



Review

Glutaredoxins in plant development, abiotic stress response, and iron homeostasis: From model organisms to crops



Qingyu Wu^{a,**}, Jian Yang^b, Ninghui Cheng^b, Kendal D. Hirschi^b, Frank F. White^c, Sunghun Park^{a,*}

^a Department of Horticulture and Natural Resources, Kansas State University, Manhattan, KS 66506, USA

^b United States Department of Agriculture/Agricultural Research Service, Children's Nutrition Research Center, Department of Pediatrics, Baylor College of Medicine, Houston, TX 77030, USA

^c Department of Plant Pathology, University of Florida, Gainesville, FL 32611, USA

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ABSTRACT

Plant growth, development, and response to environmental stress require the judicious balance of reactive oxygen species (ROS). Glutaredoxins (GRXs) are a group of oxidoreductases that participate in the control of ROS and are traditionally defined as redox regulators. New studies suggest the members of the GRX family may be involved in more biological processes than previously ascribed. While the core structure of GRX proteins are similar, localization and expression differences afford a multiplicity of functions between species and individual isoforms. Emerging evidence indicates that various plant monothiol GRXs perform diverse functions, including transcriptional regulation of defense responses, flower development, oxidative stress response, redox signaling, hormonal regulation, iron homeostasis, and environmental adaptation. This review highlights the recent progress in our understanding of the roles played by class II CGFS-type and class III CC-type GRXs in plant development, abiotic stress adaptation, iron homeostasis, and crop productivity. In particular, the abiotic stress tolerance functions of class II GRXs make them attractive targets for genetic engineering, potentially providing enhancements in salt, drought, heavy metal, and temperature stress responses.

1. Introduction

Reactive oxygen species (ROS) are formed as by-products in all oxygenic organisms during aerobic metabolism (Halliwell, 2006). In angiosperms, chloroplasts/plastids and mitochondria contribute to production of ROS during photosynthesis and carbon metabolism (Apel and Hirt, 2004). Glutaredoxins (GRXs) are disulfide oxidoreductases (thioltransferase) that catalyze reversible reduction of disulfide bonds of substrate proteins by using the reducing power of glutathione (GSH) and function in scavenging cellular ROS and regulating redox homeostasis within these organelles (Rouhier et al., 2004) (Fig. 1A). Since the first cloning of plant GRX genes in the mid-1990s, GRX genes have been partially characterized in angiosperms, including *Arabidopsis thaliana* (50 genes), *Populus trichocarpa* (36) and *Oryza sativa* (27) (Belin et al., 2015; Garg et al., 2010). The GRXs can be subdivided into four groups based on the active site motifs (Couturier et al., 2009). GRXs of class I and class II have CxxC/S and CGFS active site motifs, respectively, and exist in all photosynthetic organisms. GRXs of class III are specific to angiosperms and have a peculiar CCxx active site motif, which is a diversified active site. Class IV GRXs harbor an N-

terminal GRX domain with a CxDC/S active site motif in angiosperms and a CPxC active site motif in green algae, which are fused to two domains of unknown functions in the C-terminal (Couturier et al., 2009). As a group, GRXs play versatile roles in plant development, abiotic stress adaptation, and iron homeostasis (Wu et al., 2012; Li, 2014; Hu et al., 2015).

Among various monothiol GRXs, recent studies showcase the breadth of physiological and cellular functions that GRXs of class II and III possess beyond ROS homeostasis, and new insights are being gleaned from both yeast and *Arabidopsis* studies (Hu et al., 2015; Knesting et al., 2015; Liu et al., 2013; Moseler et al., 2015; Nagels Durand et al., 2016; Stroher et al., 2016; Wu et al., 2012). Further, genome mining has identified a wide diversity of GRXs while high-resolution protein structural characterization has also begun (Abdalla et al., 2016; Garg et al., 2010; Li et al., 2010; Wang et al., 2014). This review will focus on the function of monothiol class II CGFS-type and class III CC-type GRXs in plant development, iron homeostasis, and abiotic stress responses and the potential of GRX manipulation for genetic improvement of crops (Table 1).

* Corresponding author.

** Corresponding author. Current address: Cold Spring Harbor Laboratory, 1 Bungtown Rd, Cold Spring Harbor, NY 11724, USA.

E-mail addresses: qwu@cshl.edu (Q. Wu), shpark@ksu.edu (S. Park).

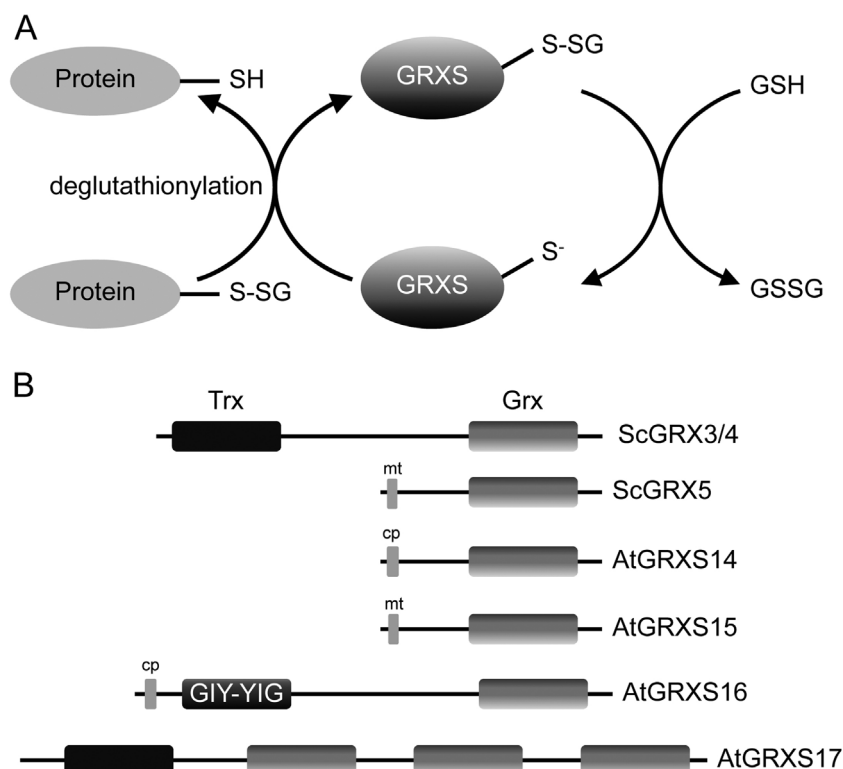


Fig. 1. Overview of plant CGFS-type monothiol glutaredoxins (GRXS). **(A)** The components of monothiol glutaredoxin system for disulfide bond reduction. **(B)** Domain organization of monothiol glutaredoxins in yeast and plants. Trx: thioredoxin module; Grx: glutaredoxin module; GIY-YIG: GlyIleTyr-TyrIleGly endonuclease motif; cp, mt: chloroplast and mitochondria signal peptide, respectively.

2. Heterologous expression in yeast and structural studies now guide plant monothiol GRXs research

GRXs of class II are conserved in all photosynthetic organisms and only reduce the mixed disulfide bond between GSH and target proteins (Lemaire, 2004). GRXs of class II have CGFS active sites and are homologous to *Escherichia coli* GRX4 and yeast *Saccharomyces cerevisiae* GRX3, GRX4 and GRX5 (Herrero and De La Torre-Ruiz, 2007). The four *Arabidopsis* class II GRXs include GRXS14, GRXS15 and GRXS16, which are low molecular weight proteins with one GRX domain, and GRXS17, which is larger with three GRX domains and an N-terminal thioredoxin (TRX)-like homology domain (Fig. 1B). Many studies have examined class II GRX biochemical and physiological properties, often using yeast heterologous expression and T-DNA insertion mutagenesis (Cheng et al., 2011; Sessions et al., 2002; Wu et al., 2012).

Initial characterizations of monothiol GRXs were achieved in yeast (Rodriguez-Manzanique et al., 1999). Two subclasses of monothiol GRXs exist, those with a single GRX domain and those with a TRX-like

region followed by one or more GRX domains (Herrero and De La Torre-Ruiz, 2007). The yeast monothiol ScGRX5 is located at the mitochondrial matrix and is used for iron-sulfur (Fe-S) cluster biogenesis. Yeast *grx5* mutants display loss of iron/sulfur enzyme activities and sensitivity to oxidative stress (Rodriguez-Manzanique et al., 2002). ScGRX5 contains a single GRX domain, while two other yeast GRXs, ScGRX3 and ScGRX4, contain a TRX-like domain fused to the GRX domain (Fig. 1B). ScGRX3 functions in the mitochondria and nucleus, and the TRX-like domain is required for nuclear localization. Mitochondrial forms of ScGRX3 and ScGRX4 partially rescue the defects of a *grx5* null mutant. Both the TRX-like and GRX domains are needed for the mitochondrial activity of ScGRX3.

AtGRXS14 is a chloroplast/plastid-localized GRX (Cheng et al., 2006). AtGRXS14 was initially isolated from *Arabidopsis* cDNA library in a yeast interaction assay (Cheng et al., 2003). In yeast functional assays, AtGRXS14 localizes to the mitochondria and suppresses the sensitivity of yeast *grx5* cells to H₂O₂ and protein oxidation (Cheng et al., 2006). Furthermore, AtGRXS14 can suppress iron accumulation

Table 1
Plant GRXs function in abiotic stress tolerance and iron homeostasis.

Gene	Group	Functions	Organisms used	References
AtGRXS14	II	Iron homeostasis	<i>in vitro</i> , yeast, structure, <i>Arabidopsis</i> protoplasts	Bandyopadhyay et al. (2008), Wang et al. (2014)
AtGRXS15	II	Arsenic tolerance, iron homeostasis	<i>in vitro</i> , <i>Arabidopsis</i>	Cheng, (2008), Moseler et al. (2015), Stroher et al. (2016)
AtGRXS16	II	Iron homeostasis	<i>in vitro</i> , yeast, <i>Arabidopsis</i> protoplast, structural study	Bandyopadhyay et al. (2008), Liu et al. (2013)
AtGRXS17	II	Heat and chilling tolerance, iron homeostasis	Yeast, <i>Arabidopsis</i> , tomato	Cheng et al. (2011), Hu et al., (2015), Inigo et al. (2016), Knesting et al. (2015), Nagels Durand et al. (2016), Wu et al. (2012)
PvGRX5	II	Heat and arsenic tolerance	<i>E.Coli</i> , <i>Arabidopsis</i>	Sundaram and Rathinasabapathi, (2010); Sundaram et al. (2008), Sundaram et al. (2009)
SIGRXI	II	Salt and drought tolerance	<i>Arabidopsis</i> , tomato	Guo et al. (2010)
AtGRXS13	III	Photooxidative stress tolerance	<i>Arabidopsis</i>	Laporte et al. (2012)
OsGRX8	III	Salt and osmotic tolerance	<i>Arabidopsis</i>	Sharma et al. (2013)

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