Redox-dependent functional switching of plant proteins accompanying with their structural changes

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INTRODUCTION

Plants produce various kinds of reactive oxygen species (ROS) from internal and external sources, such as hydrogen peroxide (H2O2), superoxide anions, and hydroxyl radicals. They can damage cellular components or act as important signal transduction molecules to trigger the cellular defense signaling cascades (Baker and Duintje, 2005; D’Asteaux and Tolezado, 2007; Schwaabmander and Finkemeter, 2013). Thus, it is crucial for cells to detect the levels of ROS and activate defense signaling pathways (Moller and Sweetlove, 2010). To initiate cellular signaling, a cellular response to a myriad of environmental signals, plants generate redox gradients across the plasma membrane, change metabolic activities, and trigger the inactivation of the oxidative burst generating enzymes (Pignochi and Fokey, 2003; Suzuki et al., 2012).

The alteration in steady-state level of ROS and subsequent changes of intracellular redox potential are important systems to regulate cellular signaling factors linking external stimuli with intracellular signal transduction pathway in response to stresses (Finkel, 2011). Plants are autotrophic organisms that are capable of undergoing photosynthesis by which they absorbed light energy that generate high electron and transport to chloroplasts, mitochondria, and peroxisomes along a cascade of redox components. During the reactions, ATP, NADPH, and other soluble reducing equivalents of ferredoxin (Fd), and thioredoxin (Trx) are generated (Schurmann and Buchanan, 2008). In addition, the thiol/disulfide state strongly regulates the light-dependent modulation of chloroplast enzyme activities (Scheibe, 1991). On the other hand, both the chloroplast and mitochondria-originated oxidative burst of peroxisomes that are usually significant in preventing harmful effects of ROS. To defend plant cells in response to stimuli, a part of redox proteins have shown to play multiple functions through the post-translational modification with a redox-dependent manner. For the alternative switching of their cellular functions, the redox proteins change their protein structures from low molecular weight to high molecular weight (HMW) protein complexes depending on the external stress. The HMW proteins are reported to act as molecular chaperones, which enable the plants to enhance their stress tolerance. In addition, some transcription factors and co-activators have function responding to environmental stresses by redox-dependent structural changes. This review describes the molecular mechanism and physiological significance of the redox proteins, transcription factors and co-activators to protect the plants from environmental stresses through the redox-dependent structural and functional switching of the plant redox proteins.

Keywords: external stress, molecular chaperone, multiple functions, redox proteins, structural and functional switching

Reactive oxygen species (ROS) can be generated during the course of normal aerobic metabolism or when an organism is exposed to a variety of stress conditions. It can cause a widespread damage to intracellular macromolecules and play a causal role in many degenerative diseases. Like other aerobic organisms plants are also equipped with a wide range of antioxidant redox proteins, such as superoxide dismutase, catalase, glutaredoxin, thioredoxin (Trx), Trx reductase, protein disulfide reductase, and other kinds of peroxisomes that are usually significant in preventing harmful effects of ROS. To defend plant cells in response to stimuli, a part of redox proteins have shown to play multiple functions through the post-translational modification with a redox-dependent manner. For the alternative switching of their cellular functions, the redox proteins change their protein structures from low molecular weight to high molecular weight (HMW) protein complexes depending on the external stress. The HMW proteins are reported to act as molecular chaperones, which enable the plants to enhance their stress tolerance. In addition, some transcription factors and co-activators have function responding to environmental stresses by redox-dependent structural changes. This review describes the molecular mechanism and physiological significance of the redox proteins, transcription factors and co-activators to protect the plants from environmental stresses through the redox-dependent structural and functional switching of the plant redox proteins.

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reactive oxygen species (ROS) can be generated. At the start of the reaction, a primary ROS which is superoxide anion (O$_{2}^-$) can be formed by the one electron reduction of molecular oxygen. The superoxide anion (O$_{2}^-$) is dismutated by superoxide dismutase (SOD) to hydrogen peroxide (H$_2$O$_2$) which is detoxified by catalase (CAT), glutathione peroxidase (GPx), and peroxiredoxin (Prx). Once the superoxide anion (O$_{2}^-$) is formed in the presence of H$_2$O$_2$, it becomes inevitable.

Antioxidant proteins protect the damages of ROS leaking from peroxisomes. H$_2$O$_2$ can easily permeate the peroxisomal membrane and play an important role in protection of cells from ROS damages. And various ROS transmitted to the mitochondrion play a role in the adaptive response of mitochondrial redox state, especially for the reduction state of respiratory pathways. The redox signals will be transmitted to the nucleus to regulate plant growth and development.

**Figure 1** | Cellular responses against reactive oxygen species. During a variety of stress conditions (UV, environmental stress, etc.), reactive oxygen species (ROS) can be generated. At the start of the reaction, a primary ROS which is superoxide anion (O$_{2}^-$) can be formed by the one electron reduction of molecular oxygen. The superoxide anion (O$_{2}^-$) is dismutated by superoxide dismutase (SOD) to hydrogen peroxide (H$_2$O$_2$) which is detoxified by catalase (CAT), glutathione peroxidase (GPx), and peroxiredoxin (Prx). Once the superoxide anion (O$_{2}^-$) is formed in the presence of H$_2$O$_2$, it becomes inevitable.
in a reversible way. The high molecular mass oligomers can be reversibly dissociated by the treatment of reducing agents, such as DTT. Only DTT-mediated dissociated AβZIP16 can bind to DNA promoter and functions as a transcription factor. The homodimeric structure of AβZIP16 can bind to the DNA promoter of antioxidant like 2-Cys peroxiredoxin and plays as transcription factor to regulate its gene expression. If the redox balance changes to more oxidized condition, the expression level of AβZIP16 is increased. But, during severe oxidative conditions, Rap2.4a expression is decreased and lost its transcriptional activity due to oligomerization. This model is modified from the reference of Shaikhali et al. (2008).

**Functional Switching of Redox Proteins Accompanying with Their Redox-Dependent Structural Changes**

Thioredoxin is a general disulfide oxidoreductase and a ubiquitous redox protein with a single disulfide bridge in all organisms. The function of Trx is involved in numerous redox-dependent cellular processes, such as activation of ribonucleotide reductase, photosynthetic activity of plant cells, modulation of transcription factors, and promotion of a variety of diseases (Aslund and Beckwith, 1999; Balmer et al., 2003; Ravi et al., 2005). Trx also control several redox-independent cellular reactions including an assembly of T7 DNA polymerase complex and formation of filamentous phage (Feng et al., 1997; Hamdan et al., 2003). The proteins belonging to Trx group share high amino acid sequence similarity and contain a common structural motif, the Trx-fold. The Trx-fold comprises approximately 80 amino acid residues with a central core of five β-strands that are enclosed by four α-helices and two hydrophobic zones (Katti et al., 1990). The interesting point we want to focus in this review is that some of redox proteins harboring the Trx-fold have been shown to behave as molecular chaperones with their endogenous reductase function. The proteins include Trx-like domain containing protein (TDX), protein disulfide isomerase, and 2-Cys-Prx (Quan et al., 1995; Jang et al., 2004), etc. To be a molecular chaperone, it should interact with target substrates and switch its protein structures in response to external stresses with a reversible fashion (Jang et al., 2004; Lee et al., 2009; Park et al., 2009). The Trx-fold containing proteins interact with substrate proteins through their hydrophobic surfaces around their active sites and reversibly change the protein structures as the following examples.
Among the various kinds of Trx isoforms, a specific type of *Arabidopsis* Trx in cytosol, AtTrx-h3, forms various protein structures ranging from low molecular weight (LMW) protein species to HMW homo-complexes, which are verified by size exclusion chromatography, native-PAGE gel, and electro-microscopic analyses (Park et al., 2009). The AtTrx-h3 performs dual functions, acting as a disulfide reductase and as a molecular chaperone, which are closely associated with its differently sized multiple protein structures. The disulfide reductase function is observed predominantly in the LMW forms, whereas the chaperone function predominates in the HMW complexes. The multimeric structures of AtTrx-h3 are regulated by redox status. The reduction of AtTrx-h3 by DTT changes the HMW structures of AtTrx-h3 into LMW protein species, and subsequent treatment of hydrogen peroxide \((\text{H}_2\text{O}_2)\) after removal of DTT almost restores the HMW structures of AtTrx-h3. Particularly, the AtTrx-h3 polymeric structures are associated not only by the forces of hydrophobic interaction but also by the redox-dependent disulfide bonds. Two active cysteine residues in AtTrx-h3 are required for disulfide reductase activity, but not for chaperone function. Thus, the active site mutant protein, C39/42S-AtTrx-h3, is not able to reduce disulfide bonds of substrate at all, but has nearly the same chaperone activity as that of native AtTrx-h3 protein. The transgenic lines overexpressing native AtTrx-h3 or C39/42S (DM) mutant AtTrx-h3 having only the chaperone function exhibit enhanced heat shock tolerance compared to wild-type plants. From the results, it can be concluded that the AtTrx-h3 plays a pivotal role in the protection of plant cells from external stresses through its chaperone function (Park et al., 2009).

In addition to the At-Trx-h3, the plant-specific Trx-like protein containing 3 tetratricopeptide repeat (TPR) domains and a Trx motif which is designated AtTDX has a highly heat-stable property. The TPR units in AtTDX are particularly important for protein–protein interaction and formation of multi-protein complexes (Blatch and Lassle, 1999), which are characteristic properties of molecular chaperones. AtTDX has diverse protein structures consisting of monomer, dimer, oligomer, and HMW complexes. The protein also displays multiple functions, acting as a disulfide reductase, foldase chaperone, and holdase chaperone. In particular, the functions of AtTDX are closely associated with its oligomerization status. Like the AtTrx-h3, multimerization of AtTDX enhances its holdase chaperone activity, whereas dissociation promotes its disulfide reductase and foldase chaperone functions. However, when the TPR domains of AtTDX is removed, the truncated protein shows a significant enhancement of its disulfide reductase activity but results in a complete loss of the holdase chaperone function of AtTrx-h3 (Lee et al., 2009). The result suggests the TPR domains of AtTDX completely block the active site of Trx motif and play a critical role in promoting the holdase chaperone function. Moreover, the Cys mutant proteins...
AtT rx-h3 and AtTDX proteins can be found from the C-type of Arabidopsis. The results suggest that the active site Cys residues critically contribute to the reductase function but not the chaperone function. For the regulation of its multiple functions, protein structure of AtTDX is varied against external conditions. The oligomerization status of AtTDX is reversibly controlled by heat shock and ROS concentrations, which cause a transition from LMW to HMW complexes with a concomitant functional switching from a disulfide reductase and foldase chaperone to a holdase chaperone. It is generally known that the chaperone function contributes resistance to cells against external stresses. Thus, when the heat-stressed Arabidopsis of the WT, AtTDX overexpression lines, AtTDX suppression lines, and Cys-mutant (C304/307S) AtTDX overexpression lines having only the holdase chaperone function are returned to their optimal temperature, the transgenic lines overexpressing the native form and C304/307S mutant form of AtTDX recover during the post-stress recovery period. In contrast, AtTDX suppression lines of Arabidopsis show a highly sensitive phenotype against heat shock. The results can conclude that the holdase chaperone function of AtTDX plays a major role in the protection of Arabidopsis from heat stress during the heat shock and/or recovery period (Lee et al., 2009).

Another redox protein sharing a similar regulation mode with AtTrx-h3 and AtTDX proteins can be found from the C-type of NADPH-dependent Trx reductase (NTRC), which is a new member of the plant-specific NADPH-dependent Trx reductase (NTR) family. During the early evolution of chloroplasts, the NTRC appears to be originated from cyanobacteria by the transfer of this gene into the plant genome. The protein contains an N-terminal Trx reductase (TR) domain and a Trx domain at the C-terminus. The functional role of this fusion of domains in NTRC has been verified as an efficient electron donor to 2-Cys-Prx (Moon et al., 2006; Perez-Ruiz et al., 2006). Particularly, Arabidopsis NTRC shows enzymatic activity characteristic for each of its separate domains and in a combination of the TR and Trx domains (Moon et al., 2006). The disulfide reductase function of NTRC is coupled with the reducing power, NADPH, which is produced by photophosphorylation and is involved in the energy transduction processes in the light conditions. The knockout mutant of Arabidopsis NTRC exhibits growth inhibition under stress conditions and shows reduced auxin levels (Serrato et al., 2001; Kim et al., 2002, 2012; Hess et al., 2004; D’Autreaux and Toledano, 2007; Salminen et al., 2008; Rodriguez-Rosales et al., 2009; Ji et al., 2013). Thus, these elaborate functional regulation patterns of NTRC have various oligomeric conformations in other species like rice, barrel medic, and barley (Alkhalfioui et al., 2007; Perez-Ruiz and Cejudo, 2009; Wuelf et al., 2011). That is, NTRC assembles into homoplastic structures of varying complexity with functions as a disulfide reductase, a foldase chaperone, and as a holdase chaperone. The multiple functions of NTRC are also associated with its protein structures. Complexes of HMW show stronger activity as a holdase chaperone, whereas the LMW species exhibit weaker holdase chaperone activity with stronger disulfide reductase and foldase chaperone activities (Table 1). Heat shock converts LMW proteins into HMW complexes and gradually increases the holdase chaperone function of NTRC. Upon the heat shock treatment, NTRC results in a decrease in its disulfide reductase and foldase chaperone activities. In conclusion, heat shock-mediated oligomeric changes of NTRC are mostly associated with a change in its functional switching from a disulfide reductase to a molecular chaperone.

### CONCLUSION AND PERSPECTIVE

To cope with external stresses, plants regulate their protein functions by employing a number of efficient regulation strategies, such as phosphorylation/dephosphorylation, covalent modification, proteolytic degradation or activation, interacting with partner proteins, and so on. However, at recent, the post-translational modification is identified as one of the most important, rapid and precise methods to respond eukaryotic cells against environmental stresses. The redox-dependent functional switching is a typical scheme for the plant defense systems. Particularly, the functional shift of the redox proteins is accompanied with their structural changes in response to redox changes. In this review, we introduce several examples of the redox proteins to respond to environmental circumstances. However, besides the redox proteins in eukaryotes, many redox-independent proteins showing similar regulation pattern with the proteins have also been identified from various sources, such as plant phosphodiesterase, sodium/proton antiporter (NHX), salt overly sensitive 1 (SOS1), mammalian nuclear factor kappa beta (mammalian NF-kB) and AP1, yeast Yap1, bacterial OxyR/S, and so on (Zheng et al., 1998; Toone et al., 2001; Kim et al., 2002, 2012; Hess et al., 2004; D’Autreaux and Toledano, 2007; Salminen et al., 2008; Rodriguez-Rosales et al., 2009; Ji et al., 2013). Thus, these elaborate functional regulation modes allow higher eukaryotic organisms to precisely respond to external stresses and to survive from the harsh and changeable environmental conditions. This review provides valuable insights into how plants can respond to the rapid changes of redox potential induced by biotic/abiotic stresses at the molecular level.

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| NTRC Redox state | Reduction | Oxidation |
|------------------|-----------|-----------|
| **Protein structures** | Low molecular weight species | High molecular weight complexes |
|                   | Monomer | Dimer    | Oligomer  |
| **Functions** | Disulfide reductase | Holdase chaperone |
| Foldase chaperone |           |          |

Table 1 | Structural and functional switching of NTRC in Arabidopsis thaliana in response to redox state.
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