

General aspects of plant thioredoxins

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ABSTRACT

Chloroplast is the organelle for photosynthesis in eukaryotic cells. In it the presence of a light-dependent ferredoxin/thioredoxin system (FTS) and a NADPH-dependent thioredoxin reductase C (NTRC), have been implicated in plant defense response and at the same time constitute important redox mechanism to provide reducing power to thioredoxins. This organelle also has a critical role in plant innate immunity against pathogen infection, where thioredoxins are the major responsible of to maintain proteins in their reduced state. The present work present a review of the scientific literature about some important aspects of plant thioredoxins.

Keywords: chloroplast, innate immunity, photosynthesis, redox control, stress

Aspectos generales de las tioredoxinas en plantas

RESUMEN

El cloroplasto es el organelo para la fotosíntesis en células eucariotas. En él la presencia del sistema luz-dependiente ferredoxina/tioredoxina (FTS) y de una tioredoxina reductasa C NADPH-dependiente (NTRC), han estado implicados en la respuesta de defensa y al mismo tiempo constituyen importantes mecanismos redox que proveen poder reductor a las tioredoxinas. Este organelo también tiene un papel crítico en la inmunidad innata de las plantas contra la infección de patógenos, donde las tioredoxinas son las principales responsables de mantener las proteínas en su estado reducido. En el presente trabajo se presenta una revisión de la literatura científica acerca de aspectos importantes de las tioredoxinas de plantas.

Palabras clave: cloroplasto, control redox, estrés, fotosíntesis, inmunidad innata

INTRODUCTION

Chloroplasts are the organelle for photosynthesis in eukaryotic cells. Besides, they carry on some other important functions like amino acids, hormones, vitamins, secondary metabolites and lipid biosynthesis, which are components of metabolic pathways and play important roles during stress response and signaling in plant cells (Rolland *et al.*, 2012; Seyfferth and Tsuda, 2014).

In this organelle, the presence of a ferredoxin-thioredoxin system (FTS) is linked to photosystem I (PSI) and regulates various chloroplast enzymes. This system together with a NADPH-dependent thioredoxin reductase C (NTRC), provide the reducing power to thioredoxins (TRXs) for their essential role on redox regulation based on disulfide-dithiol conversion of numerous target proteins (Montrichard *et al.*, 2009).

Plants contain several genes encoding TRXs, ubiquitous small oxidoreductases (12 to 14 kDa) which are involved in cell redox regulation. The TRX system in plants is very complex respect to other organisms and based on their primary structure and subcellular localization TRXs have been classified in seven types. The TRXf, TRXm, TRXx, TRXy and TRXz are localized in chloroplasts, TRXo in mitochondria and TRXh mainly in the cytosol. In addition, some TRXh isoforms have also been identified in the apoplast, mitochondria, nuclei and phloem. All of them shared an active site WCG/PPC and a redox-active dithiol CxxC motif (Tovar-Méndez *et al.*, 2011).

TRXs mainly act as electron donors in various metabolic pathways, regulate enzymatic activities and keep the reduced state inside the cell (Montrichard *et al.*, 2009). By other side, a tight control of cellular homeostasis by TRXs is essential for maintenance of normal

metabolism and redox-dependent signaling. TRXs are also involved in plant defense response to pathogen infection which has been already seen by several authors (Shim *et al.*, 2004; Campo *et al.*, 2008; Martí *et al.*, 2011). More recently, Lehmann *et al.* (2015) informed that TRXs mediate the activation of the signaling cascade triggered after pathogen recognition.

The chloroplast performs an important role in innate immunity against pathogen attack. However, knowledge about the essential mechanisms involve in regulation of the photosynthetic apparatus and its relationship with the metabolic and regulatory networks of the plant is limited (Tikkanen and Aro, 2014). In this sense, a more comprehensive understanding of this interconnections and the regulatory elements involve in it still awaits future discoveries.

This review is focus on the current knowledge about the role of plant TRXs.

MAIN ROLES OF PLANT THIOREDOXINS

Redox systems

Chloroplast is the factory for photosynthesis in higher plants, a process where the solar energy is converts to chemical energy in organisms such as bacteria and plants. This photosynthetic activity influences the general energy state and redox status by providing NADPH, ATP and carbon skeletons. At the same time, it support the growth of plants and also fuels the initiation and maintenance of responses against external stress factors (Kangasjarvi *et al.*, 2012).

In the chloroplast, FTS is a well-known mechanism that triggers metabolic reactions in response to light-darkness. It comprised ferredoxin (Fd), ferredoxin-thioredoxin reductase (FTR) and TRXf, TRXm, TRXx, TRXy and TRXz. In the presence of light, the photosynthetic electron transfer chain of thylakoid membranes allows reduction of Fd, which can afterward transfer electrons to TRXs through FTR. Then, the reduced TRXs activate target enzymes by reduction of the intramolecular and intermolecular disulfide bridges formed within and between proteins, based on the dynamic changes in the redox potential. Thus, metabolism switches to anabolic pathways (Montrichard *et al.*, 2009).

In such a way, a link is established between the activity of photosynthetic light reactions and the activation of key enzymes of photosynthetic carbon fixation. In this sense, Meyer *et al.* (2005) from a proteomic approach in *Arabidopsis thaliana* revealed that 11 enzymes of the Calvin cycle can be regulated by TRXs. Later, Nuruzzaman *et al.* (2008) informed that both TRXf and TRXm are involved in the regulation of them and other key metabolic enzymes.

The NADP/TRX system is another important redox mechanism that provides reducing power to TRXs that includes NADPH, a TRX and NADPH-dependent TRX reductase (NTR), although chloroplasts contain a modified type designated NTRC. It is widely distributed among organisms and thought to be ubiquitous in aerobes. In this system, the electrons transfer from NADPH to TRXh takes place according to the sequence: NADPH-NTR-TRX-target protein (Montrichard *et al.*, 2009).

In chloroplast, another link is established between photosynthesis and translation. From the photosynthetic machinery, reducing equivalents are transmitted to EF-G (Elongation factor G) via TRXs and that protein synthesis is activated by it in a redox-dependent manner. The elongation of the polypeptide chain is sensible to oxidative stress and their apparent suppression by reactive oxygen species (ROS) could interrupt the redox regulation to prevent further oxidative injury according to Nishiyama *et al.* (2011).

Besides of the importance of these redox systems in chloroplast functionality some evidences have showed their significance during plant response to stress. In this way, Lim *et al.* (2010) informed for the first time that silencing of the tomato (*Solanum lycopersicum* L.) SIFTR-c resulted in spontaneous necrosis development related with higher ROS levels. Moreover, these silenced plants displayed higher resistance to *Pseudomonas syringae* pv. *tomato* DC3000 (Pto DC3000) by the activation of defense-related genes. Later on, another authors revealed that the loss-of-function of NTRC resulted in spreading accelerated Pto DC3000 disease-associated cell death with enhanced ROS accumulation in tomato and in *A. thaliana* (Ishiga *et al.*, 2012). In a similar study plants lacking functional NTRC showed

localized cell death (LCD) accompanied by a higher accumulation of hydrogen peroxide (H_2O_2) in response to nonhost *P. syringae* pathogens, which suggested the critical role of NTRC in plant innate immunity (Ishiga *et al.*, 2016).

In chloroplast, some important cellular functions are related with the activity of these redox systems. However, just few information support the relevance of them. Based on the current knowledge about FTS system in plants it seems that it works as an important regulator of plant cell death and defense responses but a more detailed biochemical or physiological analyses will be required to confirm it. Besides, a little more emphasis in the study of NADP/TRX system is needed due to their biological role is currently an interesting area to be explored.

Since the discovery of the role of TRXs in the context of photosynthesis, many functions have been adjudged to them. However, some biochemical, molecular and proteomics approaches are still needed to identify putative targets of TRX, which can help to elucidate the main reactions in which they are involved. At the same time, a better understanding of TRX-dependent regulation of several target enzymes is still need it mainly in the thylakoid lumen.

Thioredoxins and oxidative stress

The buildup of ROS is one of the fastest plant defense reactions in response to abiotic and biotic stress. In plants, ROS are formed by the leakage of electrons onto O_2 from the electron transport in chloroplasts, mitochondria and plasma membrane or as a byproduct of various metabolic pathways localized in different cellular compartments. The ROS produced after incomplete reduction of oxygen include superoxide anion, H_2O_2 , hydroxyl radical, while singlet oxygen is formed from energy transfer. Among these species, H_2O_2 acts as signaling molecule regulating several processes such as cell division, cell wall strengthening, systemic response induction, photosynthesis, phytoalexins production, senescence and stomatal opening (Petrov and Van Breusegem, 2012; Sharma *et al.*, 2012; Lehmann *et al.*, 2015).

Under stress conditions, the balance between the production and elimination of ROS is

disturbed. To cope with the detrimental effects of ROS for scavenging or detoxification of them, higher plants have evolved some efficient enzymatic and non-enzymatic antioxidative systems that prevent over-accumulation of redox intermediates and formation of these species. The enzymatic systems include catalase, guaiacol peroxidase, superoxide dismutase and enzymes of ascorbate glutathione cycle. At the same time, ascorbate, carotenoids, glutathione, tocopherols and flavonoids serve as potent non-enzymatic antioxidants within the cell (Aloui *et al.*, 2011; Sharma *et al.*, 2012). Regarding to TRXs, they have been included in the enzymatic antioxidant group where they have the main function of to reduce the disulphide bonds of oxidized proteins.

In plants, the functionality of the antioxidant defenses in the cellular regulation takes place through a complex network involving redox input elements, transmitters, targets and sensory proteins such as TRXs, glutaredoxins and peroxiredoxins (Dietz and Pfannschmidt, 2011).

ROS generation as one of the first plant defense responses after pathogen attack has been associated with disease resistance in plant-fungus interactions, being the hypersensitive response (HR) the most characteristic plant defense reaction (Lehmann *et al.*, 2015). In this context TRXs can act as inhibitors of cell death either directly inhibiting proteins that trigger this process or providing reducing power to proteins that scavenge ROS (Dos Santos and Rey, 2006).

The possible role of *Trx* in plant disease resistance was informed for the first time by Rivas *et al.* (2004). These authors founded that a *CITRX* interacts with the short cytoplasmic tail of *Cf-9* and regulates the signaling pathways leading to tomato defense responses against to *Cladosporium fulvum* Cooke. Furthermore, Laloi *et al.* (2004) indicated a possible implication of the cytosolic thioredoxin *AtTRXh5* in the defense response of *A. thaliana* to Pto DC3000 and in the oxidative stresses response. Besides, according to Sweat *et al.* (2007), TRXs are related with plant defense of oats (*Avena sativa* L.), because its activity is necessary for programmed cell death in response to victorin produced by *Cochliobolus victoriae* R.R, Nelson.

Another studies carried out from the analysis of cDNA libraries constructed in different pathosystems, based on the polymerase chain reaction-suppression subtractive hybridization (PCR-SSH) (Diatchenko *et al.*, 1996), have offered new evidences about the role of TRXs during host response to pathogen infection. The differential expression of *Trx* (s) was obtained in rice (*Oryza minuta*) challenged by *Magnaporthe oryzae* B.C. Couch (Shim *et al.*, 2004), during early response of 'Calcutta 4' plants to *Mycosphaerella fijiensis* Morelet infection (Mendoza-Rodríguez *et al.*, 2006) and in *Oryza sativa* L. plants at early time points after *M. oryzae* inoculation (Campo *et al.*, 2008).

The role of mitochondrial thioredoxin PsTRXo1 as a component of the defense system in pea (*Pisum sativum* L. cv. Lincoln), in providing tolerance against the salt stress was reported by Martí *et al.* (2011). Recently, Mukaihara *et al.* (2016) founded a cytosolic TRX, acting as a molecular switch for the activation of effector protein RipAY from *Ralstonia solanacearum* which degrade GSH, resulting in the suppression of plant pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI) in plants.

Previous information supports the role of TRXs during plant defense response to stress conditions. However, just few studies has been focus on the possible relevance of this gene (s) during host response to pathogen infection.

Now, it is known that the photosynthetic process is essential in plant defense to stress conditions. However, in scientific literature has been made more emphasis in the study of regulation of plant defense responses than in the effects of pathogen infection on metabolic processes such as photosynthesis. For this reason, to elucidate the impact of photosynthesis in the cell reprogramming is still a fundamental question awaiting further molecular and physiological analysis.

Chloroplasts and innate immunity

Chloroplasts have a critical role in plant innate immunity against invading pathogens. Their perception commonly promotes transient increases of ROS generation, secondary messengers that can elicit an HR in infected tissues. According to Kangasjarvi *et al.* (2014),

in plants after an oxidative bursts a transcriptome reprogramming and the induction of disease resistance takes place.

The activation of plant immunity is associated with changes in the cellular redox status, where TRXs are the main responsible of to maintain proteins in their reduced state. This mechanism of redox regulation based on disulfide-dithiol conversion of numerous target proteins, is emerging as a main regulatory system in signal transduction during plant response to biotic and abiotic stress.

Pioneering studies have linked photosynthesis and chloroplast ROS imbalances to plant immunity (Mühlenbock *et al.*, 2008). In addition, it has been informed that the mechanisms controlling photosynthetic light reactions can be involved in plant responses to biotic stress agents. At the same time, chloroplast is the main source of pro-defense molecules, which communicate and coordinate with other organelles during defense, being the H₂O₂ and salicylic acid (SA) the most significant (Kangasjarvi *et al.*, 2012; Karpinski *et al.*, 2013).

During plant defense response some signals like ROS are produced to control the nuclear gene expression to maintain the cellular homeostasis, or optimizing chloroplast functionality under stress conditions, including pathogen attacks. Low levels of ROS can exert as a retrograde signal, whereas higher levels induce oxidative damage resulting in LCD. Among them H₂O₂ function as a signaling compound in plant innate immunity (Chi *et al.*, 2015; Hossain *et al.*, 2015).

Previous researches have shown that chloroplast ROS production regulate disease-associated cell death in tomato and *Arabidopsis* (Ishiga *et al.*, 2009; Ishiga *et al.*, 2012). More recently Caplan *et al.* (2015) announced the importance of the inter-organellar communication as a vital resource for a successful innate immune response that confer defense against pathogens. At the same time, the relevance of pro-defense molecules in cell-to-cell signaling for stromules induction along the borders of HR-PCD during plant immunity was observed.

An important defense mechanism in plants called systemic acquired resistance (SAR)

confers immunity to a broad-spectrum of pathogens and results in accumulation of the signal molecule SA. Changes in gene expression during SAR require SA and is modulated by the interaction between the non-expressor of pathogenesis-related genes1 (NPR1) protein, a master regulator of plant immunity and members of the TGA family of transcription factors. This is a very well known mechanism, where under reductive conditions a biphasic change mediated by TRXs converts the inactive oligomeric complex NPR1 to an active monomeric state. Afterwards, this protein is translocated into the nucleus where it interacts with the oxidized TGA and induces the defense response genes in plants facing pathogen infection (Lehmann *et al.*, 2015).

Some experimental evidences have shown this relationship. In wheat (*Triticum aestivum* L.) overexpression of *A. thaliana* NPR1 gene (*AtNPR1*) confers resistance to *Fusarium* head blight (FHB) caused by *Fusarium graminearum* Schwabe (Makandar *et al.*, 2006). By other side, the overexpression of *NPR1* in *Arabidopsis* and tobacco enhances resistance to the bacterial blight-causing *Xanthomonas oryzae* pv. *oryzae* (Yuan *et al.*, 2007).

Even though, a more comprehensive understanding of the underlying mechanisms and regulatory networks imply in plant innate immunity after pathogen challenged have started to emerge, more studies about this theme are still needed to deciphering this complex relationship in different pathosystems.

CONCLUSION

The results presented confirm the advances reached in the understanding of chloroplast functionality and their role during plant response to pathogen infection. However, deeper studies about the role of photosynthesis in plant defense is still a question awaiting further molecular and physiological elucidation, if it is considered that different pathogenesis mechanisms can be triggered by pathogens based on their life cycle.

In spite of the huge knowledge about SA signal generation, regulation and transduction during HR cell death, defense gene expression, and/

or SAR the main question concerns about their initial recognizing and how this event triggers resistance signaling. By other side, due to the importance of reductive conditions in the development of an effective plant defense response, a better comprehension of the signaling pathways involved in photosynthesis and detoxification of ROS produced during plant-pathogen interaction is necessary.

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