Journal of Plant Growth Regulation
https://doi.org/10.1007/s00344-023-10965-6

Role of Heterotrimeric G-Proteins in Improving Abiotic Stress Tolerance of Crop Plants

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Received: 22 July 2022 / Accepted: 24 February 2023

Abstract
As sessile organisms, plants are constantly exposed to a variety of environmental stresses that have detrimental effects on their growth and development, leading to major crop yield losses worldwide. To cope with adverse conditions, plants have developed several adaptive mechanisms. A thorough understanding of these mechanisms is critical to generate plants for the future. The heterotrimeric G-protein complex, composed of Gα, Gβ, and Gγ subunits, participates in the regulation of diverse cellular signaling pathways and has multiple roles in regulating plant stress responses. The complex has two functional entities, the GTP-bound Gα subunit and the Gβγ dimer, both of which by interacting with additional proteins can activate various signaling networks. The involvement of G-proteins has been shown in plants' response to drought, salinity, extreme temperatures, heavy metals, ozone, and UV-B radiation. Due to their versatility and the number of processes modulated by them, G-proteins have emerged as key targets for generating stress-tolerant crops. In this review, we provide an overview of the current knowledge of the roles of G-proteins in abiotic stress tolerance, with examples from the model plant *Arabidopsis thaliana*, where these processes are most widely studied and from additional agriculturally relevant crops, where their potential is realized for human usage.

Keywords Heterotrimeric G-proteins · Abiotic stress · Drought · Salinity · Temperature · Crops · Stress tolerance · Adaptation

Introduction

Any divergence from optimal growth conditions adversely affecting an organism's growth, metabolism, and development can be termed as stress (Lichtenthaler 1998). Plants being sessile are continuously challenged by multiple stresses, both biotic and abiotic (Zhang et al. 2022). The common abiotic stresses in plants include drought, salinity, extreme temperatures (high/freezing), heavy metal contamination (cadmium, aluminum and arsenate in soil), ozone and UV-B radiation, which individually or in combination affect almost every aspect of their growth and development. Global climate change over the past few decades had compounded the effects of abiotic stresses on plants by significantly affecting crop productivity world-wide, raising major concerns for future food security (Bita and Gerats 2013; Jagermeyr et al. 2021).

Plants' response to abiotic stresses can be adaptive, nonadaptive, or a combination of both. Nonadaptive responses are typically deleterious due to compromised biomolecule function and altered membrane dynamics (Zhang et al. 2022). The adaptive responses, on the other hand, are suitable to the sessile lifestyle of plants. Plants exhibit dramatic developmental plasticity brought about by rapid changes in ion channel activities, gene expression, chromatin remodeling, post-transcriptional modifications, and translational/post-translational modifications (Bita and Gerats 2013; Niu and Xiang 2018; Zhang et al. 2022), which is beneficial when responding to stresses. Studies performed over the years have also emphasized that the adaptive, plastic behavior of plants is an outcome of the regulation by multiple interconnected pathways and gene networks (Laitinen and Nikoloski 2019). Thus, it is pertinent to elucidate the molecular framework of stress responses in plants, with the aim of identifying key stress sensors, stress modulators, and

Handling Editor: Sudhir K. Sopory.

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Published online: 17 March 2023

stress-responsive genes. This will eventually lead to breeding stress-resistant crops to meet the future food demands.

Heterotrimeric guanine nucleotide binding proteins (G-proteins) comprised Gα, Gβ and Gγ subunits are key signaling intermediates in eukaryotes (Offermanns 2003; Pandey 2019). In metazoans, G-proteins are key mediators of most sensory perceptions, hormones, and neurotransmitter signaling, and consequently affect almost all aspects of normal growth and development (Neves et al. 2002). Due to their involvement in controlling multiple diseases, the signaling mechanisms of G-proteins have been extremely well-characterized in humans. According to recent estimates, G-protein signaling pathways are targets of more than 30% of all pharmaceutical drugs (Li et al. 2020; Yang et al. 2021).

In plants, G-proteins affect every aspect of growth and development and response to a multitude of exogenous and endogenous cues (Jose and Roy Choudhury 2020; Pandey 2019; Tiwari and Bisht 2022; Wang and Botella 2022; Zhou et al. 2019). The subunit composition of the heterotrimer and the core biochemistry of the Gα, Gβ and Gγ proteins is similar between plants and metazoans. However, there are also several unique components as well as distinct regulatory mechanisms that are thought to have evolved in response to the unique lifestyle of plants (Chakravorty and Assmann 2018; Pandey 2017, 2019; Wang et al. 2018; Zhou et al. 2019). Plant G-proteins are involved in modulation of a multitude of physiological processes at the subcellular, cellular, tissue, and organ levels. These include control of stomatal movement, regulation of phytohormone signaling and response to biotic and abiotic stresses (Chakravorty et al. 2011; Hao et al. 2012; Jose and Roy Choudhury 2020; Lee et al. 2018). These diverse responses are controlled by affecting fundamental processes such as regulation of ion channel activities (Chakravorty et al. 2011; Fan et al. 2008), cell division, expansion, and differentiation (Chen et al. 2003, 2006; Para et al. 2016; Ueguchi-Tanaka et al. 2000; Ullah et al. 2003; Urano et al. 2015), changes in membrane dynamics, and cell wall composition (Chakravorty et al. 2011; Roy Choudhury et al. 2019; Wu et al. 2007; Zhang et al. 2011). In addition, G-proteins are also affect key agronomic traits such as water and nitrogen use efficiency and grain yield by influencing inflorescence and root architecture, seed number and size, and germination potential (Botella 2012; Cui et al. 2020; Kaur et al. 2018; Liang et al. 2018; Roy Choudhury et al. 2019; Sun et al. 2014; Urano et al. 2015; Vavilova et al. 2017; Wendt et al. 2016; Wu et al. 2018; Zhang et al. 2015).

Plant Heterotrimeric G-Proteins Composition

In plants with non-duplicated genomes, the repertoire of heterotrimeric G-proteins is relatively simple compared to the metazoan systems (Pandey 2019). Plants have two types of Gα subunits, canonical Gα, which shows similarity to other known non-plant Gα proteins and the larger form of Gα, known as extra-large Gα (XLG), in which the Gα domain is fused with an extra, N-terminal region (Chakravorty et al. 2015; Ding et al. 2008; Hackenberg et al. 2016). The Gα protein possesses an intrinsic Ras-like GTPase domain and a unique alpha helical domain with conserved N-terminal myristoylation site at (Gly2), crucial for its membrane anchorage (Fig. 1A) (Galbiati et al. 1994). The N-terminal region of XLGs possesses a cysteine-rich region and a nuclear localization signal (NLS; Chakravorty et al. 2015). The Gα-like domain in XLG proteins has lost some of the residues crucial for nucleotide hydrolysis, but has been shown to bind to GTP (Hackenberg et al. 2016; Urano et al. 2016). Recent phylogenetic analysis shows that there are instances of the canonical Gα loss in some plant groups (*e.g.,*Bryopsida mosses) but the XLG proteins are present in all plant groups except Chlorophyceae algae (Mohanasundaram et al. 2022). The Gβ protein harbors N-terminal coiled-coil helices and seven WD40 (Trp and Asp) repeat containing domains, which is implicated in multi-protein complex formation (van Nocker and Ludwig 2003). Plants have three types of Gγ proteins-types I, II, and III (also known as types A, B, and C) (Fig. 1A) (Roy Choudhury et al. 2011; Trusov et al. 2012). Phylogenetic analysis suggests that the Gγ proteins diverged before the evolution of land plants and underwent considerable changes in their domain structures, resulting in three subtypes (Mohanasundaram et al. 2022). Type-I is the prototypical Gγ subunit with N-terminal coiled-coil domain and C-terminal prenylation motif, CAAX ("C" represents cysteine, "A" for any aliphatic amino acids, and X denotes any amino acid) involved in post-translational modification and membrane anchorage. The type-II Gγ proteins differ from the type-I Gγ only by the loss of the prenylation motif (Fig. 1A), although the proteins are still hypothesized to be localized to the plasma membrane (Botella 2012; Zeng et al. 2007). The type-III are vascular plant-specific Gγ proteins with the N-terminal region similar to prototypical type-I Gγ fused with a highly divergent C-terminal cysteine-rich region (Botella 2012; Roy Choudhury et al. 2011; Trusov et al. 2012). In Arabidopsis, the G-protein trimeric complex is represented by one canonical Gα (GPA1), three extra-large Gα (XLG1, 2 and 3), one Gβ (AGB1), and three Gγ proteins (AGG1, 2 and 3) (Mason and Botella 2000, 2001; Pandey 2019). The repertoire of G-proteins in many angiosperms is similar to that of Arabidopsis; however, plants with recently duplicated genomes have retained most copies of G-protein genes. For example, the soybean genome codes for 4 Gα, 4 Gβ, 10 XLG and 12 Gγ proteins (Bisht et al. 2011; Roy Choudhury et al. 2011). Similar higher numbers are reported from camelina, wheat, and brassica species (Gawande et al. 2022; Kumar et al. 2014; Roy Choudhury et al. 2014).

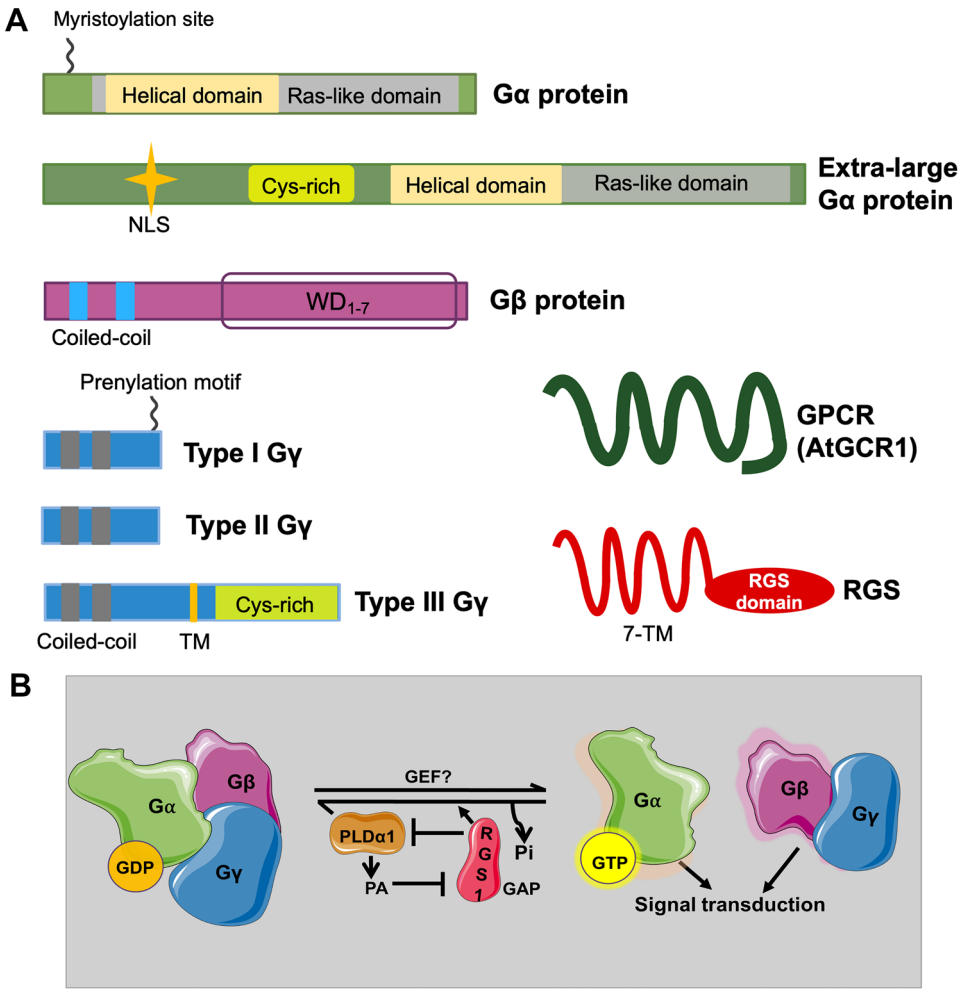

Fig. 1 Heterotrimeric G-protein signaling components and mechanism. **A** Domain architecture of G-protein signaling components in plants. Gα proteins have an N-terminal myristoylation site followed by helical domain and C-terminal RAS-like domain. The plant-specific XLG proteins possess an extra-large domain of unknown function fused with the canonical Gα-like domain. The N-terminal domain has a NLS, and a cysteine (Cys)-rich region. Gβ proteins have an N-terminal coiled-coil domain and seven WD repeats containing domain. The Gγ proteins are classified into type-I, type-II, and type-III subtypes. Type-I Gγ (canonical) proteins have the Gγ domain that interacts with the coiled-coil domain of Gβ subunit and a C-terminal prenylation motif for its membrane anchorage. Type-II Gγ proteins have Gγ domain but lack the prenylation motif. Type-III proteins have the Gγ domain followed by a transmembrane domain and Cys-rich region of variable length. A prototypical GPCR protein with seven-transmembrane regions is also identified in plants (e.g., GCR1 from Arabidopsis). The plant RGS proteins have an N-terminal seven-transmembrane domain similar to GPCRs fused with the C-terminal RGS domain. **B** Basic G-protein signaling mechanism in plants. The core heterotrimeric G-protein complex comprises of Gα, Gβ and Gγ subunits. The signaling complex shuttles between inactive Gα-GDP and active Gα-GTP forms. Conventionally, the GDP to GTP exchange reaction is catalyzed by GPCR, which acts as guanidine nucleotide exchange factor (GEF). In plants, no such GEF is identified, to date. A phosphorylation-dependent mechanism may be operative during plant G-protein signaling. The Gα subunit has an inherent GTP hydrolysis activity, which is stimulated by the GTPase-activity accelerating protein (GAP), RGS1. RGS1 inhibits PLDα1, whose product phosphatic acid (PA) in-turn inhibits RGS1 and regulates the GTPase activity of Gα protein. Once activated, the Gβγ obligate dimer dissociates from Gα-GTP subunit and both can activate downstream signaling through various effectors

Plant Heterotrimeric G-Protein Signaling Mechanisms

The Gα subunit of the heterotrimer binds to guanine nucleotides and switches between the GDP-bound inactive, and GTP-bound active forms. In metazoan, the exchange of GTP for GDP on Gα is facilitated by a plasma membrane-localized, 7-transmembrane containing G-protein coupled receptor (GPCR), which acts as a guanine nucleotide exchange factor (GEF; Oldham and Hamm 2008). Upon activation by a GPCR, GTP-bound Gα dissociates from the trimer and releases Gβγ dimer. Both these entities (GTP-Gα and Gβγ) can independently interact with various downstream effectors to relay the G-protein mediated

signals (McCudden et al. 2005; Siderovski and Willard 2005). The inherent GTPase-activity of Gα proteins causes the hydrolysis of bound GTP, generating its GDP-bound form, which associates with the Gβγ dimer to reconstitute the inactive trimer. This transition from active to inactive state is also accelerated by the GAP (GTPase-activity Accelerating Proteins) activity of RGS1 (Regulator of G-protein Signaling) proteins (McCudden et al. 2005; Siderovski and Willard 2005). These core properties i.e., guanine nucleotide-binding-dependent trimeric or monomeric Gα proteins, signaling by freed Gα and Gβγ, and regulation of signaling by the GAP activity of the RGS proteins is conserved in plant G-protein signaling as well, but several deviations also exist (Fig. 1B). In addition to the unique features of XLG and type-III Gγ proteins, the plant RGS proteins possess a domain containing 7-transmembrane regions and are localized to the plasma membrane (Chen et al. 2003; Hackenberg et al. 2017; Mohanasundaram et al. 2022; Roy Choudhury et al. 2012). Classical GPCRs with GDP/GTP exchange activity have not been identified in plants, to date. The only GPCR-like proteins identified in Arabidopsis through a reverse genetic approach, GCR1, has a protein-fold similar to non-plant GPCRs and act in G-protein-dependent pathways (Pandey and Assmann 2004), but its GEF activity remains unknown. Instead, the involvement of plasma membrane-bound receptor-like kinases (RLKs) in the regulation of G-protein signaling by phosphorylation/dephosphorylation-based mechanisms appears to be more prevalent in plants (Chakravorty and Assmann 2018; Liang et al. 2016; Roy Choudhury and Pandey 2015, 2016a; Wang et al. 2018). Similarly, RGS-dependent regulation of G-proteins exists in plants, but many plant groups do not have an RGS homolog in their genome (Bhatnagar and Pandey 2020; Hackenberg et al. 2017; Mohanasundaram et al. 2022). Various phospholipases may also be involved in the regulation of G-protein signaling (Brandenburg et al. 2014; Jeon et al. 2019; Pandey 2016, 2017; Roy Choudhury and Pandey 2016b, 2017). Furthermore, a guanine-nucleotide-independent mechanism of regulation has also been proposed (Maruta et al. 2021), implying that the regulation of G-protein signaling mechanisms in plants is flexible, potentially suitable for the sessile nature of plants and their need to integrate multiple signaling pathways.

Roles of G-Proteins in the Regulation of Abiotic Stress Responses

G-proteins are known to regulate multiple abiotic stresses in plants. However, most of our current knowledge is based on the results from the model plants *A. thaliana*, with some information from crops such as rice, maize, soybean or barley. In the next sections, we will describe the roles of G-proteins in the regulation of abiotic stress responses with the foundational knowledge from Arabidopsis and the extent to which it has been expanded to crop plants.

Drought Stress

Drought stress leads to poor germination, challenges in seedling establishment, wilting of leaves with reduction in leaf number and surface area, reduced plant height, an overall change in root system architecture affecting primary root length, lateral root density and morphology of root hairs, reduced flowering and diminished seed filling, all resulting in significantly reduced yields (Koevoets et al. 2016; Seleiman et al. 2021). Drought stress is primarily sensed by roots and the information is transmitted to the aerial parts of plants through long-distance root–to-shoot signaling, leading to the production of abscisic acid (ABA) in leaves, a key phytohormone that regulates the stress response in plants through the regulation of stomatal movement and stress-responsive molecular changes (Li et al. 2021; McAdam et al. 2016; Schachtman and Goodger 2008). It is not surprising that several of the ABA-regulated gene expression networks are shared between roots hair cells and stomatal guard cells (Li et al. 2012).

Regulation of water-loss through stomatal pores by modulating the aperture of the guard cells is an important adaptive response of land plants (Buckley 2019). ABA plays a key role in maintenance of stomatal physiology through regulation of ion fluxes across the guard cell membrane (Assmann and Jegla 2016; Huang et al. 2019b; Kim et al. 2010; Munemasa et al. 2015). ABA regulates the inward potassium and the calcium channels and transporters, influencing the levels of K^+ and Ca^{2+} and consequently of anions such as Cl^- and malate, essentially promoting the closure of open stomata and inhibiting the opening of closed stomata, in response to water limitation (Assmann and Jegla 2016; Eisenach and De Angeli 2017; Kim et al. 2010; Munemasa et al. 2015). This regulation ensures plant fitness by controlling water-loss. Several genetic and biochemical studies have identified G-proteins as key regulators of ion channel activities and stomatal physiology, implying their direct role in mitigating drought stress (Fan et al. 2008; Jeon et al. 2019; Wang et al. 2001). In Arabidopsis, the availability of knockout mutants of each of the G-protein subunit genes (and their combinations) has allowed the investigation of the roles of G-proteins in regulating drought stress using multiple approaches (Fan et al. 2008; Nilson and Assmann 2010; Pandey and Assmann 2004). These include elucidating the effects of G-protein function on guard cell ion channel activities, transpiration efficiency, gene expression and proteomic changes, as well as whole plant drought responses. Overall, these data present a complex regulatory picture, where G-protein subunits have distinct tissue-specific roles in the regulation of plant

drought responses (Alvarez et al. 2015; Chakraborty et al. 2015; Fan et al. 2008; Nilson and Assmann 2010).

The stomatal responses of G-protein mutants are studied in detail. The *gpa1* mutant shows wild-type (WT)-like response to ABA-dependent promotion of stomatal closure, but hyposensitivity to ABA-dependent inhibition of stomatal opening (Wang et al. 2001). The *agb1* and *agg3* mutants also show impaired inhibition of inward K^+ channels in guard cells (Fan et al. 2008), while the *agg1* and *agg2* mutants have WT-like stomatal ABA responses (Chakravorty et al. 2011; Trusov et al. 2008). These data predict that overexpression of specific G-protein genes can lead to better stress tolerance, by making guard cells more responsive to ABA/drought stress. However, overexpression of *AGB1* in WT or in the *agb1* backgrounds did not alter ABA-mediated inhibition of the K^+ inward current and the stomata showed ABA sensitivity similar to the WT plants (Fan et al. 2008).

Drought stress (and other abiotic stresses) also causes significant spatio-temporal changes in intracellular Ca^{2+} concentration, which acts as an important secondary messenger in the activation of ABA-dependent ion channels (Huang et al. 2019b; Konrad et al. 2018). A theoretical Boolean model of gene expression changes related to stomatal opening/closing following the removal of ABA or external Ca^{2+} predicts that the cytosolic Ca^{2+} oscillation is a deterministic factor for maintaining stomatal physiology (Albert et al. 2017; Li et al. 2006; Maheshwari et al. 2020). Genetic studies have revealed that AGB1 is required for sensing guard cell Ca^{2+} and calcium-induced release of Ca^{2+} to amplify the signal for stomata closure in the presence of ABA (Jeon et al. 2019). An involvement of extracellular calmodulin (extCaM) and calcium-binding caleosin proteins (RD20/CLO) has also been identified (Brunetti et al. 2021).

In addition to the regulation of specific K^+ and Ca^{2+} channels, a recent study has also shown the involvement of the RAPID ALKALIZATION FACTOR1-FERONIA (RALF-FER) signaling module in regulation of stomatal movement, where binding of RALF1 peptide ligand to its receptor kinase FER promotes stomatal closure and inhibits stomatal opening. Biochemical studies have shown that AGB1 interacts with FER and RALF-FER-mediated stomatal regulation requires AGB1, as *agb1* was impaired in such response. Importantly, AGGs and XLGs are also implicated in RALF1-FER-dependant stomatal response (Yu et al. 2018).

Another signaling module involved in the regulation of ABA and stomatal physiology is the interaction of lipid-mediated signaling with G-proteins. In Arabidopsis, Phospholipase Dα1 (PLDα1) catalyses hydrolysis of membrane lipids into phosphatidic acid (PA), which is an important secondary messenger in the ABA signaling pathway (Mishra et al. 2006; Roy Choudhury and Pandey 2016b; Zhao 2015). In the presence of exogenous ABA, PA produced by PLDα1 activity binds to PP2C phosphatases, which are the key negative regulator of the ABA perception module (Mishra et al. 2006). Interestingly, both PA and PLDα1 interact with GPA1 to mediate ABA inhibition of stomatal opening. Furthermore, recent studies have shown that PLDα1 also acts as a GAP for GPA1 in Arabidopsis and acts in a negative feedback loop where RGS1 inhibits PLDα1 activity, whereas PA produced by PLDα1 binds to RGS1 to inhibit its activity, eventually resulting in a dynamic, active pool of GPA1 (Roy Choudhury and Pandey 2017).

The G-protein-dependent effects of ABA on stomatal guard cells have two more aspects, which play an important role in regulating the drought responses of the plant. First, AGB1 has also been proposed to promote ABA biosynthesis (Liu et al. 2017). Since the loss of AGB1 function is effectively similar to the loss of entire G-protein function in plants like Arabidopsis (i.e., a single Gβ protein that interacts with multiple Gα or Gγ) (Pandey 2019; Roy Choudhury et al. 2020; Smythers et al. 2022; Urano et al. 2016), one would predict the role of G-proteins in regulating not only ABA signaling, but also ABA biosynthesis, during drought stress. Second, G-proteins also regulate key developmental phenotypes such as primary root length and lateral root density as well as stomatal density. The Arabidopsis *gpa1* mutants have significantly lower and the *agb1* mutant has significantly higher root mass and stomatal density than the WT plants (Chen et al. 2006; Ullah et al. 2003; Zhang et al. 2008). Both these traits will affect the whole plant drought response. Furthermore, the role of specific G-protein subunits and of their core interaction partners such as XLGs, RGS1 and PLDα1 in regulation of stomatal development is exceedingly complex, and mostly unexplored (Pandey 2019; Roy Choudhury et al. 2020). These intersecting sets of regulations make the prediction of the exact role of G-proteins at the whole plant level even more complex. To address this, several studies have evaluated changes in G-protein-dependent transcriptome (Li et al. 2012; Pandey et al. 2010; Wang et al. 2011), proteome (Alvarez et al. 2015; Gookin et al. 2008; Song et al. 2018; Zhao et al. 2010), metabolome (Jin et al. 2013) and redox proteome (Smythers et al. 2022) in Arabidopsis. These results suggest that during G-protein-dependent ABA/drought signaling several regulatory pathways intersect, causing key changes in primary and secondary metabolism, photosynthetic efficiency, redox homeostasis, and ion balance, eventually leading to the optimal plant response. This complexity of response regulation is also reflected in the analysis of the whole plant drought response of the G-protein mutants. For example, based on the ion channel activities alone, one would predict that the *gpa1* mutants would have open stomata even under water stress and therefore lower transpiration efficiency (ratio of carbon assimilation and transpiration). However,

these plants show higher transpiration efficiency under drought stress and after exogenous application of ABA (Nilson and Assmann 2010), likely due to fewer stomata per leaf. Such observations necessitate detailed evaluation of multiple interconnected networks, before specific traits or genes are modified in crop plants.

To evaluate the effects of specific genes in conferring stress tolerance, the *AGG3* gene of Arabidopsis was overexpressed in *Camelina sativa*, an emerging oil seed crop. Constitutive and seed-specific overexpression of *AGG3* resulted in tolerance to drought due to higher photosynthetic rate with greater stomatal conductance leading to an elevated transpiration rate (Roy Choudhury et al. 2014). The seed-specific proteome from these transgenics identified proteins involved in drought tolerance corroborating its role as a positive regulator of plant stress responses (Alvarez et al. 2015). The effects of efficiently managed stress response also translated to better productivity, as seen by an overall increase in biomass, seed size, and seed yield, in these transgenic camelina plants under greenhouse conditions (Roy Choudhury et al. 2014) and in field trials (unpublished data).

Several studies have demonstrated the roles of different G-protein subunits in regulating drought responses in *Oryza sativa* (rice). The G-protein complex in rice consists of one Gα (RGA1), one Gβ (RGB1) and five Gγ subunits, RGG1, RGG2, DEP1 (RICE DENSE AND ERECT PANICLE 1), GS3 (GRAIN SIZE3) and GGC2 (Perfus-Barbeoch et al. 2004; Sun et al. 2018). Among these, the *RGA1*, *RGB1*, *RGG1*, and *RGG2* transcripts are up-regulated under drought stress, implying their plausible involvement in mitigating this response (Cui et al. 2020). The *d1* mutant of rice, which possesses a non-functional RGA1 protein, exhibits higher stomatal conductance under drought stress with increased photosynthetic rate and a higher root to-shoot ratio, suggesting that RGA1 is a negative regulator of drought stress response (Ferrero-Serrano and Assmann 2016). Further characterization of *d1* mutants in rice cultivars Nipponbare and Taichung revealed improved photosynthesis and CO_2 conductance, corroborating this hypothesis (Zait et al. 2021). Transcriptomic analysis of the *d1* mutant showed several differentially expressed genes related to the drought stress response (Jangam et al. 2016), supporting the role of G-proteins in regulating such response at the gene expression level, in addition to the improved stomatal conductance. The use of CRISPR/Cas9-mediated mutagenesis to generate precisely edited G-protein genes in rice and consequent mutant analysis confirmed the results obtained with the *RGA1* gene (Cui et al. 2020). The *rga1* mutants showed a better survival rate under drought stress. Of the four putative XLGs in rice, *pxlg4* knockout mutant also showed better survival following drought treatment compared to the WT (Cui et al. 2020), suggesting the Gα proteins, in general, may act as negative regulators of drought responses in rice. The molecular mechanisms underlying these responses have not yet been determined.

Contrary to the regulation by the Gα proteins, the RGB1 subunit is a positive regulator of drought tolerance in rice. RGB1 has been shown to promote ABA biosynthesis, similar to the role of Arabidopsis AGB1 (Zhang et al. 2015). Genetic analysis shows that the knockdown of *RGB1* causes hypersensitivity to drought stress due to elevated water-loss (Zhang et al. 2015). Similar responses were observed in different Gγ gene-edited mutants i.e., *rgg1*, *rgg2*, *gs3*, and *ggc2* which exhibited hypersensitivity to drought stress (Cui et al. 2020). Genetic ablation of the Gγ gene (*qPE9-1* allele) in rice is also reported to have conferred tolerance to drought due to reduced water-loss and higher stomatal conductance. Furthermore, qPE9 was shown to suppress ABA responsive transcription factors involved in stress tolerance and therefore acts as a negative regulator of drought stress in rice (Zhang et al. 2015). It should be noted that the phenotypes of G-protein mutants in dicot versus monocot plants are distinct- the monocot Gα mutants are of smaller stature, with bushy leaves; a phenotype not seen in the dicot Gα mutant plants (Bhatnagar and Pandey 2020; Bommert et al. 2013; Cui et al. 2020; He et al. 2013). Complete knockout of the monocot *Gβ* gene results in seedling lethality (Utsunomiya et al. 2012; Wu et al. 2020) and, consequently, the available data are from plants expressing lower levels of *Gβ* gene (Gao et al. 2019; Utsunomiya et al. 2012; Wu et al. 2020). In eudicots, complete loss of the *Gβ* gene results in multiple phenotypic changes, inherently and in response to a signal, but plants are viable and capable of completing their life cycle (Roy Choudhury et al. 2020; Ullah et al. 2003). Monocot plants expressing lower levels of the *Gβ* transcript also exhibit several morphological differences from the WT plants, such as short stature, bushy and narrow leaves (Utsunomiya et al. 2012; Wu et al. 2020). The extent to which these developmental phenotypes contribute to the overall plant drought responses is yet to be explored.

The role of G-proteins in regulation of drought stress is reported from crops such as pea, tobacco, sugarcane, cucumber and mulberry (Bhardwaj et al. 2020; Liu et al. 2021b; Ramasamy et al. 2021). In most of these cases, the results are reported based on the change in transcript level of G-protein genes in response to drought stress; overexpression in the heterologous system (e.g., the mulberry gene overexpressed in tobacco Liu et al. 2018), or protein–protein interactions, and mechanistic knowledge about the signaling pathways involved remains limited (Table 1). Additional studies exploring the roles of G-proteins in conferring drought tolerance in greenhouses and in field settings are required to fully utilize their potential in generating drought-tolerant crops.

Salinity and Osmotic Stress

When exposed to high salt, plants experience a combination of osmotic shock due to reduced water availability in the soil and ionic stress imparted by excess Na^+ uptake which eventually interferes with the uptake of other ions like K^+ leading to ionic imbalance (van Zelm et al. 2020). Salinity-driven osmotic stress attenuates plant growth due to arrest of cell proliferation in meristems and results in cell death by ion toxicity (Liu et al. 2015). In particular, salinity stress in the plants results in accumulation of reactive oxygen species (ROS), which is detrimental to proper biomolecule functioning and restrains plant growth and productivity (Miller et al. 2010). Thus, maintenance of ion homeostasis and detoxification of ROS are the major adaptive responses of plants during salinity stress.

G-proteins are involved in modulating plant's growth during salt stress. Several studies have highlighted the possible involvement of G-proteins in maintaining ion fluxes and scavenging ROS during salinity stress (Liu et al. 2018; Peng et al. 2019). Transcriptomic analysis also revealed that the core G-protein subunits Gα, Gβ and Gγ are significantly up-regulated under salt stress in Arabidopsis and other crop plants such as rice, rape seeds, and peas (Gao et al. 2010a; Jangam et al. 2016; Yadav et al. 2012).

The Arabidopsis *gpa1* mutants exhibit higher tolerance to salt stress compared to the WT plants, in term of seed germination, root-shoot ratio, relative water content and ROS detoxification (Chakraborty et al. 2015), implying that the Gα subunit is a negative regulator of salt stress. On the other hand, *agb1* mutants exhibit higher sensitivity to salinity stress, as NaCl treatment results in smaller and chlorotic leaves with increased Na^+ and reduced K^+ in the roots, leading to ion imbalance (Colaneri et al. 2014). Molecular characterization of *agb1* showed that the mutant was compromised in translocation of Na^+ from root to-shoot, resulting in altered Na^+ fluxes. Genes involved in Na^+ homeostasis are significantly downregulated in *agb1* (Ma et al. 2015b). The hypersensitivity of *agb1* mutant to salinity stress was also correlated with the reduced peroxidase (POD) activity required for ROS detoxification (Ma et al. 2015b). A recent study has shown that AGB1 interacts with N-Myc 1 (NDL1), which acts as a modulator of the salt stress response in Arabidopsis (Gupta et al. 2021). Similarly to *agb1*, *xlg1/2/3* triple and *agg1/2/3* triple mutants also show hypersensitivity to salinity stress and exhibit smaller and chlorotic leaves when grown in the presence of high NaCl (Colaneri et al. 2014; Roy Choudhury et al. 2020). While AGGs are involved in salt stress tolerance by activating ROS detoxification, XLGs do so by interacting with the salt-inducible, zinc finger transcription factors SZF1 and SZF2. It has been proposed that AGB1 interacts with XLGs to promote plant growth during salt stress through the expression of SZF1 and SZF2 (Liang et al. 2017). These findings highlight the role of AGB1 (or the XLG.AGB1.AGG trimer) as a positive regulator of salinity stress by ROS detoxification and maintaining ionic balance, although the detailed underlying molecular mechanisms are only beginning to be discovered.

Maintenance of cell wall integrity during salinity/osmotic stress is crucial for plants to withstand the turgor pressure (Rui and Dinneny 2020; Vaahtera et al. 2019). A key component in maintaining cell wall integrity is the recently identified LRX-RALF-FER signaling module in Arabidopsis (Feng et al. 2018). The leucine-rich repeat extensin (LRX) crosslinks with cell wall pectin. FER also binds pectin through its extracellular malectin-binding domain. Cell type-specific increases in Ca^{2+} fluxes are also required to maintain cell wall integrity through crosslinking of pectins in FER-dependant fashion. These interactions are disrupted under salt stress and the integrity of the cell wall is lost in *fer* loss-of-function mutant. Because AGB1 has been identified as a key interactor of FER (Yu et al. 2018), an AGB1/LX-RALF-FER signaling module may also be involved in pectin-crosslinking-associated cell wall damage during salinity stress (Feng et al. 2018; Zhao et al. 2018).

A forward genetic screen in rice identified a novel mutant allele of *RGA1*, *sd58*, which showed better salt tolerance due to reduced ROS accumulation, consistent with higher enzymatic activity of ROS detoxification enzymes (Peng et al. 2019). Quantitative proteomics identified differentially expressed proteins involved in the regulation of photosynthesis, metabolic processes, and ROS homeostasis in *sd58*. Similarly, CRISPR/Cas9 edited Gα mutants in rice, *rga1-1,* and *rga1-2* also exhibit better survival after salinity stress (Cui et al. 2020). These mutants showed delayed leaf senescence, lower chlorophyll degradation and reduced electrolyte leakage from the cytoplasm during salt stress (Cui et al. 2020). The *Gα* subunit, CT2 (COMPACT PLANT2) in maize is an important regulator of agronomic traits including upright leaf, higher spikelet density and kernel row number (Bommert et al. 2013). The *ct2* null mutant exhibited better salt tolerance with reduced cytoplasm electrolyte leakage, delayed leaf senescence and chlorophyll degradation, similar to *rga1* in rice (Urano et al. 2014). All these studies support the role of Gα proteins as a negative regulator of the response to salt stress in plants. In contrast, the results obtained from the overexpression of the *Gα* genes in pea led to improved salt tolerance (Misra et al. 2007), whereas knockdown of the *Gα* gene expression in cucumber led to hypersensitivity to salt stress with increased leaf wilting and reduced water content (Yan et al. 2020), suggesting their role as positive regulators. The extent to which these results are due to different stress conditions, age of the plants, or additional experimental factors is not known.

Similar to what was observed with the response to drought stress, the Gβ and Gγ proteins seem to be positive

Table 1 Role of G-proteins in regulating plant abiotic stress responses

Plant species	G-protein subunit	Stress	Positive or negative regulation	Explored mechanisms, pathways or responses	Reference
Arabidopsis	GPA1	Drought	Negative	Transpiration efficiency and stomatal density	Nilson and Assmann (2010)
	AGB1	Salinity	Negative		Chakraborty et al. (2015)
	AGG1.2.3	Cold	Negative	Seed germination, root–shoot ratio, relative water content and ROS detoxification	Chakraborty et al. (2015)
	XLG1.2.3	UV-B	Unknown		He et al. (2013)
	AGG3	Ozone	Unknown		Joo et al. (2005)
		Drought	Positive	Cold stress-responsive gene expression	Fan et al. (2008)
		Salinity	Positive		Colaneri et al. (2014), Ma et al. (2015b) and Yu et al. (2018)
		Ozone	Unknown	Stomatal movement under high UV-B treatment	
		Salinity	Positive		
		Salinity	Positive	Sensitivity to O_3-induced damage	Joo et al. (2005)
		Cd toxicity	Positive	ABA-dependent ion channel activity in guard cells, plant's fitness and seed yield	Colaneri et al. (2014) and Yu et al. (2018)
					Liang et al. (2017)
				ROS detoxification and ion homeostasis, chlorophyll degradation and plants survival	Alvarez et al. (2015)
				Sensitivity to O_3-induced damage	
				ROS detoxification	
				Salt stress-responsive gene expression changes	
				Expression of proteins involved in heavy metal tolerance	
Camelina	AGG3-OE	Drought	Positive	Stomatal conductance, photosynthetic and transpiration rate	Roy Choudhury et al. (2014)
Rapeseed	*Bn*GA1, *Bn*GB1, *Bn*GG2	Heat and cold	Negative	Temperature responsive gene expression	Gao et al., (2010a, 2010b)
Tomato	*Le*GPA1	Cold	Positive	ROS detoxification and synthesis of protectants e.g., proline, soluble sugars	Guo et al. (2020)
Pea	*Ps*Gα	Salinity	Positive	Improved water content	Misra et al. (2007)
	*Ps*Gα *Ps*Gβ	Heat	Positive	Stomatal movement, gene expression changes	Bhardwaj et al. (2020)
Rice	RGA1	Drought	Negative	Stomatal conductance, photosynthetic rate and root–shoot ratio	Ferrero-Serrano and Assmann (2016)
	PXLG4	Salinity	Negative		
	RGB1	Cold	Positive	ROS detoxification	Peng et al. (2019)
	qPE9-1(Gγ)	Drought	Negative	Activation of Ca^{2+} channel for temperature sensing	Ma et al. (2015a)
	RGG1	Drought	Positive		Cui et al. (2020)
	DEP1	Salinity	Positive	Unknown	Zhang et al. (2015)
	DEP1	Heat	Positive	Regulation of water-loss and ABA biosynthesis	Biswas et al. (2019) and Swain et al. (2019)
	GS3	Drought	Negative		
		Salinity	Positive	Electrolyte leakage, chlorophyll content and ROS detoxification	Biswas et al. (2019)
		Salinity	Negative		Zhang et al. (2015)
		Cd toxicity	Positive	Effective mitigation of ROS and activation of heat shock proteins	Swain et al. (2019)
		Salinity	Negative		Cui et al. (2020)
		Heat	Negative	Regulation of water-loss and stomatal conductance	(Kunihiro et al. 2013) (Cui et al. 2020)
				ROS detoxification	Kan et al. (2022)
				Survival rate and crop yield	
				Heterologous expression, may act through its Cys-rich region	
				Survival rate and crop yield	
				Regulation of heat-triggered Ca^{2+} signaling and wax biosynthesis	
Maize	CT2	Salinity	Negative	Electrolyte leakage from the cytoplasm, leaf senescence and chlorophyll degradation	Urano et al. (2015)
Wheat	GPBL	Cold	Negative	ROS scavenging and cold responsive gene expression	Dong et al. (2019)

Table 1 (continued)

Plant species	G-protein subunit	Stress	Positive or negative regulation	Explored mechanisms, pathways or responses	Reference
Mulberry	*Ma*Gα	Drought and salinity	Negative	Modulates ROS detoxification	Liu et al. (2018)
	*Ma*Gβ, *MaGγ1*, *MaGγ2*	Drought and Salinity	Positive	ROS detoxification and proline content	Liu et al. (2021a, 2017)
Cucumber	*Cs*Gα	Salinity	Positive	Improves water content and leaf wilting	Yan et al. (2020)
	CsGG3.2	Cold	Positive	Affects ROS detoxification and membrane lipid peroxidation	Bai et al. (2018)

regulators of salinity stress in rice. Overexpression of *RGB1* resulted in better salt tolerance with reduced electrolyte leakage and higher chlorophyll content (Biswas et al. 2019). At the molecular level, the better salt tolerance was correlated with increased expression of ROS detoxification enzymes like superoxide dismutase (SOD). Concurrent overexpression of *RGB1* and *RGG1* in rice improved salt tolerance by increasing the expression of stress-responsive genes and better management of ROS (Swain et al. 2019). However, an *rgb1* mutant generated by CRISPR/Cas9 mutagenesis showed better survival after salinity treatment (Cui et al. 2020), which confounds previous observations.

The non-canonical Gγ subunits in rice, DEP1 and GS3 may also act as negative regulator of salt stress as *gs3* and *dep1* mutants showed better survival rate following salinity treatment and both the mutants had higher yield (Cui et al. 2020). In a few other crop species where the roles of G-proteins in salt stress has been analysed, a similar confounding picture emerges—the overexpression of a *Gβ* gene in pea led to no effect (Misra et al. 2007), whereas the overexpression of mulberry *Gβ*, *Gγ1* or *Gγ2* genes led to increased salt tolerance (Liu et al. 2017, 2018). As mentioned earlier, the contrasting results could be due to the experimental conditions or due to the inherent nature of the G-protein complex regulation (discussed in the next sections) and need further confirmation.

Temperature Stress

Extreme hot and cold temperatures affect both the vegetative and reproductive phases of plant life cycle resulting in a significant decrease in crop productivity (Zhang et al. 2022). At the molecular level, heat stress adversely affects various biomolecules, resulting in altered membrane fluidity leading to loss of cell membrane integrity, reduced protein synthesis, improper protein functionality due to their aggregation and altered enzyme kinetics (Niu and Xiang 2018). The morphological changes include delayed seedling establishment with an overall reduction in plant growth rate, smaller leaves, early senescence and abscission, elongated hypocotyl, petiole and damaged fruit (Bita and Gerats 2013). Heat stress also affects reproductive development in plants such as reduced pollen and ovule viability, resulting in poor fertilization, slower pollen tube elongation, improper floral organ development, and closed floral buds with reduced seed vigor (Endo et al. 2009; Kumar et al. 2013; Snider et al. 2011). Among physiological changes, reduction in the rate of photosynthesis, respiration, and transpiration is more evident during heat stress, accompanied by an overall increase in the ROS and phytohormone production (Kumar et al. 2012; Yin et al. 2008).

In response to cold stress, plants need to synthesize cryoprotectants such as soluble sugars, proline and cold-resistance proteins to protect themselves from the freezing temperatures by regulating osmotic potential, avoiding ice crystal formation and providing stability of the cell membrane (Kaplan and Guy 2004). Calcium channels have been involved in low temperature detection in plants (Knight and Knight 2012). Ca^{2+}, along with other secondary messenger molecules such as ROS and NO are involved in the regulation of the plant response to cold stress (Knight and Knight 2012; Zhao et al. 2009), although the downstream events involved in the cold signalling pathway are poorly understood.

As with other types of abiotic stresses, the involvement of G-proteins has been shown in response to tolerance to temperature stress. In Arabidopsis, these responses are mostly evaluated at the transcriptomic level, where a number of transcripts related to temperature stress were differentially expressed in *gpa1* mutants (Chakraborty et al. 2015). The *gpa1* mutants exhibit significantly increased tolerance to cold stress and a subtle increased tolerance to heat stress, corroborating the transcriptomics data (Chakraborty et al. 2015). However, unlike other stresses, where the response mechanisms have been characterized to some extent, no mechanistic data exist on the response to temperature stress of G-protein mutants in Arabidopsis. The transcriptional regulation of different G-protein subunits themselves has been

reported in rapeseed (*Brassica napus*). The *Gα* (*BnGA1*), *Gβ* (*BnGB1*) and *Gγ* (*BnGG2*) transcripts show downregulation in response to heat and cold stresses (Gao et al. 2010a, 2010b), suggesting that the G-protein subunits may act as negative regulators of temperature stress responses in plants. This was supported by the heterologous overexpression of a wheat Gβ protein, *Ta*GPBL in Arabidopsis, which causes reduced plant growth at 16 °C. These plants also show reduced expression of cold-inducible genes and lower activity of ROS scavengers, compared to WT plant, corroborating the role of Gβ proteins as a negative regulator of temperature stress signaling (Dong et al. 2019).

In other species, such as Chinese pear (*Pyrus pyrifolia*), six out of eight *Gα* genes were up-regulated in response to high temperature in leaves (Chen et al. 2022). Similarly, the transcript levels of the pea *Gα* and *Gβ* genes showed higher expression after heat treatment (Misra et al. 2007). Furthermore, transgenic tobacco plants constitutively expressing *PsGα* or *PsGβ* showed tolerance to heat stress when tested by leaf disk senescence assay and germination/growth of T_1 seeds/seedlings (Misra et al. 2007). Further characterization of tobacco plants overexpressing *PsGβ* suggest that the heat stress response is mediated by nitric oxide (NO)-induced stomatal closure during heat stress (Bhardwaj et al. 2020), and may also include mitogen activated protein kinase (PsMPK3). These results suggest a positive role of G-proteins during temperature stress response, in contrast to what has been suggested for Arabidopsis. Studies in tomato plants expressing an altered level of *Gα* gene by *RNAi* and overexpression approaches also support the positive role of these proteins in the tolerance to cold stress (Guo et al. 2020). *The LeGPA1-RNAi* and *LeGPA1-OX* plants exhibit reduced and improved tolerance to cold stress, respectively, compared to the WT tomato plants. The *LeGPA1-OX* plants showed higher activities of antioxidant enzymes such as SOD, POD, and catalase (CAT) leading to a lower accumulation of H_2O_2 and O^{2-}. Moreover, there was an upregulation of the transcripts involved in cold signaling, resulting in an increased levels of proline and soluble sugar that protect against cellular damage (Guo et al. 2020).

The involvement of G-proteins in controlling temperature stress in rice has been studied at multiple levels. Transcriptomic analysis of the rice *d1* mutant identified hundreds of differentially expressed transcripts related to temperature stress tolerance. Specific G-protein subunits themselves are also regulated at the transcript level and show altered expression in response to cold and heat stress. As with other stresses, the regulation seems to be complex. For example, the level of *RGA1* was reduced in response to elevated temperature. On the contrary, the *RGB1, RGG1,* and *RGG2* transcripts were up-regulated in response to both heat and cold stress (Yadav et al. 2013, 2014). The G-protein-dependent cold stress response in rice has been also linked to a quantitative trait locus COLD 1 (Chilling-tolerance divergence 1), a homolog of Arabidopsis GTG proteins, which interact with GPA1 (Pandey et al. 2009). COLD1 interacts with rice RGA1 and affect its GTPase-activity and calcium channel activation. Overexpression of COLD1 significantly improved chilling tolerance, whereas its downregulation was reported in cold-sensitive rice lines (Ma et al. 2015a). Overexpression of the *RGB1* gene in rice also led to improved heat stress tolerance, potentially via effective mitigation of ROS and activation of heat shock proteins (Biswas et al. 2019).

One of the rice type-III Gγ proteins, GS3, is recently identified as the causal gene underlying the quantitative trait locus for heat stress tolerance, thermotolerance 2, TT2 (Kan et al. 2022). Heat-treated plants with the natural allele of disrupted TT2 function exhibited a reduction in wax content, therefore an enhanced thermotolerance in comparison with plants carrying the functional TT2 allele. The transcription factor SCT1 (Sensing Ca^{2+} Transcription factor 1) is a calmodulin (CaM)-interacting Ca^{2+} decoder, that negatively regulates the *OsWR2* gene (*Wax Synthesis Regulatory 2*). The CaM-SCT1 interaction was affected in plants with disrupted TT2, revealing that the G-protein TT2 regulates thermotolerance by mediating heat-triggered Ca^{2+} signaling and Ca^{2+}/CaM-dependent suppression of SCT1 transcriptional activity to control wax biosynthesis in rice (Kan et al. 2022).

The roles of G-proteins in mediating temperature stress have been evaluated in a few additional crops. In wheat, the *Gα* gene, *GA1-D*, and two of the *Gγ* genes, *Gγ2-B* and *Gγ2-D*, were significantly up-regulated by cold and heat stress, respectively (Gawande et al. 2022). In cucumber, a type-III Gγ protein, CsGG3.2, has been shown to be involved in the regulation of tolerance to cold stress by modulating the CBF (Cold Binding Factor) signaling module and resulting in increased activities of antioxidant enzymes and consequently decreased production of ROS, reduced membrane lipid peroxidation after cold stress (Bai et al. 2018). A recent study in sugarcane (*Saccharum* spp.), implies a role of G-protein signaling in stress responses. The sugarcane GPCR-like protein (ShGPCR1), a homolog of the Arabidopsis GCR1, was upregulated by cold, drought and salinity stresses (Ramasamy et al. 2021). GCR1 is a known interactor of GPA1 and regulates stress response in Arabidopsis, potentially via G-protein signaling (Pandey and Assmann 2004). Constitutive overexpression of *ShGPCR1* in sugarcane conferred tolerance to multiple abiotic stresses and showed up-regulation of multiple cold stress marker genes such as *NAC23* (*NAM/ATAF1/2/CUC*), *CBF2* (*COLD BINDING FACTOR 2*), *ScADH3* (*ALCOHOL DEHYDROGENASE 3*), as well as several drought and salinity marker genes (Ramasamy et al. 2021).

Heavy Metal Stress

Heavy metals such as cadmium or arsenic impose significant stress on plants under specific growth environments. In particular, Cd due to its chemical similarity to metal co-factors such as Zn, Fe, and Ca, can inactivate and denature proteins by binding to free sulfhydryl groups (DalCorso et al. 2008; Lewandowska et al. 2020). Plants typically cope with Cd toxicity by sequestration into the vacuoles, a process that largely involves cysteine (Cys)-rich proteins that can chelate heavy metals (Freisinger 2008). Several studies have demonstrated the role of unique type-III Gγ proteins in Cd tolerance. Overexpression of rice DEP1 (a type-III Gγ protein) in heterologous systems, such as yeast and in Arabidopsis resulted in tolerance to high levels of Cd (Kunihiro et al. 2013). Similarly, the overexpression of Arabidopsis *AGG3* gene in camelina improved Cd tolerance, which was also supported by a quantitative proteomics analysis, where several proteins related to heavy metal toxicity were differentially abundant (Alvarez et al. 2015). Such response to Cd is proposed to be mediated via the Cys-rich C-terminal region of these proteins. In contrast, the role of Gα and Gβ subunits in the response to heavy metal stress is poorly understood in plants. Based on transcript profiling in rice, it appears that *RGA1* is involved in heavy metals such as cadmium and arsenate tolerance/sensitivity, while *RGB1* expression was not affected by these heavy metals (Yadav et al. 2013, 2014).

Other Environmental Stresses

In addition to their relatively well-documented roles in droughts, temperature and salinity stress, the involvement of G-proteins has been demonstrated in other adverse atmospheric conditions such as UV-B radiation and ozone (O_3) (He et al. 2013; Joo et al. 2005).

In plants, high-energy enriched UV-B radiation causes thickening of leaves and cuticular wax layers and reduction of photosynthetic efficiency, plant growth, and pollen fertility (Caldwell et al. 2007). Stomatal regulation is central to the plants' response to UV-B. Exposure to UV-B results in increased production of reactive oxygen and reactive nitrogen species in the stomatal guard cells, which ensures stomatal closure under high light/UV-B radiation (Jansen and van den Noort 2000). ABA elicits the production of ROS including H_2O_2 under such conditions (He et al. 2013). In Arabidopsis, the plasma membrane-bound NADPH oxidases RbohD and RbohF are involved in the generation of H_2O_2 in an ABA-dependant manner (Kwak et al. 2003). Being an important mediator of the stomatal ABA response, the *gpa1* mutant is compromised in stomatal closure under high UV-B treatment due to reduced H_2O_2 and NO production. However, exogenously added H_2O_2 and NO can rescue the stomatal closure defect of *gpa1*, suggesting that GPA1-mediated signaling is upstream of UV-B-mediated H_2O_2 and NO production (He et al. 2013). The cytosolic synthesis of phenylalanine (Phe) ensures the timely production of antioxidants and photoprotective molecules against high-frequency radiation (Para et al. 2016). ADT3 (AROGENATE DEHYDRATASE 3) is one of the final enzymes participating in the biosynthesis of Phe and it has been shown that ADT3 is positively regulated by GPA1 in response to blue light that controls the synthesis of phenylpyruvate, Phe, and a variety of UV- and blue light absorbing compounds (Warpeha et al. 2006, 2008). It has also been demonstrated that when *adt3* Arabidopsis seedlings were exposed to UV-C light, ROS production was significantly increased, and that Phe could prevent this significant ROS accumulation (Para et al. 2016), revealing the crucial role of ADT3 in ROS homeostasis and its regulation by GPA1. The involvement of other G-protein subunits in UV-B response is largely unknown.

In addition to UV-B, ozone is also harmful for plants as it can enter through stomata (Torsethaugen et al. 1999) and generate oxidative stress intracellularly, resulting in massive cellular damage (Joo et al. 2005). Elevated ozone (O_3) levels affect crop productivity by reducing yield and grain quality. For example, wheat and rice exposed to high levels of O_3 produced significantly smaller grains with decreased starch content, increased protein and nutrient (P, K, Mg, Ca, Zn, Fe) content, affecting the grain texture and its baking properties (Broberg et al. 2015; Ueda et al. 2015). Similar to UV-B radiation, O_3 also induces ROS production primarily in the chloroplasts of the stomatal guard cells (Evans et al. 2005). The signal is transmitted to the adjoining cells where extracellular ROS act as a molecular trigger for generation of intracellular ROS production through membrane-localized NADPH oxidases RbohD and RbohF. The mutants *gpa1* and *agb1* have reduced and increased sensitivities, respectively, to O_3-induced damage. It was proposed that the Gβγ complex mediates the early chloroplastic oxidative burst, while the Gα induces the late ROS production that leads to the activation of the membrane-bound NADPH oxidases, necessary for transmitting the ROS signal and trigger cell death (Joo et al. 2005). Ozone and UV-B radiation stress mediated effects may be correlated, as the depletion of the stratospheric ozone layer exacerbates the harmful effect of UV-B on crop productivity. However, the role of G-protein subunits in ozone and UV-B tolerance in crop plants largely remains unknown.

Signaling Modules Affected by G-Proteins in Regulation of Stress Responses

The overall description of the role of G-proteins in mediating abiotic stress responses in plants presents a complex picture. However, a closer examination of several of these

responses supports scenarios where G-proteins potentially affect a few fundamental signaling modules, which by interconnecting with discrete signaling networks may result in signal-specific responses (Fig. 2). For example, the role of G-proteins in affecting ABA signaling pathways places them in a central position to regulate almost all abiotic stress responses (Fan et al. 2008; Liu et al. 2021a; Yu et al. 2018; Zhang et al. 2015). G-proteins regulate the signaling pathways of several other phytohormones, which intersect and feedback into ABA synthesis and signaling networks (Alvarez et al. 2015; Bhardwaj et al. 2020; Smythers et al. 2022; Zhang et al. 2015). ABA responses are also related to ROS production (Bohmer and Schroeder 2011; Mittler and Blumwald 2015). Regulation of ROS levels is central to the normal growth, development and productivity of plants. By their ability to affect the ROS levels, either by their interactions with NADPH oxidases, or via the high Cys containing regions of the type-III Gγ proteins, or other unknown mechanisms, G-proteins have the ability to affect several of these stress responses (Bai et al. 2018; Guo et al. 2020; Liu et al. 2017). There is additional information that links the G-proteins with ROS signaling. For example, the proteomic analysis of Arabidopsis *adt3* (*arogenate dehydratase3*) mutant shows misregulation of proteins involved in cell wall organization (Para et al. 2016), which were also identified as interactors of GPA1 (Klopffleisch et al. 2011). ADT3 catalyzes the last step of phenylalanine (Phe) biosynthesis. Activation of ADT3 increases the Phe content and the production of phenylpropanoids which are implicated in ROS homeostasis (Huang et al. 2019a; Warpeha et al. 2006, 2008), and it has been demonstrated that GPA1 and GCR1 are involved in blue light-mediated Phe biosynthesis in ADT3-dependant manner (Warpeha et al. 2006, 2008). In addition, the similar phenotypes of the *adt3*, *gpa1*, and *gcr1* Arabidopsis mutants, including the reduced number of guard cells, broader cotyledons, and defects in chloroplasts development (Nilson and Assmann 2010; Para et al. 2016; Zhang et al. 2008) provide strong evidence of the relationship between G-proteins and ROS homeostasis in a pathway where ADT3 is involved.

Another module potentially involves the change in membrane potential and dynamics as well as in plasma membrane composition, which can eventually affect fundamental cellular properties and response, as well as ion channel activities (Assmann and Jegla 2016; Huang et al. 2019b; Kim et al. 2010; Munemasa et al. 2015). G-proteins are known to interact with and regulate several phospholipases, sphingosine phosphatases and kinases, potentially affecting multiple aspects of lipid biosynthesis and signaling (Coursol et al. 2003; Roy Choudhury and Pandey 2016b; Zhao and Wang 2013). Additionally, developmental regulations, such as the stomatal density, which are key to plants interaction with its environment, interactions with intracellular membrane systems, such as ER biogenesis and regulation and potentially cell wall composition also contribute to the G-protein-dependent responses (Feng et al. 2018; Para et al. 2016; Roy Choudhury et al. 2019; Roy Choudhury and Pandey 2016b; Rui and Dinneny 2020). Even though the cause-and-effect relationships of these signaling/developmental modules is not clear, future research geared towards identifying these will certainly result in critical knowledge needed to harness the power of these proteins in generating stress-tolerant plants.

The Challenges and Future Perspectives

One of the biggest challenges in synthesizing available data on the roles of G-proteins in plant abiotic stress responses is the seemingly random and often contrasting phenotypes observed in various studies. This is primarily confounded by the inherent composition and signaling mechanism of G-proteins. An initial level of complexity is introduced at the level of trimer composition itself. In plants such as Arabidopsis and rice that have simpler repertoire of G-proteins, a single Gβ protein can interact with one of multiple Gα or Gγ proteins. When studying the effect of the loss of an individual Gα or an individual Gγ gene (e.g., *gpa1, rga1, dep1* mutants), it is not clear if the observed effects are due to the loss of this individual protein or an effect of a varied stoichiometry between different subunits (Pandey

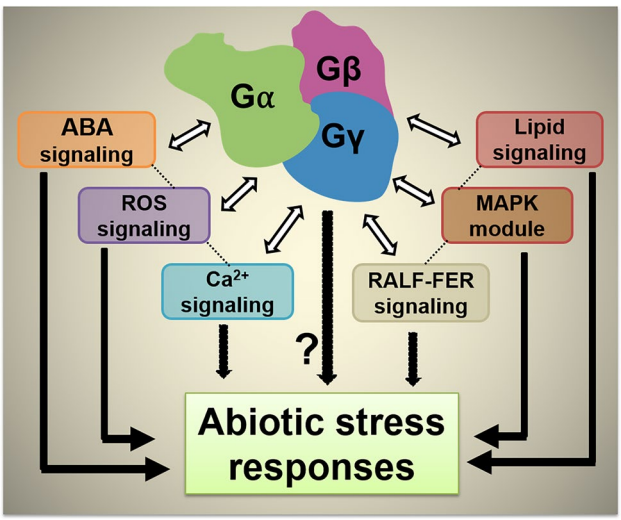

Fig. 2 Signaling pathways involved in G-protein mediated abiotic stress responses in plants. Involvement of abscisic acid (ABA), $Ca.^{2+}$, reactive oxygen species (ROS), rapid alkalization factor-Feronia (RALF-FER), lipid-mediated signaling and mitogen activated protein kinase (MAPK) modules has been shown during G-protein modulated abiotic stress signaling pathways. The cause/effect relationships between these modules is not fully elucidated (depicted as double arrowheads)

2019; Roy Choudhury et al. 2020; Urano et al. 2016). For example, the phenotype of a *gpa1* mutant could be due to the loss of GPA1 function, due to the altered availability of AGB1 for XLG proteins or due to constitutive signaling by freed Gβ (Roy Choudhury and Pandey 2022). In such situations, the effects of the loss of a gene function may not be exact opposite of the its overexpression. The situation becomes significantly more complex when studying plants with higher numbers of each of the G-protein subunits such as soybean or wheat. Moreover, the protein complex is trimeric, but it is active when the trimer is dissociated. Both Gα and Gβγ can be functional signal transducers, but can also affect each other's availability/localization (Chakravorty and Botella 2007; Trusov et al. 2007; Wang and Botella 2022). Therefore, results with gain- or loss-of-function of an individual protein should be interpreted cautiously. The modular structures of specific proteins also add to this complexity. For example, the C-terminal of the type-III Gγ protein has been proposed to be an inhibitor of its N-terminal Gγ-like domain (Botella 2012; Tiwari and Bisht 2022). In this case, mutations that result in the removal of only the C-terminal may actually result in a highly active Gγ protein, similar to its overexpression. Examples of such effects have been seen during grain size regulation in rice by the *GS3* gene, where site-specific mutations in the same gene may result in smaller or longer grains (Botella 2012; Cui et al. 2020; Fan et al. 2009; Mao et al. 2010).

Another level of complexity is added by the potential tissue or organ-specific roles of these proteins. Although such studies are limited mostly to Arabidopsis, it appears that significant differences exist. For example, Arabidopsis *gpa1* and *agb1* mutants show hyposensitivity to ABA during stomatal opening responses, these same mutants are hypersensitive to ABA during seed germination (Fan et al. 2008; Smythers et al. 2022; Yu et al. 2018). It is therefore important to consider the plant's response to specific signals in totality, not only in a specific tissue type.

A further key point to consider is the experimental designs themselves. Plant growth condition, plant age, stress treatment conditions, severity of stresses, and time, all vary considerably between experiments. Many of these are performed in heterologous systems, most under laboratory conditions, which has little relevance to actual plant growth in fields. The timings and methodologies of how plants are subjected to stress conditions is also important, but rarely considered. For example, stress experienced by the plants at their vegetative growth stage maybe tolerated better than the stress experienced at the time of flowering, or seed filling. Similarly, the way plants perceive these stresses needs to be optimized for each species. A rice seedling submerged in water during early growth may not experience the same severity of heat stress compared to a wheat seedling growing at a similar higher temperature. Finally, plants growing in fields experience several stresses simultaneously and thus will respond differently than what is assessed with plants grown under control laboratory conditions, subjected to one specific stress at a time.

In summary, it is obvious that the global climate change has already exacerbated the harmful effects of various abiotic stresses in crop plants, drastically reducing their overall productivity worldwide. It is of utmost importance to design and breed stress-resilient crops to meet the needs of future generations. The information obtained so far places the G-proteins in a central position to serve this role. However, an integrated approach that combines current 'cause/effect' information with precise genome editing technologies, multi-omics analysis and modeling, extensive crop physiology, agriculture economics and management is required to apply it directly to crops of interest, in field settings in order to enable food security.

Acknowledgements Research in the Pandey Lab is supported by Grants from the National Science Foundation (MCB-1714693 and MCB-2207012) to S.P.

Author Contributions PM, DRTR and SP wrote the review.

Declarations

Conflict of interest The authors have no conflict of interest related to the work described in this manuscript.

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