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Recent advances in the signalling function of glutathione on plants

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Abstract

Plants favour a variety of signaling networks that maintain physiological functions of the plants for managing stressful conditions. Glutathione (GSH), a non-protein thiol compound, plays an important role in maintaining redox signaling in plants against stress conditions. However, a gap remains to state the functional activities of glutathione on hormonal signaling and growth of plants under stress conditions. In the past centuries, GSH gradually gained significant interest and importance to the researchers due to diverse functional activities in plants. To date, researches and reviews documented the protective role of GSH in plants against stress conditions. Nevertheless, signalling behaviour of GSH is still lacking with regards to the mechanism of GSH underlying the hormonal signaling to the plants. This review highlights the improvements made on the functions of GSH to the hormonal signaling in plants under stressful conditions.

Keywords: Glutathione, Stress defense, Light harvesting complexes, Stomatal closure, Signaling cascade, Plant growth.
Abbreviations: γ-ECS_γ-glutamylcysteine synthetase; GSH2_glutathione synthetase; GSH_glutathione; ROS_reactive oxygen species; *ch1-1_chlorinal-1*, ABA_abscisic acid; *atgpx3*_Glutathione peroxidase3; MeJA_Methyl jasmonate; AITC_allyl isothiocyanate; GSSG_oxidized GSH; NAC_N-acetyl-cysteine.

Introduction

Two enzymatic steps are catalyzed by γ-glutamylcysteine synthetase (γ-ECS, GSH1) and glutathione synthetase (GSH2), which are involved in the biosynthesis of glutathione in plants (Wachter et al., 2005). The GSH arises in animals, plants and bacteria up to the concentration of 10 mM under the stress condition (Sharma et al., 2000). Glutathione performs a major player in the redox chemistry as an electron donor, stress defense gene expression, plants' growth, in addition to show the sensitivity to the certain hormone (Okuma et al., 2011; Jahan et al., 2016). Glutathione reduces the effect of certain diseases in human and detoxifies reactive oxygen species (ROS) and xenobiotics in animals under stress conditions (Ball et al., 2004). Different stress conditions such as drought, salinity, chilling, metal toxicity, UV-B radiation, pathogens attack induced ROS production in plants due to disruption of the cellular homeostasis. The condition causes a danger to cells mortality by triggering peroxidation of lipids, proteins oxidation, and injury of nucleic acids and inhibition of enzymes (Mittler, 2002). In the past eras, GSH involved in defense responses alongside a variation of stress conditions (Ball et al., 2004).

Several recent reports confirm the signalling behaviour of glutathione to the cells in response to hormones in regulating the detrimental effects of stress conditions on plants (In Arabidopsis: Jahan et al., 2008; Khokon et al., 2011; Okuma et al., 2011; Jahan et al., 2016; In corn: Munirah et al., 2015; Inani et al., 2015; Syuhada and Jahan, 2016; In rice: Choe et al., 2013; Fangbin et al., 2015). This review shows the recent updates in understanding the signalling function of GSH in adjusting hormonal regulation in plants under stressful conditions.

Metabolomics of GSH on plants to stress responses

Metabolomics is a common in physiology and biochemistry of plants, which deals with biotic and abiotic stresses. Climate change limits water availability for crop production. It is needed to effort understanding GSH function on the crucial and common stress of water that affects the growth and production of crops. Glutathione play an important role in regulating photosynthesis rate and light-related parameters in the response of drought stress in *Arabidopsis* plants (Jahan et al., 2016) and corn plants (Munirah et al., 2015). Glutathione reduced H_2O_2 to H_2O under stress condition (Foyer and Noctor, 2011). Under oxidative stress, *de novo* biosynthesis of glutathione maintains the redox balance of GSH/GSSG ratio (Ruiz and Blumwald, 2002; Nahar et al., 2015). Freezing environments leads serious damage of cells due to dysfunction of cellular membranes (Guy, 1990). Glutathione induces tolerance mechanisms in loquat plants under low temperature (Wu et al., 2011). High temperature reduced different parameters of plants (Wahid et al., 2007), which were significantly alleviated by the application of exogenous GSH (Ding et al., 2016). Therefore, GSH plays a critical mechanism under temperature stress due to climate change.

The role of glutathione in plants

Plants accumulate GSH in respond to different stress conditions through modulating metabolic trails in cells of plants by quenching oxygen species (Noctor and Foyer, 1998), regulating cell proliferation, expansion of root, salt acceptance, and chilling protection (Vernoux et al., 2000; Islam et al., 2009; Diaz-Vivancos et al., 2010). Several recent reports stated that GSH associated with abscisic acid signaling in guard cells of Arabidopsis (Jahan et al., 2008; Okuma et al., 2011; Jahan et al., 2014; and 2016) that might implicate physiological mechanisms in plants to grow, reproduce, maintaining cell structures, in respond to the climate change. The phenotype of the plants with low GSH formation is affected through the cell division during postembryonic root enlargement (Ogawa et al., 2004; Vernoux et al., 2000). Glutathione acts as a phytochelatins and ligand peptides to mitigate stress-induced redox imbalance and tolerance mechanism in cells of plants (Hernandez et al., 2015).

Glutathione initiates and cares cell partition in root (Vernoux et al., 2000) as well as embryo and seed (Cairns et al., 2006). GSH regulates root development through adjustment of redox mechanism in auxin transportation in roots of Arabidopsis plants (Koprivova et al., 2010). This result suggests that GSH involved in root development that control nutrients' uptake and the growth of plants. In this connection, glutathione-deficient mutant, *chlorinal-1* (*ch1-1)*, shows that GSH influenced the growth and physiology of the mutant (Frottin et al., 2009; Jahan et al., 2014). Glutathione synthesis is necessary for germination of pollen in vitro (Zechmann et al., 2011). This result is consistent with Jahan et al. (2014) that seed production of the GSH deficient mutant, *ch1-1,* was significantly lower than that of wild types. This result suggests that GSH linked to the seed production of *Arabidopsis* plants. Pauly et al. (2006) stated that glutathione might have a major role in symbiotic N_2-fixing in the nodule to control the growth and development of legume crops. Therefore, GSH-controlled growth and physiology of plants could be a crucial point to sustain production under stressful conditions.

The light-antenna complexes regulate glutathione functions in plants

The light-harvesting complex is a collection of protein and chlorophyll particles, which allocate light energy to chlorophyll-*a* molecule in the photosystem reaction centre. GSH regulates physiological functions (Jahan et al., 2008) via redox state of GSH pools in plants (Noctor et al., 1998). The light-antenna complexes regulate photosynthetic electron flow, light-dependent energy production and GSH biosynthesis (Ogawa, 2005; Ogawa et al., 2004). Therefore,accumulation of lower GSH contents in the *ch1-1* mutant likened to the modulation of physiological functions of the plant (Ogawa, 2005; Jahan et al., 2014; Jahan et al., 2011; Jahan et al., 2008). Furthermore, lower GSH biosynthesis limits photosynthesis rate, which controls flowering time of *Arabidopsis* plants (Ogawa et al., 2004) and leaf development of the *ch1-1* mutants (Jahan et al., 2014). Light reaction regulates GSH biosynthesis in Arabidopsis plants indicates that photosystem pathway consumes GSH level (Ogawa et al., 2004). This result supports to the increment of photosynthesis rate in GSH-treated corn plants compared to the control condition (Munirah et al., 2015, Inani et al., 2015). Deficient GSH in the *ch1-1* mutant due to a lack of light-antenna complexes in photosystem II (Jahan et al., 2008) impaired the growth and development of Arabidopsis plants (Jahan et al., 2014; Jahan et al., 2016) may result in lacking the light-dependent photosynthesis rate. Based on findings, it is proposed that the growth of plants is to be controlled by the GSH biosynthesis and the ATP-dependent gamma-glutamylcysteine synthetase (γ-ECS) reaction that linked to the photosynthesis rate (Ogawa et al., 2004).

Glutathione regulates signalling network of abscisic acid on guard cells

It is well established that abscisic acid (ABA) is the key controller of stomatal movement in guard cells under water deficit condition. During water stress condition, ABA translocated from mesophyll and vascular cells to the guard cells then close stomatal pore through a signaling cascade (Okuma et al., 2011). Guard cells accumulate a significant amount of ABA in contrast to the concentration of the surrounding cells under stress condition (Behl and Hartung, 1986). Several studies extensively presented the signal transduction pathways underlying ABA-regulated stomatal aperture under water shortages (Seo and Koshiba, 2011). Abscisic acid operates as a biochemical signal in reply to the stress, which stimulated physiological and developing processes of the plant to acclimatize stress conditions (Robert-Seilaniantz et al., 2007; Murata et al., 2015).

Glutathione peroxidase3 (*atgpx3*) controls H_2O_2 homeostasis in ABA and drought stress signaling in guard cells to arbitrate stomatal movement (Miao et al., 2006). Therefore, *atgpx3* mutant exhibited lessened ABA- and H_2O_2-treated stomatal closure and quicker water loss (Miao et al., 2006). This result indicated that glutathione appears to be linked with the ABA signaling to the guard cell of *Arabidopsis* (Okuma et al., 2011). The connection concerning between GSH biosynthesis and ABA signaling was studied previously in guard cells of Arabidopsis (Jahan et al., 2008; Jahan et al., 2011; Okuma et al., 2011; Munemasa et al., 2013; Jahan et al., 2016). ABA differentially touched the GSH levels, the ratio of GSH: GSSG, glutathione reductase, γ-ECS transcript in maize genotypes (Kellos et al., 2008).

ABA mediates ROS and cytosolic Ca $\{(Ca^{2+})_{cyt}\}$ in guard cells during ABA-treated stomatal closure in wild types (Murata et al., 2015) as well as GSH deficient mutant, *cad2-1,* plants (Okuma et al., 2011). In addition, guard cells of *ch1-1* and *cad2-1* displayed advanced sensitivity to ABA than that of WT plants (Okuma et al., 2011; Jahan et al., 2008; Jahan et al., 2014). Guard cells of mutants and WT plants showed similar response to the Ca-induced stomatal closure (Jahan et al., 2012). In addition, chemically and genetically depletion of GSH did not alter ROS creation in guard cells of the *Arabidopsis* plants (Akter et al., 2013; Okuma et al., 2011). Therefore, in the GSH-induced ABA signalling cascade, ROS production is not conditional to the stomatal aperture (Munemasa et al., 2013). Moreover, supplementation of GSH monoethyl ester and *N*-acetyl cysteine restored GSH levels in guard cells to revoke ABA sensitivity to guard cells (Okuma et al., 2011; Jahan et al., 2008; Jahan et al., 2014, and 2016). Different studies suggested that apoplastic ROS signals regulate the stomatal movement (Hossain et al., 2013; Khokon et al., 2011; Munemasa et al., 2013). Therefore, it is suggested that GSH signaling in the regulation of ROS production in apoplastic

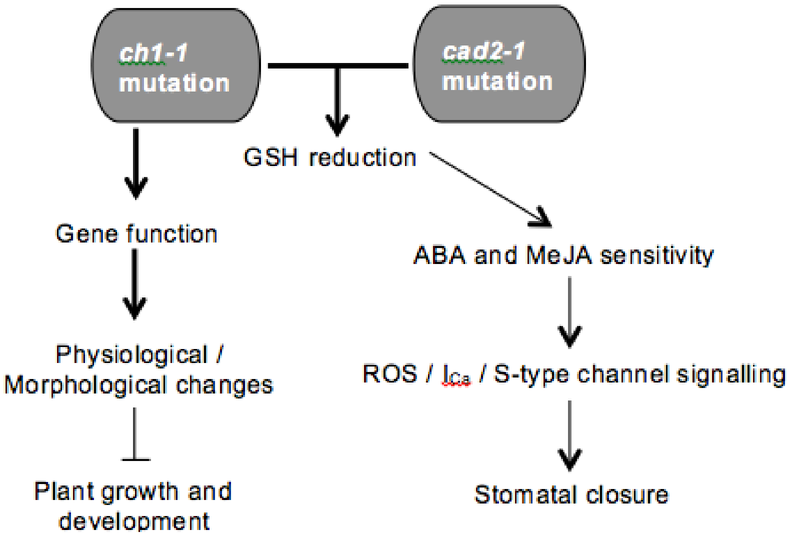

Fig 1. A proposed schematic diagram shows the reduction GSH biosynthesis in *ch1-1* and *cad2-1* mutant plants. The thick arrows indicate metabolic flows, thin arrows indicate incremental pathways and the reverse T-bar indicates limited paths. Depletion of GSH biosynthesis in guard cells modifies ABA / MeJA sensitivity to the stomatal aperture through inflection of ROS, I_{Ca} channel and S-type channel signaling. The *ch1-1* mutation, on the other hand, affects plant growth and development.

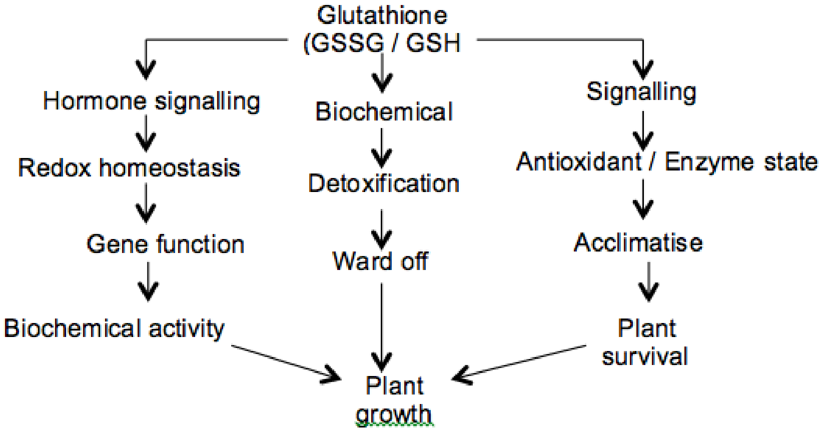

Fig 2. Differentiating functions of glutathione to the plants.

area during ABA-treated stomatal closure (Munemasa et al., 2013). Therefore, GSH played a role in coupling to ROS production to the downstream of ABA signaling cascade in *cad2-1* mutant plants (Okuma et al., 2011). Accordingly, GSH function in ABA signaling cascade is a complex system to control the stomatal movement of guard cells of *Arabidopsis* plants (Fig. 1).

Glutathione regulates signalling network of methyl jasmonate-induced stomatal closure

Methyl jasmonate (MeJA) plays imperative characters in controlling stress reactions to the growth and progress of plants (Creelman and Mullet, 1997). Different stress conditions such as, cold, water, insect increase endogenous jasmonates in cells of the plants (Lan et al., 2004; Pedranzani et al., 2007). The expression of jasmonate-regulated genes (JRGs) increased resistant capacity in plants against stress conditions (Sasaki-Sekimoto et al., 2005).

Jasmonic acid reduces GSH-dependent formaldehyde dehydrogenase levels and enzymatic activities in tobacco (Diaz et al., 2003). MeJA decreases GSH contents in guard cells of *Arabidopsis* plants (Akter et al., 2013). The role of GSH in plants is complex and has potential characters in jasmonic acid-related genes expression (Han et al., 2013). Besides that Akter et al. (2013) stated that GSH did not affect ROS homeostasis in MeJA signaling flow in guard cell (Akter et al., 2013) to regulate MeJA-treated stomatal aperture (Munemasa et al., 2007; Munemasa et al., 2013). It is possible that GSH plays a role in the coupling of ROS to downstream of MeJA-induced signaling cascade comparable to the GSH function in ABA signaling cascade in *cad2-1* mutants (Okuma et al., 2011). In addition, allyl isothiocyanate (AITC) is a phytochemical induced in plants of Brassicaceae family in response to the defense against herbivores or pathogens (Halkier and Gershenzon, 2006). GSH is also involved in AITC-induced stomatal aperture (Khokon et al., 2011) indicating the involvement of GSH in

MeJA signalling in plants under stress conditions. Furthermore, GSH monoethyl ester completely reversed AITC-treated stomatal aperture (Khokon et al., 2011) indicates the involvement of GSH in plants under biotic stress. Jasmonate levels induced in the cells of the plants suggested the sensing and signalling actions in response to the wounding and insect-induced reactions (Mithöfer et al., 2014). Glutathione regulates jasmonate acid signalling cascade in account to the intracellular oxidation (Han et al., 2013). Therefore, these shreds of evidence supports that the relationship between GSH functions and MeJA signalling pathway provides defense mechanisms in plants against stress conditions.

Glutathione regulates signalling network of the salicylic acid

The elevation of salicylic acid in plants mediates systemic acquired resistance in response to the activation of pathogenesis-related genes in *Arabidopsis* (Shirasu et al., 1997). Salicylic acid leads the biosynthesis of GSH in cells to reduce the harmful effect of ozone on Arabidopsis plants (Yoshida et al., 2009). This result indicates that salicylic acid activates de novo biosynthesis of GSH under oxidative stress (Tausz et al., 2004). GSH metabolize ROS to mitigate salinity stress injury in plants (Csiszár et al., 2014). The transcript level of ascorbate-GSH pathway enzymes enhanced salicylic acid and reduced detrimental effects of salt and temperature to wheat and corn plants (Janda et al., 1999; Li et al., 2013). Therefore, glutathione enhanced salicylic acid-related defense mechanism (Koornneef et al., 2008) and salicylic acid-induced signaling processes as well as to mimic fungal or pathogen infection (Edwards et al., 1991).

Glutathione regulates the growth and production of plant

It is well established that glutathione controls plant growth and development through cell differentiation, reducing cell death and senescence under stress condition (Ogawa, 2005). Higher quantities of oxidized GSH (GSSG) are associated with the growth and reduction of cell death (Kranner et al., 2006). Therefore, optimum biosynthesis of GSH content in plants is significant aimed to enhance or maintain the growth and production of the plants under stress condition.

N-acetyl-cysteine (NAC), a free radical scavenger and GSH precursor, preserves the redox state then improves the cellular environment (Kerksick and Willoughby, 2005) and the physiological condition of the corn plants under low fertile soil condition (Munirah et al., 2015; Inani et al., 2015). Increment of GSH by the treatment of NAC increased chlorophyll related parameters in leaves of corn plants (Munirah et al., 2015), which is consistent with the increment of Chl content and GSH contents in leaves of GSH deficient mutant of *ch1-1* plants (Jahan et al., 2014; Jahan et al., 2016). These results confirmed that GSH functions are related to the light reaction of photosystem II and photosynthesis rate. Therefore, GSH might enhance energy production through increasing the photosynthesis rate to regulate the growth and development of plants (Zhu et al., 2010). The light antenna function would be a dominant factor in GSH signalling pathway that might increase the growth of the Arabidopsis plants (Jahan et al., 2014) and corn plants (Munirah et al., 2015; Inani et al., 2015). Fangbin et al. (2015). In addition, the application of GSH significantly increased rice yield in both of Cd sensitive and resistant plants. In this relation, glutathione induces various physiological parameters of plants and improves the yield (Inani et al., 2015; Munirah et al., 2015; Syuhada and Jahan, 2016; Jahan et al., 2016). Therefore, it is suggested that GSH signalling pathway is closely related to the light reaction and photosynthesis rate of plants.

A higher GSH/GSSG ratio in rice plants shows higher chlorophyll-fluorescence, germination rates, increased yield and improved biomass production of rice (Choe et al., 2013). For that reason, glutathione improves redox homeostasis in plants under stress conditions and plays the significant role in increasing the yield of crops through improving physiological functions of the plant (Fig. 2).

Conclusion

To date, there are insufficient evidences of the signalling behaviour of glutathione on the growth and development of plants concerning the hormonal activity during stress conditions. In this mini review, evidences showed that GSH activates hormonal signaling to change various physiological parameters of the plant. Considering the latest discoveries, GSH showed a diverse standpoint in the hormonal signaling pathway in plants. Further studies and experimental proofs are needed for accepting the cross connection of the GSH signaling with different hormones under stress conditions. This would comply a complete scenario of GSH signalling in regulating signaling-web of the various hormones for sustainable growth and production of plants under stress conditions due to climate changes.

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