stress conditions, the functions of plant PTOX in stress responses are still disputed now. In this paper, the possible physiological roles of PTOX in plant stress responses are discussed based on the recent progress.

1. Introduction

Plastid terminal oxidase (PTOX), a plastid-localized plasto-quinol (PQ)/O_2 oxidoreductase, exists widely in photosynthetic species including algae and higher plants (Carol and Kuntz 2001; Kuntz 2004). Evidence indicates that PTOX is encoded by a single gene in the genomes of higher plants, and by two genes in the genomes of some eukaryotic algae (Wang *et al*. 2009). Protein sequence analysis implies that PTOX from different species are conserved in several domains, such as iron-binding residues and trans-membrane segments. Therefore, PTOX was proposed to be an interfacial membrane protein with a di-iron carboxylate centre in the active site (Aluru and Rodermel 2004; Wang *et al*. 2009). Under the guidance of a transit peptide, PTOX could enter into the chloroplast, and locate to the stromal lamellae of thylakoid membrane with the orientation towards stromal side (Joët *et al*. 2002; Kong *et al*. 2003; Lennon *et al*. 2003). Since its first isolation in *Arabidopsis*, PTOX has been cloned from many plant species, and its role in plant metabolism is getting increased attention (Carol and Kuntz 2001; Kuntz 2004). Many studies showed that PTOX could be a co-factor of carotenoid biosynthesis and play an

important role in chloroplast biogenesis (Carol and Kuntz 2001; Aluru *et al*. 2006). There was also evidence that PTOX is the terminal oxidase of chlororespiration and regulates the redox state of the PQ pool (Aluru and Rodermel 2004; Peltier and Cournac 2002).

In addition, PTOX displays clear sequence similarity to the plant alternative oxidase (AOX), which performs as terminal oxidase in the alternative pathway of mitochondrial respiration by transferring electrons from ubiquinol to molecular oxygen (O_2) (Aluru and Rodermel 2004). The PTOX enzymatic activity was also sensitive to the known AOX inhibitors, e.g. *n*-propyl gallate and salicylhydroxamic acid. Thus, PTOX in chloroplasts has been suggested to be functionally analogous to AOX in mitochondria (Aluru and Rodermel 2004; Kuntz 2004). Many studies revealed that AOX plays important roles during particular processes, such as florescence, and during environmental stresses, because of the induced AOX level and its function in reducing reactive oxygen (ROS) generation (Zhao *et al*. 2007; Lei *et al*. 2010). An increased level of PTOX under changing environmental conditions, e.g. temperature/light, etc., was detected in many plants (Rumeau *et al*. 2007). Therefore, it is likely that PTOX plays a physiological role in plant stress responses. This

paper will focus on recent discoveries on the relationship between PTOX and environmental stresses, and discuss the possible functions of PTOX in plant stress responses.

2.   Involvement of PTOX in the synthesis of photoprotective carotenoids

Carotenoids, which serve as accessory pigments of photosynthesis, are also known as photoprotective agents against photo-oxidation in plants. The coloured carotenoids are synthesized within plastids from a non-coloured precursor called phytoene and catalysed by enzymes including the indispensable phytoene desaturase (PDS) and downstream zeta-carotene desaturase (ZDS) (Carol and Kuntz 2001). Catalytic activity of PDS and ZDS has been shown to require several redox components including PQ and O_2. As a PQ/O_2 oxidoreductase, plant PTOX has been regarded as an important co-factor of carotenoid biosynthesis by transferring the electrons derived from PDS and ZDS steps to O_2 via the PQ pool (Carol and Kuntz 2001; Aluru and Rodermel 2004) (figure 1).

Therefore, the lack of PTOX will lead to the blockage of carotenoids synthesis at the PDS step due to the over-reduction of the PQ pool (Carol and Kuntz 2001). This is the case in the well-known *Arabidopsis* mutant *immutans*, which has variegated white and green sectors in leaves and is sensitive to photo-oxidative stress. Absence of PTOX in *immutans* plants results in the inhibition of phytoene desaturation, and then causes phytoene accumulation and lack of photoprotective carotenoids. Without the protection of carotenoids, chlorophylls and other contents of the plastid would suffer from photo-oxidation, and photo-bleached white sectors will appear (Aluru *et al*. 2006). Consistent with this idea, the white sector formation was shown to be enhanced under increasing light intensity and temperature conditions, due to increasing photo-oxidation (Rodermel 2002). Enhanced formation of white sectors in variegated leaves probably aggravates the impairment of photosynthesis capacity, and reduces the adaptation to environment changes. The same situation was also observed in the tomato mutant *ghost*, in which PTOX deficiency leads to poorly coloured flowers and fruits, in addition to bleached leaves (Aluru and Rodermel 2004). Therefore, PTOX may be beneficial in preventing significant decrease of chlorophyll content during carotenogenesis, thus maintaining essential photosynthesis capacity under environmental stresses, especially when photo-oxidation occurs.

Apart from high light irradiation, carotenogenesis coupled with PTOX was also suggested to play a role against oxidative stress caused by many other environmental conditions. For example, the PTOX-dependent biosynthesis of red carotenoid astaxanthin in algae *Haematococcus pluvialis* could consume
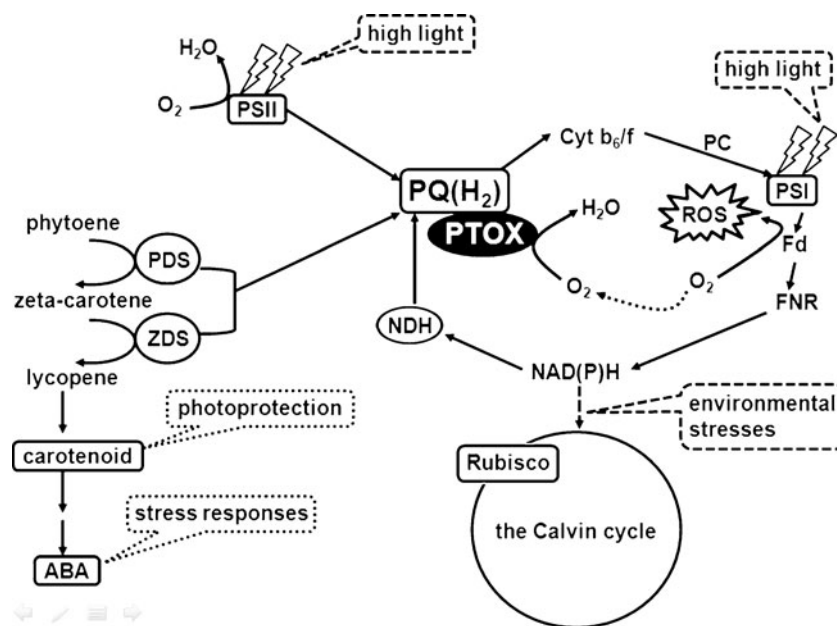

Figure 1.   A scheme for the proposed roles of plant PTOX under environmental stresses. PTOX is suggested to be involved in the stress responses through (1) serving as an important co-factor of photoprotective carotenoids synthesis; (2) reducing ROS generation by preventing the over-reduction of PQ pool when exposed to stress conditions (e.g. absorbing light energy at a rate faster than it can be utilized for CO_2 assimilation under high light, or lower demand for electrons required for carbon fixing reactions under stresses such as salinity and drought); (3) other pathways such as PTOX-dependent O_2-consumption reactions and ABA biosynthesis.

excess oxygen effectively (Li *et al.* 2008). Under environmental stresses, such as salinity or excess metals, subcellular O_2 concentration (in particular surrounding the thylakoid membrane) would be reduced since the stimulated PTOX expression and astaxanthin synthesis prevent the O_2-dependent generation of ROS (Li *et al.* 2008, 2010). Besides, the use of PTOX inhibitor to *H. pluvialis* was shown to cause severe membrane lipid peroxidation with reduced astaxanthin content under stress conditions (Wang *et al.* 2009). Therefore, a protective role for PTOX under stresses may be hypothesized.

Carotenoids are not only directly involved in protection but also act as precursors of abscisic acid (ABA), which is a plant hormone known to relieve damage caused by environment stresses (Carol and Kuntz 2001). A study on rice further indicated that ABA was an inducer of PTOX expression (Kong *et al.* 2003). Therefore, a possible role of PTOX in ABA-induced plant stress responses by facilitating carotenoid production could be also proposed.

3. Induced PTOX level and chlororespiration activity under environmental stresses

Chlororespiration, which refers to a respiratory electron transfer chain (ETC), interacts with the photosynthetic ETC in thylakoid membranes of chloroplasts. It represents an alternative electron transfer pathway and involves the reduction of PQ by NAD(P)H dehydrogenase (NDH) and the oxidation of reduced PQ by PTOX as the terminal oxidase (Peltier and Cournac 2002)

(figure 1). In plants grown under normal conditions, PTOX is only present at about 1% of the level of photosystem II (PSII), and is believed to be a minor component of thylakoid membranes (Lennon *et al.* 2003). However, many studies detected an induced PTOX level in plants exposed to various stress conditions (table 1). For example, the activity of both PTOX and NDH were stimulated to be associated with their increased amounts in oat plants under high light and heat treatments (Quiles 2006; Tallón and Quiles 2007). Increased PTOX level was also observed in rice under salt stress and in Lodgepole pine when acclimated to winter cold (Kong *et al.* 2003; Savitch *et al.* 2010). Besides higher plants, up-regulation of PTOX expression was also detected in algae, such as *H. pluvialis* under high light and *Chlamydomonas reinhardtii* under phosphate deprivation (Moseley *et al.* 2006; Li *et al.* 2008; Wang *et al.* 2009). Furthermore, an analysis on the promoter of *H. pluvialis* PTOX gene revealed several light responsive elements and environmental stress *cis*-acting elements response to drought and low temperature (Wang *et al.* 2009). These potential regulatory elements suggested that PTOX could be induced and might be involved in multiple functions in response to various stress conditions.

More persuasive evidence comes from studies on plant species with different stress tolerances. For example, the wild species *Brassica fruticulosa* has higher stress tolerance than the related agricultural species *Brassica oleracea*. Although the level of PTOX in both species increased when exposed to high light intensity and heat, much higher amount and activity of PTOX was detected in *B. fruticulosa* than in *B. oleracea* (Díaz *et al.* 2007). Chen and Guo (2008)

Table 1. A summary of up-regulated level of PTOX detected in various higher plant and algae species under different stress conditions

Groups	Species	Stress conditions	Detected levels	References
Higher plants	*Avena sativa*	Heat; high light	Protein; activity	Quiles 2006; Tallón and Quiles 2007
	Brassica fruticulosa	Heat; high light	Protein; activity	Díaz *et al.* 2007
	Brassica oleracea	Heat; high light	Protein; activity	Díaz *et al.* 2007
	Coffea arabica	Drought	mRNA	Simkin *et al.* 2008
	Oryza sativa	Salinity	mRNA	Kong *et al.* 2003
	Pinus banksiana	Cold; short daylight	Protein	Busch *et al.* 2008
	Pinus contorta	Cold	Protein	Savitch *et al.* 2010
	Ranunculus glacialis	Cold; high light	Protein	Streb *et al.* 2005
	Solanum lycopersicum	High light	Protein	Shahbazi *et al.* 2007
	Spathiphyllum wallisii	Drought; heat; high light	Protein	Gamboa *et al.* 2009; Ibáñez *et al.* 2010
	Thellungiella halophila	Salinity	Protein; activity	Stepien and Johnson 2009
Algae	*Chlamydomonas reinhardtii*	Phosphate deprivation	mRNA	Moseley *et al.* 2006
	Haematococcus pluvialis	High light; iron excess; salinity	mRNA	Li *et al.* 2008; 2010; Wang *et al.* 2009

also detected an enhanced expression of PTOX in stress-tolerant rice plants, which overexpressed OPBP1 (a stress-related transcription factor), in comparison with the control plants. In addition, *Thellungiella*, a salt-tolerant close relative of *Arabidopsis*, accumulated significantly more PTOX than *Arabidopsis* under salt stress. The application of PTOX inhibitor obviously reduced photosynthetic electron transfer in salt-stressed *Thellungiella*, but had no effect under normal conditions (Stepien and Johnson 2009). These results all suggested that PTOX might play a protective role in stressed plants. It is well known that the chloroplast is an important ROS-generating place and is susceptible to the attack of free radicals, especially when the major photosynthetic electron transfer is inhibited under stresses. On the other hand, inhibition of the major electron transfer pathway could trigger alternative pathways including cyclic electron flow around PSI and chlororespiration in chloroplasts to alleviate ROS generation (Rumeau *et al*. 2007). Therefore, as the terminal oxidase of chlororespiration, PTOX would be considered to play a role in regulating the photosynthetic electron flow and in minimizing the generation of ROS when induced under environmental stresses (Aluru and Rodermel 2004; McDonald *et al*. 2011). Besides, PTOX was indicated to be induced more than 10-fold in a tobacco *psbA* gene deletion mutant, which was devoid of PSII complexes (Baena-González *et al*. 2003). The level of PTOX was detected about 210% higher in a tobacco *rbcL* deletion mutant, which lacks the key enzyme Rubisco for photosynthetic carbon assimilation (Allahverdiyeva *et al*. 2005). It is well known that deletion of these important components would ravage the photosynthetic ETC seriously. Thus, the protective function of PTOX when stress-caused inhibition of photosynthetic ETC happens could be proposed.

PTOX has been suggested to reduce the generation of ROS by preventing the over-reduction of PQ pool in chloroplasts, just like its analogue AOX dose in mitochondria (Aluru and Rodermel 2004). As an alternative electron sink, when plants are exposed to stress conditions, induced PTOX could effectively transfer excess electrons to O_2, and maintain the relative redox balance of photosynthetic ETC, and then lower the possibility for oxidative damage (McDonald *et al*. 2011) (figure 1). Streb *et al*. (2005) detected significantly high PTOX content in a high mountain plant species *Ranunculus glacialis*, which has weak chloroplastic antioxidation system. The high PTOX content could be regarded as a crucial strategy for *R. glacialis* to transfer electrons without generating ROS, in order to survive on high mountains with extreme and changeable environmental conditions. Rizhsky *et al*. (2002) reported that in double antisense tobacco plants lacking two H_2O_2-detoxiying enzymes, catalase and ascorbate peroxidase, the expression

of PTOX was stimulated. This result also implied that PTOX contributed to the antioxidation mechanisms of plants. This suggestion was further supported by the evidence that plants that provided higher amount of PTOX accumulated lower level of ROS (Díaz *et al*. 2007; Ibáñez *et al*. 2010), and inhibition of PTOX activity resulted in more severe membrane lipid peroxidation under stress conditions (Wang *et al*. 2009).

In addition, a study on rice revealed the co-existence of two splicing mechanisms in PTOX gene expression: the normal splicing resulted in functional PTOX transcript *OsIM1*, and the abnormal splicing led to the pseudo-transcript *OsIM2* (Kong *et al*. 2003). Alternative splicing has been suggested to participate in the plant stress responses (Barbazuk *et al*. 2008). So, the co-existence of two PTOX splicing mechanisms may have important functions in rice, even in a wide range of plants under stress conditions. Kong *et al*. (2003) further indicated that the ratio of *OsIM1*/*OsIM2* increased steadily under salt stress in stress-tolerant varieties, while the ratio reached a peak in a short time and then declined in stress-sensitive varieties. This difference implied that PTOX-related stress tolerance probably not only resulted from the increased expression of PTOX, but also the regulation of alternative splicing.

4. Does PTOX act as a universal safety valve for the adaptation of photosynthesis to environmental stresses?

Although many studies detected an increased level of PTOX in stressed plants, there were also studies arguing that PTOX did not act as a safety valve in protection on photosynthesis but more likely played important roles in development (Shahbazi *et al*. 2007; Busch *et al*. 2008; Okegawa *et al*. 2010). Rosso *et al*. (2006) tested the level of *Arabidopsis* PTOX under several stress conditions. Results showed that the expression of PTOX was modulated minimally by stresses (e.g. salt, cold) and stress-related hormones (e.g. ABA), but was clearly related to development. Overexpression of PTOX did not result in increased capacity to keep the PQ pool oxidized compared to the wild type and *immutans* type, even under stresses. Therefore, PTOX was suggested to play an important role in chloroplast biogenesis rather than in stress responses (Rosso *et al*. 2006). However, further investigation indicated that PTOX-related stress resistance existed in *Thellungiella*, a salt-tolerant close relative of *Arabidopsis* (Stepien and Johnson 2009). Recent studies on *Chrysanthemum morifolium* (a sun species) and *Spathiphyllum wallisii* (a shade species) suggested that chlororespiration involving NDH and PTOX was an important stress response in the shade species, whereas in sun species, cycle electron transfer around PSI depending on PGR5 (proton gradient regulation 5) was more

active in response to stresses (Gamboa *et al.* 2009; Ibáñez *et al.* 2010). These results suggested that different plants might have different strategies to adapt to stress conditions, and that induced PTOX could be regarded as a beneficial safety valve for certain plants such as *Thellungiella* and some shade species.

Studies on transgenic tobacco showed that PTOX over-expression did not protect PSII against photo-inhibition, and even promoted oxidative stress under high light (Joët *et al.* 2002; Heyno e*t al.* 2009). It was indicated that intermediate formation in a side reaction was difficult to avoid during the reduction of O_2 to H_2O by PTOX. This process may lead to the generation of ROS like superoxide or peroxide in chloroplasts. In this case, if PTOX activity is not tightly coupled with an efficient antioxidant system like superoxide dismutase (SOD), protection from PTOX would not occur and the stresses plant would suffer increased oxidative damage (Heyno *et al.* 2009). Thus, a high level of PTOX alone may not be sufficient to improve the stress tolerance of plants. PTOX-related stress tolerance relies not only on the induced level and activity of PTOX but also on the necessary coupling between PTOX activity and other stress responses.

Acclimation of photosynthesis and other physiological process to environmental stresses is a complex process and may vary in different plants. We propose that PTOX could be helpful under stress conditions in certain plants just like *Thellungiella* and *R. glacialis*, in which additional PTOX-related physiological regulation may exist in response to stresses, but probably does not acts as a universal or essential safety valve in the whole plant kingdom. Pathways such as cycle electron transfer around PSI depending on PGR5 may act as preferred protective strategies in other plants. This explanation is expected to resolve the contradictions in previous studies with different plant species and kinds. However, how to distinguish the PTOX-dependent species or kinds of plants remains to be clarified.

5. Concluding remarks and future perspectives

In summary, a role for PTOX in stressed plants is proposed due to its involvement in carotenoid biosynthesis and its PQ oxidase activity in chlororespiration (figure 1). Although the protective functions may not be universal in the whole plant kingdom, increased PTOX level and the coupling between PTOX activity and other stress tolerance systems could be regarded as effective strategy in many plants to alleviate the effects of particular environmental stresses. However, since stress responses in plants are complex mechanisms, the functions of PTOX in stressed plants are still disputed. There is limited evidence to clarify the exact role of PTOX in plant stress responses. Further studies are needed to understand why PTOX can benefit many stress-tolerant plants like *Thellungiella* and *R. glacialis* in response to environmental stresses while different strategies are chosen by other plants. And further investigations on PTOX expression and activity, as well as PTOX-related physiological mechanisms, are necessary in order to understand the function and regulation of PTOX in plant stress responses.

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