



Plant G-protein signaling cascade and host defense

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Abstract

The heterotrimeric guanine-nucleotide-binding proteins (G-proteins) play a crucial role in signal transduction and regulate plant responses against biotic and abiotic stresses. Necrotrophic pathogens trigger G α subunit and, in contrast, sometimes G $\beta\gamma$ dimers. Beneficial microbes play a vital role in the activation of heterotrimeric G-proteins in plants against biotrophic and necrotrophic pathogens. The subunits of G-protein (α , β , and γ) are activated differentially against different kinds of pathogens which in turn regulates the entry of the pathogen in a plant cell. Defense mediated by G-proteins in plants imparts resistance against several pathogens. Activation of different G-protein subunits depends on the mode of nutrition of the pathogen. The current review discussed the role of the three subunits against various pathogens. It appeared to be specific in the individual host–pathogen system as well as the role of effectors in the induction of G-proteins. We also discussed the G-protein-mediated production of reactive oxygen species (ROS), including H₂O₂, activation of NADPH oxidases, hypersensitive response (HR), phospholipases, and ion channels in response to microorganisms.

Keywords Phytohormonal signaling · Plant defense · Plant–pathogen interaction · Jasmonic acid signaling

Introduction

Heteromeric G-proteins (GPCRs, G α , G β , and G γ) are crucial for signal transduction in the plant immune system in response to phytopathogens. It triggers the expression of several downstream genes (Escudero et al. 2019). G-proteins are composed of three different subunits which includes, G α , G β , and G γ . They are activated by seven transmembrane G-protein coupled receptors (GPCRs). The G α subunit has an inherent GTPase activity, and upon binding to GTP, the activated G α dissociates from the G $\beta\gamma$ complex. The activated GTP-bound G α subunit functions autonomously, while G β and G γ subunits form a heterodimer. The separated G α subunit and G $\beta\gamma$ complex then regulate the downstream

signaling cascades (Oldham and Hamm 2008). Knock-down *RGB1*, which is a G β gene, affects several developmental aberrations, such as browning of the lamina, dwarf plant, sterile seeds, and narrow leaves (Utsunomiya et al. 2011).

The missing links of the complex network of plant immunity are being revealed layer by layer. However, several missing links between the pathways are yet to be studied. G-protein-coupled receptors (GPCR) encompass a large family of intrinsic transmembrane receptors. Upon binding to a ligand, the GPCR activates a cognate G-protein, which in turn triggers a myriad of secondary messengers that regulate many physiological responses within the plant cell. Recent studies in plants confirmed the direct role of G-proteins in plant biotic and abiotic stress responses, which includes the production of reactive oxygen species (ROS), activation of NADPH oxidases, ion channels, and phospholipases (Escudero et al. 2019). A heterotrimeric G-protein in *Arabidopsis thaliana* activated the jasmonate-mediated signaling response against necrotrophic pathogen *Alternaria brassicicola*. The barley homolog to the *Mlo* gene, which modulates plant defense responses, was known to be structurally similar to seven transmembrane GPCR protein family members. Plant NADPH oxidases produce ROS in response to pathogens

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that have diverse functions in different cellular contexts. The production of ROS by NADPH oxidase activates several signaling molecules resulting in the suppression of necrotrophic pathogens like *A. brassicicola* (Table 1). In contrast, a recent study confirmed an increased accumulation of G α transcripts against the biotrophic pathogen *Erysiphe pisi* in pea (Patel et al. 2016).

The key objectives of the present review include (1) role of G-protein signaling in plant–microbe interaction has been unraveled. (2) The specific mode of nutrition of the phytopathogens in activation of specific heterotrimeric G-protein. (3) Beneficial microbes activate specific heterotrimeric G-protein in favor of the plant. (4) Role of G-protein-mediated signaling in plant disease resistance against specific pathogens. We have also discussed the role of G-proteins in the induction of plant cell death during interaction with biotic and abiotic stressors. Even though a lot of recent studies focused on the G protein signaling, this review throws light on the cascade of events in the signaling mechanism that activates the defense responsive genes.

Role of effectors in triggering the G-protein signaling

The molecules, such as virulence factors or toxins, which are responsible for the alteration of structure and function of the host cell, are effectors and accountable for the activation of plant defense response. The effectors can be apoplasmic (interact with extracellular targets) or cytoplasmic (translocated to cytoplasm) (Park et al. 2012).

In addition to receptors and modulator molecules, four effector molecules interact with G-protein which includes, thylakoid formation 1 (THF1) (Huang et al. 2006), the Arabidopsis cupin domain protein (AtPirin1/PRN1) (Lapik and Kaufman 2003), prephenate dehydrogenase 1 (PD1) (Holland and Jez 2018), and phospholipase (Zhao and Wang 2004; Mishra et al. 2006). It is reported that one Arabidopsis G-protein receives the external signals through more than three different kinds of GPCR-like molecules and transfers the information through at least four different types of effector molecules (Urano and Jones 2014).

A recent report demonstrated the role of G α in the induction of resistance in Arabidopsis against

Table 1 Activation of different heterotrimeric G-proteins in response to different pathogens

S. no.	Name of the pathogen	Mode of nutrition	Plant name	Subunit of G-protein activated	References
1	<i>Pseudomonas syringae</i>	Biotrophic, hemibiotrophic or Necrotrophic	<i>Arabidopsis thaliana</i>	G $\beta\gamma$ dimer	Lee et al. (2009)
2	<i>Fusarium oxysporum</i> , <i>Alternaria brassicicola</i>	Necrotrophic	<i>A. thaliana</i>	G β	Trusov et al. (2010)
3	<i>Magnaporthe grisea</i>	Necrotrophic fungus	<i>Oryza sativa</i>	G α	Li et al. (2019)
4	<i>Xanthomonas oryzae</i> , <i>Magnaporthe oryzae</i> , <i>Phytophthora boehmeriae</i>	Necrotrophic fungus	<i>Nicotiana benthamiana</i>	G α , G β 1	Zhang et al. (2012)
5	<i>Fusarium oxysporum</i>	Necrotrophic fungus	<i>A. thaliana</i>	G γ	Thung et al. (2013)
6	<i>Agrobacterium tumefaciens</i>	Hemibiotrophic	<i>A. thaliana</i>	G β 1	Ishikawa (2009)
7	<i>Pseudomonas aeruginosa</i>	Biotrophic, hemibiotrophic or Necrotrophic	<i>A. thaliana</i>	G protein	Cheng et al. (2015)
8	<i>Pseudomonas syringae</i> pv <i>tomato</i> DC3000	Biotrophic, hemibiotrophic or Necrotrophic	<i>A. thaliana</i>	G α	Zheng et al. (2015)
9	<i>Erysiphe pisi</i>	Biotroph	<i>Pisum sativum</i>	G α	Patel et al. (2016)
10	<i>Pseudomonas syringae</i>	Biotrophic, hemibiotrophic or Necrotrophic	<i>A. thaliana</i>	G $\beta\gamma$	Liu et al. (2013)
11	<i>Hyaloperonospora arabidopsidis</i> Noco2	Biotrophic	<i>A. thaliana</i>	G β	Escudero et al. (2017)
12	<i>Cucumber mosaic virus</i> and <i>Turnip mosaic virus</i>	Biotrophic	<i>A. thaliana</i>	G β	Brenya et al. (2016)
13	<i>Fusarium oxysporum</i>	Hemibiotrophic	<i>Lycopersicon esculentum</i>	G γ	Urano et al. (2016)
14	<i>Pyricularia oryzae</i>	Necrotrophic fungus	<i>Arabidopsis thaliana</i>	G β	Takahashi et al. (2018)
15	–	Bacterial flg22 elicitor	<i>Arabidopsis thaliana</i>	G α	Xue et al. (2019)
16	<i>Rhizoctonia solani</i>	Necrotrophic	<i>Oryza sativa</i>	G $\beta\gamma$	Swain et al. (2019)

Pseudomonas syringae (Lee et al. 2013). Overexpression of $G\alpha$ and $G\beta$ reduced the multiplication of nonhost bacterial pathogens and overexpression of $G\beta$, but not $G\alpha$ reduced growth of host pathogens (Lee et al. 2013). Another report showed that heteromeric G-protein, primarily $G\alpha$, regulates the genes of JA signaling pathways in Arabidopsis (Okamoto et al. 2009; Li et al. 2019). Several defense responses mediated by *AGB1* is (Escudero et al. 2019) independent of pathogen-dependent SA signaling. Accumulation of SA in the *agb1 sid2* (isochorismate synthase 2), a double mutant showed enhanced disease susceptibility to *P. syringae* and *Plectosphaerella cucumerina* compared to single mutants.

Activation of G-protein signaling by beneficial microbes

Plants recognize external and internal signals, which regulate diverse responses in development and assimilation. Biochemical studies have confirmed the role of heterotrimeric G-proteins in different signaling pathways, which are regulated by several hormones produced by the plant in response to abiotic and biotic factors such as temperature, pathogen, etc. (Assmann 2005). Previous studies confirmed the essence of G-proteins in phytohormone signaling. Mutants lacking *AGB1* and *AtGPA1* affect the activity of phytohormones such as ABA (Wu and Urano 2018; Xu et al. 2015), brassinolides (Chen et al. 2004), gibberellin (Xu et al. 2015), and auxin (Zhang et al. 2018). Rice dwarf1 mutant (*d1*) lacking a functional $G\alpha$ gene reduced HR and thus is susceptible to the infection of an avirulent rice blast fungal strain of *Magnaporthe grisea* (Kawano et al. 2010). The closure of the stomata by pathogen-associated molecular patterns (PAMPs) needs inhibition of inward K^+ channels by the $G\alpha$ subunit in *Arabidopsis* (Melotto et al. 2017). $G\beta$ subunit is required to impart resistance against necrotrophic fungus *P. cucumerina* in *Arabidopsis* (Jorda et al. 2016; Pandey and Vijayakumar 2018). Patel et al. (2016) described the role of G-protein signaling mainly through $G\alpha$ subunit during the tripartite interaction of the pea powdery mildew pathogen *E. pisi* in the presence of *Trichoderma* and *Pseudomonas* either in single or in combination. The study also revealed that activation of the $G\alpha$ subunit during the interaction with bioagents which activates JA-mediated signaling (*CO11* and *LOX1* activation) upon challenging with *E. pisi*. The inhibition of pathogen development via ROS generation was observed following the activation of the $G\alpha$ subunit. Activation of ABA (abscisic acid) signaling following ROS generation (H_2O_2 production), therefore, linked to the closure of stomata in both combined as well as single treatment of the beneficial microorganisms.

Role of G-protein in ROS production

Reactive oxygen species are superoxide anions and their dismutase product hydrogen peroxide (H_2O_2). Upon biotic and abiotic stresses, these ROS molecules activate a series of signal cascades (Mittler 2017). In *Nicotiana benthamiana*, both $G\alpha$ and $G\beta 2$ heterotrimer subunits account for H_2O_2 production. However, the hypersensitive response (HR) by *Nep1* and *bohmerin* does not require a functional G-protein. Silencing of $G\alpha$ and $G\beta 2$ in plants compromise harpin-triggered cell death, suggesting the role of $G\alpha$ and $G\beta 2$ in plant harpin-induced cell death. G-protein mutants exhibited reduced expression of *PR2b*, *EDS1*, *NbrbohA*, and *NbrbohB*, giving an insight into the role of G-proteins in plant defense and signaling. Induced illustration of *Arabidopsis ADH1* by ethylene shows the intricate signal network involving ethylene, G-protein, and H_2O_2 (Zhang et al. 2012).

Role G-proteins in the pathogenesis

The rice dwarf mutant *d1* with a non-functional $G\alpha$ gene reduced HR, which makes plants susceptible to avirulent strain of the rice blast fungus *Magnaporthe grisea* (Ashikari et al. 1999; Fujisawa et al. 1999; Kawano et al. 2010). The $G\alpha$ subunit also helps in the closure of stomata during the pathogen attack by inhibiting K^+ channels through PAMPs (Melotto et al. 2017). Further, Trusov et al. (2006) described the role of $G\beta$ in imparting resistance in *Arabidopsis* against necrotrophic pathogens. $G\alpha$ protein *XLG2* interacts directly with *BIK1* (central cytoplasmic kinase) and *FLS2* (*Arabidopsis* immune receptor). $G\alpha$, together with $G\gamma$ proteins (*AGG1/2*) and $G\beta$ protein (*AGB1*), attenuates the degradation of *BIK1* through proteasomes, which results in maximum plant immune activation (Liang et al. 2018). Upon activation of G-protein, the receptors *flg22* and *XLG2* dissociates from *AGB1* and *BIK1* phosphorylates its N terminus. Phosphorylation of *XLG2* enhanced the production of ROS, and the most probable reason for the activity is the modulation of NADPH oxidase *RbohD* (Qi et al. 2017).

The role of extra-large G-proteins (XLGs) in defense regulation

A. thaliana deploys $G\beta\gamma$ dimer instead of $G\alpha$ for multiple defense responses. Dimer of $G\beta\gamma$ partners directly with extra-large G-proteins (XLGs) for the activation of plant immunity. The phenomenon was confirmed by the use of mutants deficient in XLGs, $G\beta$, and $G\gamma$, where resistance is compromised against several pathogens and production

of ROS. Analysis of some other mutants such as double, triple, and quadruple XLGs and G $\beta\gamma$ functionally has been confirmed by the interaction of these in the same defense cascade (Maruta et al. 2015). The well-known fact is that heterotrimeric G-proteins have a role in the activation of plant immunity. The activation demonstrates the onset of innate immunity in the Arabidopsis by two different G $\beta\gamma$ dimers (G $\beta\gamma$ 1 and G $\beta\gamma$ 2), which majorly contributes in the resistance against several fungal pathogens (Jorda et al. 2016; Trusov et al. 2010; Delgado-Cerezo et al. 2012). However, these studies have not shown the role of G α , due to mutant plant for the G α unit have a truly insignificant effect on the plant immunity (Jorda et al. 2016; Escudero et al. 2019). The presence of three genes encoding G α -like proteins in the Arabidopsis genome and are classified as extra-large G-proteins (XLGs) (Lee and Assmann 1999; Ding et al. 2008). These XLGs have two distinct regions, C-terminal and N-terminal. The C-terminal area is having conserved helical and GTPase domains like the established G α . However, the N-terminal region has 400 amino acids for the nuclear localization in the plant cell (Ding et al. 2008).

G-protein regulates phytohormonal signaling

Heterotrimeric G-proteins are involved in plant stress signal network, which is tightly regulated by various phytohormones to cope-up with biotic and abiotic stress conditions (Assmann 2005). Transcriptomics studies in *Arabidopsis* G β mutant, *agb1-2* suppressed many auxin-inducible genes such as GH3, Aux/IAA, and GST (Xu et al. 2015). At present, a very little transcriptomics data are available on the G α mutant of Arabidopsis plants. Studies on G-protein regulated gene expression were performed in a G α mutant *gpa1-1* using an Affymetrix (ATH22K) microarray system (Okamoto et al. 2001). Analysis of the microarray results suggested the role of G α subunit in regulating the expression of Jasmonic acid (JA)-induced genes. The study confirmed the response of plants to methyl jasmonate (MeJA) in chlorophyll loss, gene regulation, and root growth. Transcriptome analysis further revealed that there was a reduction in expression of 29% of JA-regulated genes, and mutation of the G α subunit altered their expression. These results suggest the probable role of G-proteins in JA-mediated stress signaling in plants. Further, GPA1 mutants affect many other physiological responses in plants that are induced by ABA (Mishra et al. 2006) and GA (Grigston et al. 2008). During *M. grisea* infection, it was also observed that the G α subunit activates the downstream GTPase *OsRac1* signaling (Kawano et al. 2010).

The role of ROS in plant defense is modulated by the interaction between NADPH oxidases and plant hormones.

Exogenous application of ROS synergistically increased SA signaling towards the onset of HR (Le Thanh et al. 2017). ROS production by the activity of *AtRbohD* developed antagonism against the SA-mediated signaling pathway and resulted in cell death in the site of infection (Torres and Dangl 2005). The role of *AtRbohD* thus associated with the negative feedback regulation of SA and the ethylene pathway and thereby decreased cell death during infection by necrotrophic pathogens (Kadota et al. 2014). Simultaneous production of ROS and nitric oxide (NO) resulted in hypersensitive response (Torres et al. 2006) and led to regulation of ABA-mediated stomatal closure (Eisenach et al. 2017). However, the production of ROS has antagonistic activity towards the breakdown of basal host defense against necrotrophic pathogens such as *Botrytis cinerea* (Asai et al. 2008). Signaling through ROS is associated with the plant growth regulators such as ABA and gibberellin, which can modulate ROS production after infection (Achard and Genschik 2009; Sivakumaran et al. 2016). This interaction regulates the production of ROS signals and contributes to the multidisciplinary function of ROS in distinct types of plant–pathogen interactions. There is evidence associated with the regulatory role of G-protein-mediated signaling during plant–pathogen interaction, along with several developmental pathways and abiotic stresses (Temple and Jones 2007; Trusov et al. 2010).

G-protein-mediated defense regulation

Higher plants have a complex system to induce innate immunity against phytopathogens, including immune responses to conserved pathogen molecules or PAMPs (Chisholm et al. 2006; Jones and Dangl 2006). Pathogens should enter in the plant to establish the disease. Phytopathogens utilize the natural openings in the plant to enter inside (Melotto et al. 2006, 2008; Underwood et al. 2007). Recent research has shown the regulation of stomatal closure by guard cells can serve as the first line of defense against phytopathogen entrance (Melotto et al. 2006).

Heterotrimeric G-proteins participate in the responses of guard cells to PAMPs. PAMPs affect stomatal opening, K⁺ ion channel regulation is targeted by PAMPs. PAMP derived from bacterial flagellin (Flg2), also inhibits light-induced stomatal opening. PAMP-triggered stomatal response involves K⁺ channel regulation, and this regulation is dependent on signaling through cognate PAMP receptors and a heterotrimeric G-protein (Zhang et al. 2008). Regulation of stomatal aperture by bacterial pathogens was altered in G α and G β (Lee et al. 2013).

A very complex system of innate immunity is present in the plant system and works against several plant pathogens, having specific conserved molecules such as PAMPs

(Chisholm et al. 2006; Jones and Dangl 2006). Most of the plant pathogens enter through plant's natural openings such as stomata (Underwood et al. 2007; Melotto et al. 2008). Heterotrimeric G-proteins are reported to control the guard cells for opening and closing the stomata, especially in response to PAMPs (Zhang et al. 2008). Lee et al. (2013) suggested the role of $G\alpha$ and $G\beta$ subunit of the heterotrimeric G-proteins in the regulation of stomatal aperture against the bacterial pathogen (*P. syringae*) in Arabidopsis plants.

The role of subunits of G-proteins in plant defense has been confirmed with mutant studies. Rice dwarf mutant *d1* is one homolog of $G\alpha$ subunit induce HR response and resistance against avirulent races of the rice blast pathogen *M. grisea* (Kawano et al. 2010). However, in Arabidopsis, mutation of $G\alpha$ subunit *GPA1* exhibits minor or no effect on the response. In contrast, GPCR subunit *AGB1* induces against some fungal pathogens (Jorda et al. 2016; Trusov et al. 2010; Delgado-Cerezo et al. 2012). Therefore, the study confirmed that the mutant of *Arabidopsis agb1* is more susceptible to disease compared to the wild-type plants against the necrotrophic pathogens such as *P. cucumerina*, *Botrytis cinerea*, and *Alternaria brassicicola*, as well as against the hemibiotrophic vascular fungus *Fusarium oxysporum*. However, *agb1* mutant showed no response against biotrophic pathogens such as oomycete *Hyaloperonospora arabidopsidis* and *P. syringae* compared to the wild-type plants (Jorda et al. 2016; Pandey and Vijayakumar 2018). It was proved that Arabidopsis $G\alpha$ has a decisive role in the activation of defense responses against *P. syringae* through stomatal closure, which ultimately restricts the pathogen entry into the plant leaves (Melotto et al. 2017; Hind et al. 2016; Lee et al. 2013). Two different pathways are involved, which includes, the action of $G\beta\gamma$ dimer independently from $G\alpha$, and another is the formation of heterotrimer by the replacement of $G\alpha$.

Three subunits of heterotrimeric G-proteins can function in diverse ways depending upon the host plant and mode of nutrition of the pathogens used in the experiment. The $G\beta$ protein *AGB1* is necessary for defense response in plants. However, $G\gamma$ subunits (*AGG1* and *AGG2*) and *AGB1* work together for generating defense responses, because mutant *agb1* and double mutants *agg1 agg2* showed similar responses against the necrotrophic fungal pathogen *P. cucumerina* (Delgado-Cerezo et al. 2012).

A report by Brenya et al. (2016) suggested the activity of G-proteins in viral diseases such as cucumber mosaic virus (CMV) and turnip mosaic virus (TuMV) in *A. thaliana*, they reported the negative regulation of salicylic acid, jasmonic acid, and abscisic by $G\beta$ during infection of CMV and TuMV. Results from Brenya et al. (2016) suggested that G-proteins play a positive role in the suppression of viral disease by promoting necrosis of the cells.

G-protein as an activator of receptor kinases

One of the largest family of proteins, receptor-like kinases (RLKs), has various roles related to the development and stress signaling in plants (Liang et al. 2018). Over 600 RLKs have been reported (Shiu and Bleecker 2001) in the model plant *A. thaliana*. RLKs have an extracellular domain, a cytoplasmic kinase domain, and a single transmembrane domain to be shared in most of the RLKs. The extracellular domain is believed to be involved in recognition of ligands, which later is responsible for activation of the cytoplasmic kinase domain. Flagellin-sensitive2 (FLS2), a receptor for PAMPs and chitin elicitor receptor kinase1 (CERK1), is the member of the RLK family. EFR and FLS2 are the receptor kinases exposed on the membrane surface involved in the activation of EF-Tu and bacterial flagellin, respectively (Gomez-Gómez and Boller 2000; Liang et al. 2018). However, CERK1 is reported (Miya et al. 2007; Wan et al. 2008) for the chitin and other components of the fungal cell wall. Other RLKs such as Brassinosteroid Insensitive1-associated receptor kinase1 (BAK1) said (Cao et al. 2013; Chaparro-Garcia et al. 2011) to be the co-receptor of EFR and FLS2. Xa21 in rice is another example of RLKs functions as a receptor for a peptide obtained from the AvrXa21 (Park et al. 2010).

G-protein subunits including *AGB1* and *AGG1/AGG2* functions downstream of RLKs such as *SOBIR1*, *FLS2*, *EFR*, and *CERK1* towards the activation of resistance responses against pathogens. Liu et al. (2013) described that RLKs function upstream of the G-protein subunits-like activity of GPCR in plant heterotrimeric G-proteins. Some of the results still question the role of *AGB1* and *AGG1/AGG2* downstream to RLKs for the activation of plant immunity (Stateczny et al. 2016). A recent report by Liu et al. (2018) confirmed that *RACK1* (receptor for activated C kinase 1) is involved in the regulation of G-protein signaling pathway for defense in woody plants.

Concluding remarks

It is interesting to know the role of G-proteins in plant defense signaling against pathogens. G-proteins are involved in the regulation of different developmental as well as physiological processes in plants, but still, so many missing links need to be bridged for complete understanding. This review also suggested the role of G-proteins in the plant defense pathways against phytopathogens. We have also suggested the role of beneficial plant-microbe such as *P. fluorescens* in defense response running through the G-protein signaling cascade. Knowledge of the role

of receptors, as well as beneficial microorganisms, could open newer eco-friendly strategies for the plant disease control. G-protein-induced programmed cell death (PCD), closure of stomata, and production of disease-resistance-related proteins could be the strategies for the protection of plants against pathogens. However, in-depth study is needed to enhance our understanding of the role of G-proteins for activation of induced immunity in the plants for plant disease management.

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Compliance with ethical standards

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