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Review Article

Role of Glutathione in Abiotic Stress Tolerance of Rice Plants

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Abstract

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Glutathione (GSH), glutathione reductase (GR), glutathione S-transferase (GST), and glutathione peroxidase (GPX) are important components of scavenging system for reactive oxygen species in plants. The importance of glutathione and its related enzymes in rice plants in response to abiotic stresses is reviewed. Evidence is provided to show that GSH plays critical role in tolerance to chilling, salinity, copper and cadmium excess, and herbicide treatment.

Key words: Glutathione, Glutathione peroxidase, Glutathione reductase, Glutathione S-transferase, Rice.

INTRODUCTION

It is well established that reactive oxygen specie (ROS) such as superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radical (•OH) are produced during normal aerobic metabolism. ROS are produced in different cell components such as cell walls, plasma membrane, chloroplasts, mitochondria, and peroxisomes (Dat *et al.* 2000). Basically, these oxygen species are highly reactive causing damage to proteins lipids, DNA, and ultimate result in cell death (Foyer & Noctor 2005). The intensity of the ROS production is determined by interplay between the ROS production and ROS scavenging capacity of the cell. During unfavorable conditions such as drought, low temperature, salinity, and heavy metals, ROS production exceeds the scavenging capacity of the cell. An overproduction of ROS results in oxidative damage (Fridovich 1986). To prevent the oxidative damage, plants have developed enzymatic and non-enzymatic systems for scavenging ROS (Dat *et al.* 2000). Plants use non-enzymatic components, such as ascorbic acid (AsA) and glutathione (GSH), and antioxidant enzymes, such as superoxide dismutase, catalase, ascorbate peroxidase (APX) and glutathione reductase (GR), to scavenge ROS (Noctor & Foyer 1998). Compared with Arabidopsis and tobacco, the role of GSH in rice plants is less well known. In this review, we discuss the most recently published data concerning the role of GSH in rice plants under conditions of chilling, salinity, copper (Cu) and cadmium (Cd) excess, and herbicide treatment.

GLUTATHIONE

The tripeptide glutathione (GSH; γ-glutamate-cysteine-glycine) is sulfur containing non-protein thiol. Reactivity of GSH depends on the thiol group (-SH). It can act as an effective electron acceptor and donor for

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many biological reactions (Xiang *et al.* 2001). The nucleophilic nature of the thiol group is also important in the formation of mercaptide bonds with metals and for reacting with select electrophilies (Xiang *et al.* 2001).The reactivity, stability, and high water solubility of GSH make it an ideal biomolecule to plants against abiotic stresses. GSH is involved in many cellular processes including detoxification of xenobiotics (Dixon *et al.* 1998), sequestration of heavy metals (Cobbett & Goldsbrough 2002), and defense against ROS (Foyer & Noctor 2005). In addition, GSH is a substrate for glutathione S-transferase (GST) and glutathione peroxidase (GPX) which are also involved in the removal of ROS (Noctor *et al.* 2002).

GSH is synthesized from two-consecutive ATP-dependent reactions. In the first step γ-glutamylcysteine (EC) is formed from L-glutamate and L-cysteine by γ-glutamylcysteine synthetase (ECS). The second step is catalyzed by glutathione synthetase which adds glycine to C-terminal of EC forming GSH. ECS is a major regulatory enzyme in GSH biosynthesis. The plastid is the compartment for GSH biosynthesis. GSH is one of the major forms of organic sulfur that translocate in the phloem (Herschbach & Rennenberg 1994) and therefore must move between cells, either apoplastically, symplastically, or both. Uptake of GSH has been reported in both cells and protoplasts (Schneider *et al.* 1992; Jamai *et al.* 1996). Several different types of transporters may be important in translocation of GSH between subcellular compartments (Noctor *et al.* 2012). The availability of γ-EC and cysteine is important for GSH synthesis (Noctor *et al.* 2012). Other factors that may affect GSH contents in plants include glycine and ATP (Ogawa *et al.* 2004).

GLUTATHIONE-RELATEDENZYMES

In almost all the biological functions, GSH is oxidized to glutathione disulfide (GSSG), which should be converted back to GSH in the cell to perform normal physiological functions. Thus, rapid recycling of GSH is more important than synthesis of GSH. The glutathione reductase (GR) catalyzes GSSG back to GSH at the expense of NADPH. It maintains the balance between GSH and ascorbate pools. GR was first reported in wheat germ (Conn & Vennesland 1951) and germinated pea (Mapson & Goddard 1951). GR has been purified and characterized from rice (Kaminaka *et al.* 1998). It is located predominately in chloroplasts, but a small amount of this enzyme has also been found in mitochondria and cytosol (Gechev *et al.* 2006). In higher plants, GR is encoded by more than one gene (Edwards *et al.* 1990). Three genes encoding GR have been described for rice: a cytosolic (*OsGR2*) (Kaminaka *et al.* 1998) and two chloroplastic isoforms (*OsGR1* and *OsGR3*) (Bashir *et al.* 2007; Wu *et al.* 2013). Wu *et al.* (2013) observed that both *OsGR1* and *OsGR3* are proteins dually targeted to chloroplasts and mitochondria in rice roots. Expression of *OSGR2* and *OsGR3* in NaCl-treated rice roots is regulated by H_2O_2 but not abscisic acid (Hong *et al.* 2009).

The GSH/GSSG ratio is decreased by oxidative stress, indicating that GSH and GSSG constitute a cellular redox buffer. GR has a role in maintaining a high GSH/GSSG ratio. A number of abiotic stresses have been shown to affect the activity of GR in plants (Gill & Tuteja 2010). To determine whether heterologous expression of *OsGR* can reduce the deleterious effects of abiotic conditions, Kim *et al.* (2012) constructed a transgenic yeast expressing *OsGR*. They demonstrated that *OsGR* expression in the yeast cells increases the ability of yeast to adapt to abiotic stresses, such as exposure to menadione (a free radical generator), heat shock, and heavy metals. Clearly, GR also has roles in defending against ROS.

Glutathione S-transferases (GSTs), also known as glutathione transferases, are enzymes involved in cellular detoxification by conjugating GSH to a wide variety of electrophilic

compounds. GSTs are localized in apoplast, cytosol, chloroplasts, mitochondria, and nucleus (Gechev *et al.* 2006). Herbicide atrazine is active on many annual broad-leaf weeds, while many commercial grass crops are naturally tolerant. An atrazine-susceptible maize strain was reported by Grogan *et al.* (1963). The identification of an atrazine-GSH conjugate was the first evidence of herbicide metabolism in plants by GSH conjugation, and this conjugation was shown to be the primary pathway for atrazine detoxification in maize (Shimabukuro & Swanson 1969). The first plant GST, which is responsible for conjugating the atrazine with GSH, was identified in maize by Frear & Swanson (1970). Plant GSTs can also function as glutathioneperoxidases (GPXs) (Bartling *et al.* 1993; Cummins *et al.* 1999), protect from oxidative stress (Hayes & McLellan 1999). Some of GSTs were originally identified as auxin- and cytokinin-binding proteins (Bilang & Sturm 1995; Gonneau *et al.* 1998), indicating that GSTs can also act in hormonal signal transduction. Based on the predicated amino acid sequences, the GSTs in plants have been grouped into several classes, including phi (F), tau (U), lamda (L), theata (T), and zeta (Z) (Dixon *et al.* 2002). The first plant GST cDNA sequence was published by Wiegand *et al.* (1986). To date, a total of 79 putative GST genes have been identified in rice (Jain *et al.* 2010). Many GST genes are regulated by plant hormones auxin and cytokinin, abiotic stresses, and biotic stresses (Jain *et al.* 2010).

GPXs are a family of multiple isozymes which catalyze the reduction of H_2O_2 and lipid hydroperoxides by GSH and the reforehelp to protect the cell from oxidative damage (Eshdat *et al.* 1977). GPXs are located in plant cytosol, chloroplasts, mitochondria, and endoplasmic reticulum (Gechev *et al.* 2006). However, one should be aware that in some of the above mentioned cases the observed GPX activity might have been due to the presence of GST. GPXs are considered as one of key enzymes involved in scavenging ROS. However, little is known about the response of GPXs in rice plants to abiotic stresses.

ROLE IN ABIOTIC STRESS OF RICE PLANTS

Chilling stress

Cold temperature can be distinguished from freezing in terms of the range of temperatures that cause the related damages. Many species of tropical or subtropical origin are injured or killed by nonfreezing low temperatures, and exhibit various symptoms of chilling injury such as chlorosis, necrosis, or growth retardation. In contrast, chilling-tolerant species are able to grow at such low temperatures (Sanghera *et al.* 2011). Rice plants are injured at the seedling stage when they are grown early spring in temperate and subtropical environment. A positive correlation between tolerance of chilling-induced photoinhibition and high GR activities has been demonstrated in rice (Kuk *et al.* 2003; Huang & Guo 2005). Proteomic analysis of chilling stress in rice also showed the upregulation of cysteine synthase (Yan *et al.* 2006). This enzyme is responsible for the final step in cysteine biosynthesis, a key limiting step in GSH synthesis. Thus, GSH and GR are important for tolerance to chilling stress.

To develop a rice cultivar that is suitable for growing in low temperature and submergence conditions, Takesawa *et al.* (2002) generated transgenic rice plants overexpressing a zeta class GST gene (GSTZ) under the control of a maize ubiquitin promoter. These transgenic rice lines enhance germination and growth of both roots and shoots at low temperature and submergence. The GSTZ in transgenic lines was observed to have higher GST/GPX activities than non-transformant. The GSTZ is suggested to have dual enzyme function (GST/GPX) in transgenic rice seedlings.

Andaya & Mackill (2003) developed a recombinant inbred line mapping population us-

ing cold tolerant California temperate japonica cultivar 'M202' and the cold sensitive indica cultivar 'IR50'. Genetic analysis of this population for seedling tolerance led to the identification of a major QTL (quantitative trait locus) on rice chromosome 12 for tolerance of cold-induced wilting and necrosis, designated as *qCTS12*. To identify the gene(s) underlying *qCTS12*, Andaya & Tai (2006) further studied the fine mapping of this locus. They demonstrated that *OsGSTZ1* and *OsGSTZ2* are the genes responsible for the tolerance to cold-induced wilting and necrosis conferred by *qCTS12*. Later work by Kim *et al.* (2011) revealed that a single amino acid change from Ile^{99} to Val^{99} in *OsGSTZ2* causes a significant reduction in its catalytic activity and the corresponding SNP (single nucleotide polymorphism) appears to be highly associated with cold sensitivity of rice seedlings. These results are in agreement with previous evidence that overexpression of GSTZ in transgenic rice seedlings enhances cold tolerance (Takesawa *et al.* 2002).

Salt stress

Soil salinity, particularly due to NaCl, can be considered as the most widespread soil toxicity problem for global rice production at present. A consequence of salt stress in rice plants is also the production of ROS, especially H_2O_2 (Lin & Kao 2001; Hong *et al.* 2009; Yamane *et al.* 2009; Yamane *et al.* 2012). Rice is a salt-sensitive cereal crop and is more affected at seedling stages. Yamane *et al.* (2012) demonstrated that H_2O_2 accumulation was observed in the chloroplasts, mitochondria, peroxisome, plasma membrane, and cell walls of rice plants under salinity.

Using two rice genotypes 'Pokkali' (salt-tolerant) and 'BRRI dhan29' (salt-sensitive), Hossain *et al.* (2013) investigated the efficacy of AsA-GSH cycle for scavenging H_2O_2 during salt stress. They demonstrated that 'Pokkali' exhibits increased GR activity, whereas 'BRRI dhan29' has no effect on GR activity during salt stress. The maintenance of sufficient GSH pool by GR in 'Pokkali' leads to increased antioxidant activity, which in turn improves tolerance to salt stress. Similarly, drought tolerant rice seedlings have higher GR and GST activities and a higher GSH content under water deficit when compared to the drought sensitive rice seedlings (Pyngrope *et al.* 2013). These results suggest that drought tolerant rice seedlings also have higher capacity to maintain GSH pool to meet the challenge of water deficit.

As mentioned earlier, *ECS* is the key enzyme of the GSH biosynthetic pathway in plants. A variety of transgenic plants overexpressing *ECS* has been reported to have higher tolerance to salt stress (Gullner *et al.* 2001; Gill & Tuteja 2010). The levels of GSH and salt stress response via *ECS* overexpression are recently reported in rice by Choe *et al.* (2013). They generated transgenic rice plants overexpressing *OsECS* under the control of an inducible promoter (*Rab21*). The transgenic rice plants increase tolerance to paraquat (PQ)- and salt-mediated oxidative stress through maintenance of cellular homeostasis via an enhanced GSH pool. Moreover, these transgenic rice plants increase grain and biomass under paddy field conditions.

Studies of GR in the past were largely carried out in dicot plants, especially tobacco (Chalapathi Rao & Reddy 2008). In most of those cases, the *E. coli GR* not endogenous genes, was overexpressed in plants. Recently, using a knockout mutant (*gr3*) and rescue line C1, Wu *et al.* (2015) investigated the role of *OsGR3* gene in NaCl tolerance of rice plants. Results showed that *gr3* mutant reduces GR activity, is sensitive to NaCl andPQ, and has low GSH content and low GSH/GSSG ratio. Moreover, the gr3-complementation line C1 recovers the GR activity and NaCl tolerance. Clearly, GR3 may play an important role in NaCl tolerance by regulating the GSH redox state in rice.

It has been shown that salt stress induced GST gene in the sensitive cultivar of indica rice 'IR29' but not the tolerant 'FL478' (Walia *et al.* 2005). Recently, Sharma *et al.* (2014) characterized a rice tau class GST gene, *OsGSTU4*. Overexpressing this gene in *E. coli* resulted in higher GST activity and better growth under salinity, osmotic, and oxidative stresses. In *Arabidopsis*, overexpression of *OsGSTU4* also shows tolerance to salinity and oxidative stress, which may be due to enhanced GST activity and decreased accumulation of ROS (Sharma *et al.* 2014). They suggested that *OsGSTU4* can be used to generate stress tolerant crop plants.

Copper and cadmium excess

Cu is essential for the plant growth. Excess Cu can generate ROS (Fernandes & Henriques 1991) and is able to stimulate the production of •OH in a Fenton-type reaction (Sadmann & Borger 1980). Cd is a non-redox metal unable to produce ROS via Fenton and/or Haber-Weiss reactions. However, evidence has demonstrated that Cd stress causes oxidative stress in plants (Hsu & Kao 2007). Thus, mechanisms by which plants can withstand toxicity of excess Cu or Cd include restriction the uptake of Cu or Cd and detoxification of Cu- or Cd-induced ROS.

Excess Cu exposure results in toxic symptoms such as stunted growth, leaf chlorosis, and leaf rolling of rice seedlings. Proteomic changes in response to excess Cu were studied by Ahsan *et al.* (2007) in germinated rice seeds. Differentially displayed proteins were identified by MALDI-TOF mass spectroscopy. The up-regulation of some antioxidants and stress-related proteins was observed in Cu-treated germinating rice seeds, indicating that excess Cu generates oxidative stress that might be disruptive to other important metabolic processes. Exogenous GSH decreases symptoms of Cu toxicity, diminishes Cu-induced production of ROS, and restricts Cu uptake (Mostofa *et al.* 2014). Using proteomic approach, Song *et al.* (2013) demonstrated that GST exhibits a greater increase in response to excess Cu in the Cu-tolerant rice cultivar B1139 compared with the Cu-sensitive B1195.

On treatment with Cd, the content of GSH decreases in rice seedlings of Cd-sensitive cultivar ('Taichung Native 1'; 'TN1') but not in the seedlings of Cd-tolerant cultivar ('Tainung 67'; 'TNG67').In earlier work, Hsu & Kao (2007) demonstrated that Cd toxicity is mainly due to H_2O_2 accumulation in 'TN1' rice seedlings. Thus, 'TNG67' seedlings experienced lower oxidative stress from Cd exposure than 'TN1'. Exogenous GSH reduces the subsequent Cd-induced toxicity of 'TN1' seedlings (Chao *et al.* 2011).The importance of GSH in regulating Cd toxicity is supported further by the facts that exogenous application of the buthionine sulfoximine (BSO), aspecific inhibitor of GSH biosynthesis, to seedlings of 'TNG67' decreases GSH content and increases subsequent Cd toxicity (Chao *et al.* 2011). Cai *et al.* (2011) alsodemonstrated that rice genotypic difference in the tolerance to Cd is positively linked to the capacity of elevation of GSH.

GST may catalyze Cd complexation with GSH (Adamis *et al.* 2004), thereby alleviating Cd toxic effects and promoting Cd retention in plant roots. Zhang *et al.* (2013b) reported that Cd can be retained and detoxified in rice roots through chelation with thiol compounds and subsequent sequestration. In another paper, Zhang *et al.* (2013a) purified GST from Cd-stressed rice roots and identified that a tau class rice GST is vital in Cd detoxification

Herbicide treatment

Herbicides are also known to generate ROS in the chloroplast in the light (Foyer *et al.* 1995). PQ, also known as methyl viologen, is a herbicide widely used in agriculture and has long been known to exert its toxic effects by catalyzing the transfer of electrons from photosystem I of chloroplast membranes to molecular oxygen producing ROS (Calderbank 1968). Chang & Kao (1995) also reported that

normally operated photosynthetic electron transport is essential for PQ-induced toxicity in rice leaves. PQ toxicity in rice leaves can be scavenged by increasing GR activity (Chang & Kao 1997).

It has been shown that GST in maize is responsible for herbicide atrazine detoxification (Shimabukuro & Swanson 1969). The function of the lambda class GST (GSTL) is not well understood. To test whether *OsGSTL1* has GSH conjugating activity, Hu *et al.* (2008) transformed yeast strains with *OsGSTL1*. They found that transgenic strains with OsGSTL1 have higher GSH conjugating activity than anon-transgenic strain. Glyphosate is a non-selective systemic herbicide, and chlorsulfuron is a selective herbicide. Later work by Hu *et al.* (2009) demonstrated that overexpression of *OsGSTL1* in rice plants enhances tolerance to glyphosate and chlorsulfuron, and the accumulation of *OsGSTL1* protein confers elevated GST and GPX activities. Recently, Hu (2014) also reported that overexpressing *OsGSTL2* in rice plants also protects plants from the injury caused by herbicides.

CONCLUSIONS AND PERSPECTIVES

This article gives a clear overview of the biochemical aspects of GSH and its related enzymes in rice plants subjected to abiotic stresses. It is now well established that GSH is synthesized from glutamate, cysteine, and glycine. It has been shown that GSH, GR, GST, and GPX play central role in scavenging ROS in rice plants under conditions of salt, low temperature, copper and cadmium excess, and herbicide treatment.

Increase in GR activity during stress should be achieved by increased GR protein synthesis and/or through changes in isoform population of GR. It is also important to characterize which isoform is crucial for a particular stress and how the expression of particular isoform is regulated in rice plants. Overexpressing or expressing antisense constructs resulting in inhibition of specific GSH related enzymes or mutants with impaired ROS generation may be extremely useful for creating transgenic rice plants to understand the role of GSH in rice plants in response to stress conditions. Most of the work regarding the functional aspects of GSH in rice plants has been done in laboratory. In future, studies are required to evaluate stress-tolerant transgenic rice plants in field trials under real stress conditions.

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穀胱甘肽與水稻環境逆境

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摘要

高景輝。2015。穀胱甘肽與水稻環境逆境。台灣農業研究 64(3):167–176。

穀胱甘肽、穀胱甘肽還原酵素、穀胱甘肽 S-轉移酵素與穀胱甘肽過氧化酵素為活化氧族清除系統之成員。本文係綜合討論穀胱甘肽及其相關酵素在水稻環境逆境下所扮演之角色。證據顯示穀胱甘肽可調控水稻在低溫、鹽分、過量銅與鎘及除草劑處理之抗性。

關鍵詞：穀胱甘肽、穀胱甘肽過氧化酵素、穀胱甘肽還原酵素、穀胱甘肽 S-轉移酵素、水稻。

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