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ROLE OF THE PLANT HETEROTRIMERIC G-PROTEINS IN THE SIGNAL PATHWAYS REGULATION

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❀ Animal and fungal heterotrimeric G-proteins are are some the well-known regulators of signaling pathways. Plant studies have shown that G-proteins may also be involved in the regulation of many processes. G-proteins are involved in hormonal regulation, control of cell proliferation, response to abiotic factors, control of biotic interactions and many others. It turned out that with a smaller variety of subunits, G-proteins of plants can have a greater variety of mechanisms for activating and transmitting signals. However, for most processes in plants the mechanisms of operation of heterotrimeric G-proteins remain poorly understood. This review is devoted to the analysis of modern ideas about the structure and functioning of heterotrimeric plant G proteins.

❀ **Keywords:** heterotrimeric GTP-Binding proteins; plants; receptors; signal transduction.

РОЛЬ ГЕТЕРОТРИМЕРНЫХ G-БЕЛКОВ В СИГНАЛЬНОЙ РЕГУЛЯЦИИ У РАСТЕНИЙ

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❀ Гетеротримерные G-белки животных и грибов являются одними из хорошо известных регуляторов сигнальных путей. Исследования на растениях показали, что в регуляцию многих процессов у них могут быть вовлечены G-белки. G-белки принимают участие в гормональной регуляции, контроле пролиферации клеток, ответе на абиотические факторы, контроле биотических взаимодействий и др. Оказалось, что при меньшем разнообразии субъединиц G-белки растений проявляют большее разнообразие механизмов активации и передачи сигналов. Однако для большинства процессов механизмы работы гетеротримерных G-белков еще малоизучены. Настоящий обзор посвящен анализу современных представлений о строении и функционировании гетеротримерных G-белков растений.

❀ **Ключевые слова:** гетеротримерные G-белки; растения; рецепторы; передача сигнала.

INTRODUCTION

The significant interest in studying heterotrimeric G-proteins is attributable to their ability to control different processes (such as growth and development, metabolism, and responses to biotic and abiotic factors) via the interaction of these proteins with different receptors. In this regard, heterotrimeric G-proteins are well known as the participants of the signal pathways of eukaryotes.

G-proteins were named thus owing to the ability to bind guanine nucleotides [guanosine triphosphate (GTP) or guanosine diphosphate (GDP)], thereby modifying of the activity of these nucleotides. Heterotrimeric G-proteins are typically distinguished based on their complex formation comprising α-, β-, and γ-subunits. Besides, a separate class is presented by monomeric small G-proteins that can hydrolyze GTP (GTPases). Small G-proteins have molecular weight of approximately 20–25 kDa, and their single polypeptide chain is homologous to the α-subunit of heterotrimeric G-proteins. Both groups of G-proteins are involved in the intracellular signaling; however, the present overview primarily focuses on heterotrimeric G-proteins.

Although heterotrimeric G-proteins are probably the universal signaling regulators of all eukaryotes, a majority of the research on G-proteins focused on their involvement in the processes of humans and plants [1].

In 1990s, the presence and functioning of heterotrimeric G-proteins was the demonstrated for the first time

in plants by means of heterotrimeric G-protein inhibitors and agonists [2–5]. These studies determined the involvement of heterotrimeric G-proteins in the plants' response to the effect of several phytohormones, development of response to the light, and other processes [6–9]. Several mutants were detected with defects in some subunits of heterotrimeric G-proteins, which facilitated a detailed examination of features of the plants' G-protein structure [10, 11]. Thereafter, the role of G-proteins in the control of biotic relations of plants and microorganisms–protection against pathogenes [12–14] and development of symbiotic relations [15–19] — were elucidated. Because these plant interactions are of great practical interest, the study of potential mechanisms of regulation of resistance or sensitivity of plants to different microorganisms with involvement of heterotrimeric G-proteins is of substantial value. However, the mechanisms of functioning of the signal pathways with involvement of heterotrimeric G-proteins of plants remain poorly elucidated.

STRUCTURE AND FUNCTIONING OF HETEROTRIMERIC G-PROTEINS

Structure and activation of heterotrimeric G-proteins

The animal G-proteins in the inactive state forms a heterotrimeric complex consisting of α-, β-, and γ-subunits associated with membrane (Fig. 1, *a*) [20]. In the inactive state, the α-subunit is associated with GDP [21]. The entire complex is associated with G-protein coupled receptor (GPCR). The presence of seven transmembrane domains in the content of GPCR-receptor is its distinctive structural feature.

GPCR is activated upon the binding of the ligand, and in this case, it stimulates the exchange of guanine nucleotides on α-subunits [serves as the factor of nucleotides exchange, i.e., guanine nucleotide exchange factor (GEF)], which is expressed in GDP disconnection and GTP binding. Activation of complex components occurs owing to the conformational changes in presence of nucleotides, thereby resulting in the dissociation of the complex into α-subunit and β- and γ-subunits; the latter ones serve as messengers for further signal forwarding (see Fig. 1, *a*). After activation, the α-subunit, which is a GTPase, catalyzes the hydrolysis of GTP to GDP, which converts it into an inactive state, and the complex of α-, β-, and γ-subunits is re-formed [22]. Soluble regulator of G-protein signaling (RGS) protein has special function–it is the signal pathway regulator activated by G-protein (see Fig. 1, *a*). These animal proteins are localized in cytoplasm and are characterized with the RGS-motive that is required for recognizing the α-subunit. RGS proteins enhance the hydrolysis of GTP to GDP of α-subunit regulating intensity and duration of effect of heterotrimeric G-protein, thereby stimulating the association of the complex of α-, β-, and γ-subunits) [23].

Heterotrimeric G-proteins are detected in fungi [25–29], with most detailed studies available for the organisms of *Ascomycota*, *Basidiomycota*, and *Zygomycota* groups. GPCR receptors are detected in fungi with seven transmembrane domains, which are similar to the GPCR of animals based on the structural and functional homology [29]. However, the less diversity of α-, β-, and γ-subunits in comparison with animals is typical of the heterotrimeric G-proteins in fungi.

Similar effect of GPCR-receptors on heterotrimeric G-proteins facilitates the discussion regarding the evolutionary congeniality of the signal pathways with an involvement of these regulators of animals and fungi [30]. Cytoplasmic RGS protein was detected in fungi, which results in the inactivation of α-subunit. In addition, unique RGS proteins were detected in fungi [31] with seven transmembrane domains. Structurally similar RGS proteins were detected in plants as well [32] and will be discussed further. This indicates the presence of various methods of signal transmission with the involvement of heterotrimeric G-proteins in fungi.

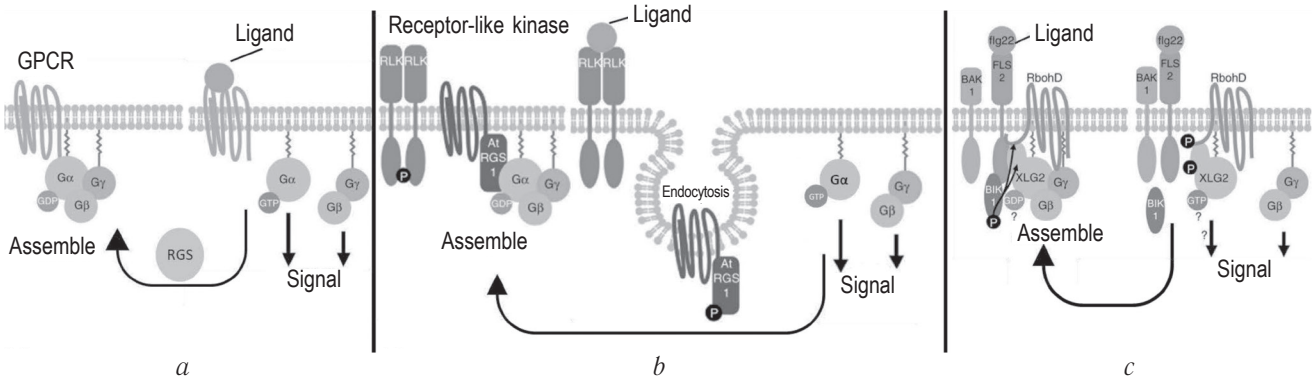

Fig. 1. Comparison of the ways of activation of heterotrimeric G-proteins in animals (*a*) and plants (*b*, *c*); *b* — RGS-dependent pathway of activation, *c* — RGS-independent pathway of activation (according to [24], as amended)

Researches on the features of the structural arrangement of heterotrimeric G-proteins as well as their functioning in plants were conducted in the last two decades. Notably, single GPCR-like proteins were detected in some plants. In particular, the GCR1 protein was detected in Arabidopsis that has seven transmembrane domains, which demonstrates its similarity with the GPCR of animals [1]. However, the ability to stimulate nucleotides exchange of G-protein subunits was not detected in GCR1-receptor, which results in an ambiguity regarding its functional activity [1, 24, 33].

Meanwhile, the unique regulator RGS protein was detected in plants, which when compared with the RGS protein of animals and besides the RGS-motive, has seven transmembrane domains similar GPCR-receptor of animals and fungi [32]. Due to similarity of structure of transmembrane domains, it was initially considered that the RGS protein of plants could serve as GPCR–receptor; however, this has not yet been proved [1, 24].

α-, β-, and γ-subunits of heterotrimeric G-proteins are in inactive state together with RGS protein (Fig. 1, *b*). In contrast to animals, the α-subunit of plants, besides the inherent GTPase activity, spontaneously exchanges GDP to GTP (spontaneous activation without GEF involvement) [34]. However, the α-subunit mostly acts as GTPase under effect of RGS protein, which performs hydrolysis of GTP to GDP, thereby supporting the inactive state of heterotrimeric G-protein (see Fig. 1, *b*) [35]. Following RGS protein activation, the hydrolysis of GTP in the α-subunit is discontinued, which results in its activation and decomposition of the heterotrimeric complex into α-, β-, and γ-subunits and subsequent signal forwarding, whereas RGS is subjected to endocytosis (see Fig. 1, *b*) [36].

Therefore, despite the structural differences, the biochemical activity of RGS protein in animals and plants is similar. RGS protein, within the complex, acts as a stimulator for the hydrolysis of GTP by the α-subunit, whereas the GPCR-receptor in animals stimulates the exchange of GDP to GTP (performs function of GEF) by activating the α-subunit. Despite the structural similarity between RGS protein and GPCR-receptor, the functioning of the analogue between these classes of proteins was detected. In this regard, RGS protein does not play the role of GPCR-receptor in plants [1, 24].

The coordination of G-protein activity in plants can be performed both via RGS protein and directly by receptors to different ligands as well as the intracellular regulators associated with them (Fig. 1, *c*). In such cases, RGS proteins are not required and signal directly received from membrane receptors. This was demonstrated for an atypical large α-subunit *At*XLG2 in *Arabidopsis thaliana*; the subunit is involved in the interaction with the complex of receptors *At*FLS2 and *At*BAK1 to the protein flagellum. When *At*FLS2/*At*BAK1 complex interacts with an active epitope of flagellin (peptide flg22), the protein kinase *At*BIK1 is intracellularly activated, which phosphorylates the large α-subunit *At*XLG2 of heterotrimeric G-protein and the NADPH oxidase *At*RBOH associated with it (see Fig. 1, *c*). This contributes to the dissociation of heterotrimeric G-protein and transfer of signal-regulating nonspecific immune response of Arabidopsis (see Fig. 1, *c*) [12].

A similar mechanism was detected during the reception of chito-oligosaccharides that are signal molecules for the LysM-receptor-like kinase (LysM-RLK) *At*CERK1. Using the ubiquitin split into N- and C-end parts (the split-ubiquitin assay) and biomolecular fluorescent complementation (BiFC), it was demonstrated that activated LysM-RLK *At*CERK1 interacts with the α-subunit of G-protein (*At*GPA1), which probably results in its phosphorylation, dissociation of the complex of subunits of G-protein, and signal transfer into the cell [19].

The RGS-independent pathway of signal transfer with the involvement of heterotrimeric G-proteins probably plays a role in monocotyledon plants. Although RGS proteins were detected in all studied dicotyledonous plants, they were lost in most monocotyledonous plants, except for the individual species [including panic grass (*Setaria italica*) and palm (*Phoenix dactylifera*] [34, 37].

Based on the analysis of the references data, it can be concluded that the conventional ideas regarding the mechanism of heterotrimeric G-proteins in the cells of animals and fungi significantly differ from the way these proteins are arranged and functioning in plants. A comparative diagram of the mechanisms of activation of heterotrimeric G-proteins is presented on Fig. 1.

Diversity of G-proteins subunit composition

In 2001, 3D models of α-, β-, and γ-subunits of G-protein of plants were created. The authors compared obtained models with similar structures of well-studied subunits of heterotrimeric G-proteins of animals and concluded regarding the similarity of their structural arrangement [38].

G-proteins of plants differ with little variability of subunits compared with animals. Although 23, 5, and 12 types of α-, β-, and γ-subunits, respectively, are detected in humans, only 1 definitive α-subunit (*At*GPA1), 3 types of non-canonical [extra-large G-protein alpha, XLG] α-subunits (*At*XLG1, *At*XLG2, and *At*XLG3), 1 β-subunit (*At*AGB1), and 3 types of γ-subunits (*At*AGG1, *At*AGG2, and *At*AGG3) of G-protein are detected in *A. thaliana* (see Fig. 2) [24]. Diagrams of the arrangement of subunits of heterotrimeric G-proteins are provided on Fig. 2.

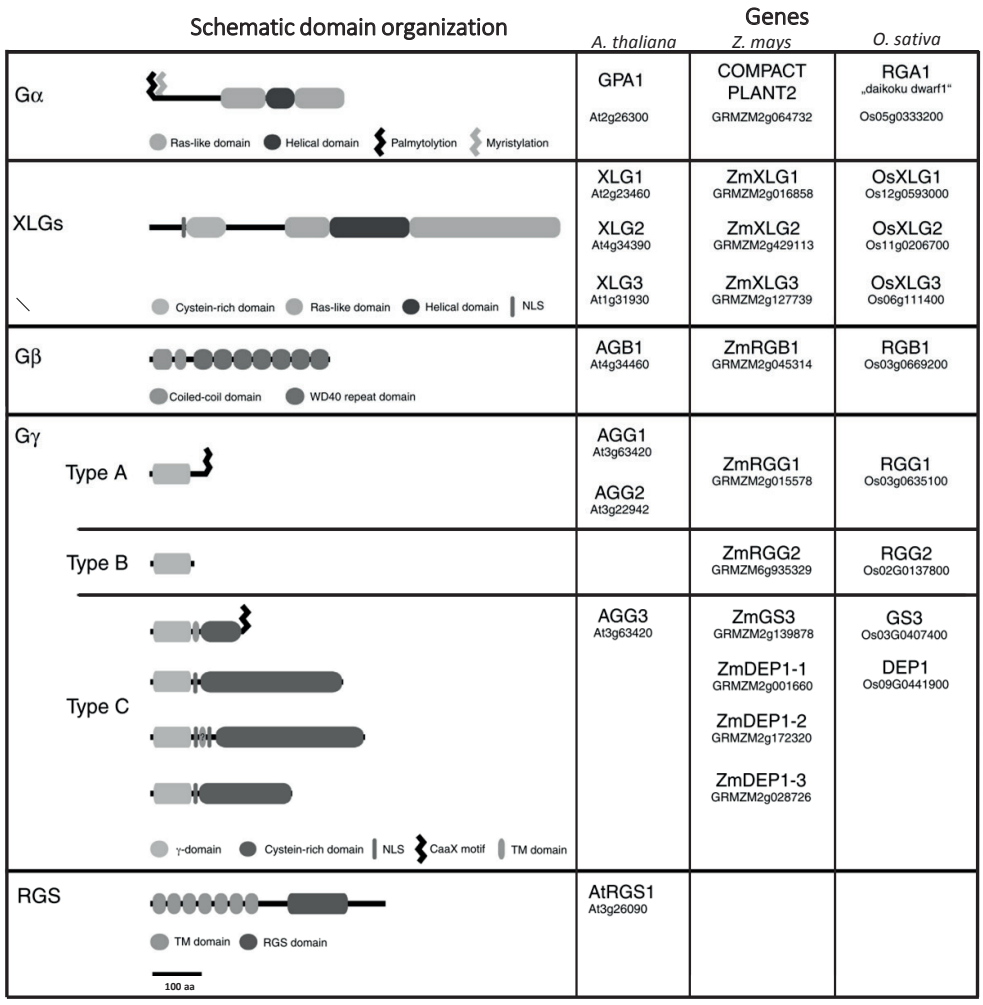

Fig. 2. Scheme of the organization of subunits of heterotrimeric G-proteins and plant RGS. Given the designation of the corresponding genes and accession numbers in the databases for some model plants. A scale bar corresponding to 100 amino acid residues is shown. TM — transmembrane domain; CaaX — prenylation domain (according to [24], as amended)

The signals of nuclear localization were detected within XLG and some other γ-subunits. It is assumed that these participants can serve as direct transmitters of signal from membrane receptors to the nucleus.

SIGNAL TRANSMISSION FROM HETEROTRIMERIC G-PROTEIN IN ANIMALS AND FUNGI

Heterotrimeric G-proteins as participants of the intracellular pathways of signal transfer receive the signal from activated receptor and transmit it to the pathway components. For animal G-proteins, the range of potential "targets" is determined to a sufficient extent that activates the subunits of heterotrimeric G-proteins. One of the first open intracellular "targets" was the enzyme adenylyl cyclase that is essential for the synthesis of the secondary secondary messenger adenosine monophosphate (cAMP) [39]. Different α-subunits as well as some complexes of β- and γ-subunits interact with adenylyl cyclase, whereas some of them activate the synthesis of cAMP and the other ones suppress it [40]. Besides, G-proteins can regulate enzyme adenylyl cyclases with the opposite function such as the cGMP phosphodiesterases, which hydrolyze phosphodiester links in cGMP [41].

Phospholipases C and D involved in the hydrolysis of membrane phospholipids and determining the synthesis of the secondary messengers of inositol-3−phosphate (IP3), diacylglycerol (DAG), and phosphatidic acid (PA) also serve as the target for effect of α-, β- and γ-subunits of heterotrimeric G-proteins. Formation of the complex with α-subunit in animals substantially increases the activity of phospholipases, whereas the contact occurs via the several sites of phospholipase C (two calcium-binding EF domains as well as the area between C2−and TIM-domains are involved in binding). The most important site of interaction of phospholipase C with β- and γ-subunits is the PH-domain. Frequent regulation of phospholipase C activity via the subunits of heterotrimeric G-proteins is indirectly performed via small GTPases [41, 42].

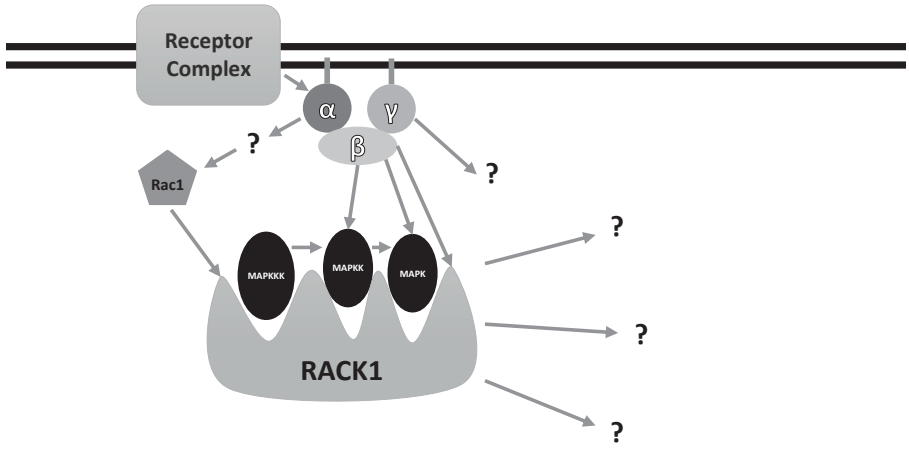

Fig. 3. Integration of heterotrimeric G-proteins, MAP-kinases with the RACK1 scaffold protein and Rac1 small GTPase in signaling pathways

IP3 is important for the regulation of calcium exchange in animal cells. Calcium channels located in the membrane of endoplasmic reticulum serves as a receptor for IP3. These channels can contain sites of binding of other secondary messengers, such as cyclic nucleotides, which can be regulated by heterotrimeric G-proteins [43].

The other targets of the effect of heterotrimeric G-proteins are the intracellular kinases. Mitogen-activated protein (MAP)-kinases are of special interest. Several MAP-kinases are collected on scaffold-proteins and both MAP-kinases and scaffold-proteins are regulated (see Fig. 3) [44].

Heterotrimeric G-proteins in fungi mostly activate two types of signal regulators—adenylyl cyclase and MAP-kinase. α-subunits activate both regulators, whereas its role in the activation of MAP-kinase way is demonstrated for complex of β- and γ-subunits [26]. Typically, it can be considered that signal pathways with an involvement of heterotrimeric G-proteins in fungi are structurally and functionally similar to that of animals. This explains the system of studying GPCR and relevant G-proteins of humans being well developed in yeast for the examination of the drug substances [45].

MECHANISM OF SIGNAL TRANSMISSION FROM HETEROTRIMERIC G-PROTEIN TO THE INTRACELLULAR REGULATORS IN PLANTS

Plant and animal heterotrimeric G-proteins have a similar range of regulated targets. However, several of these targets are almost not studied. For example, although the adenylyl cyclases of plants are poorly studied, the membrane and cytoplasmic adenylyl cyclases of plants can be involved in formation of cAMP [46]. Bioinformatic analysis demonstrated that motives specific for the adenylyl cyclase of plants can be present in the content of other proteins [47]. For example, five plant proteins of Arabidopsis have such motives, which include the membrane protein *At*KUP7 that is responsible for potassium transportation to the cage. Protein *Zm*PSiP as well as some other proteins regulate the germination of pollen tube in corn [47]. Similar results was observed with enzymes synthetizing cGMP—guanylyl cyclases [48]. The nature of interaction of such proteins with heterotrimeric G-proteins in plants remained to be studied.

Phospholipases

Connection between the activation of G-proteins and operation of phospholipases C and D that control the occurrence of the secondary lipid messengers IP3, DAG, and PA was established in a study on the signal regulation of symbiosis between plants and rhizobial bacteria. Hartog et al. [49] detected that in case of treatment with mastoparan, an agonist of G-proteins, the level of DAG and PA increased in the roots of *Vicia sativa*, which became one of the first evidences of heterotrimeric G-proteins and phospholipases C and D involvement in this signal pathway.

Evidences of the direct interaction of G-protein and phospholipase C in *Lillium davidii* were obtained [50], wherein two phospholipases C (*Ld*PLC1 and *Ld*PLC2) could form complexes with an activated α-subunit, which corresponds to the model of phospholipase C regulation in animals. However, mechanisms of activation of phospholipases C of G-proteins remain unclear.

In animals, phospholipases D do not play any significant role in the interaction with heterotrimeric G-proteins, whereas in plants, these enzymes are involved in signal transfer. It was demonstrated that in *A. thaliana*, the α-subunit of heterotrimeric G-protein (*At*GPA1) interacts with phospholipase D that is associated with DRY-motive [51]. Probably, *At*GPA1 can be associated with several phospholipases D, as several families of phospholipase D [α, β, and γ (except for γ2) and ε] had DRY-motive. In the

inactive state, *At*GPA1 is associated with phospholipase D, whereas in the active state, it can result in dissociation with phospholipase D, which stimulates formation of DAG and PA.

In 2016, the authors Choudhury and Pandey [17] studied signal transfer via heterotrimeric G-proteins in symbiotic plants with nitrogen fixing bacteria and demonstrated, by the means of coimmunoprecipitation method, that the phospholipase D of α1 was included in complicated signal complex that also included α-, β-, and γ-subunits of G-protein and RGS protein. During activation of this complex, the α-subunit is associated with GTP, which results in its dissociation with phospholipase D, thereby catalyzing the formation of DAG and PA.

Interestingly, phospholipases D of α, β, γ, and ε families have C2-motive changing their activity in response to change of calcium concentration [52], which probably allows ferment to receive from heterotrimeric G-proteins, with calcium as the secondary messenger, and to integrate them.

Cytoplasmatic protein kinases and small GTPases

As mentioned above, the association between the activation of heterotrimeric G-proteins and signal transfer to MAP-kinases is well studied in animals and fungi. Experiments with plants demonstrated that the components of the MAP-kinase pathway [MAP-kinase of kinase of kinase (MAPKKK), MAP-kinase of kinase (MAPKK), and MAP-kinase (MAPK)] could be activated with G-proteins. For example, in Arabidopsis, the β-subunit of G-protein is involved in the process of signal transfer from the receptor *At*FLS2 at the immune response, which activates cytoplasmatic protein kinase RACK1. RACK1, being a scaffold protein, directly interacts with the components of the MAP-kinase pathway—MAPKKK (MEKK1), MAPKK (MKK4/5), and MAPK (MPK3/6) [53] (see Fig. 3). The activation of RACK1 possibly stimulates further signal transfer via MAP-kinase. G-proteins can similarly activate MAP-kinases at the early stages of embryogenesis in *A. thaliana*, in particular, the interaction of β-subunit of G-protein with MAP-kinase of kinase 4/5 (MPKK4/5) is demonstrated [54].

Involvement of heterotrimeric G-protein in signal transmission with participation of RACK1 and small GTPhase Rac1 was detected in rice during the development of immune responses [55]. Moreover, small GTPase Rac1 can be activated with the α-subunit of heterotrimeric G-protein at the immune response of rice during infection with phytopathogenic fungus *Magnaporthe grisea* [56]. However, experimental data regarding the direct interaction of Rac1 with the α-subunit of heterotrimeric G-protein was not obtained. It remains unclear whether heterotrimeric G-protein directly or indirectly interacts with GTPases.

REGULATION OF THE REACTIVE OXYGEN INTERMEDIATES FORMATION

Heterotrimeric G-proteins of plants are involved in the control of reactive oxygen species (ROS) formation via NADPH-oxidase. ROS formation by ferments of NADPH-oxidases plays an important role in the development of the immune responses during the interaction of plants with phytopathogenes. These processes are similar in plants and animals [57, 58]. Notably, the activation of NADPH-oxidases, under the effect of heterotrimeric G-proteins, can occur as a result of direct interaction of the subunits of G-protein with NADPH-oxidases as well as a result of the interaction of these subunits with other regulators—small GTPase Rac1 [59], protein kinases [60], calcium, and calcium-dependent kinases [61]. As mentioned above, these regulators are closely connected with heterotrimeric G-proteins.

A complete study on the intracellular signal transfer with ROS synthesis is provided with regard to plant response to abscisic acid (ABA). ABA is involved in different plant processes, such as the regulation of seeds and resting buds, transpiration processes, and formation of heterophylly [62]. It was demonstrated that mutants in gene coding subunits of heterotrimeric G-proteins have disturbances connected with ABA perception. This data suggests that G-proteins are important participants of reception and plant response to ABA. The mutants of *A. thaliana gpa1*, *agb1*, *and agg3* (containing defects in genes coding α1-, β1-, and γ3-subunits of G-protein, respectively) demonstrate the ABA suppression of ABA-dependent stomata closing, which is attributable to the indirect effect of G-proteins on the operation of the ion channels [63, 64]. Mutants *agg1*, *agg2*, and double mutant *agg1 agg2* (defects in genes coding the γ1- and γ2-subunits of G-protein) did not exhibit any such disturbance of sensitivity to ABA.

Regulation via calcium-dependent and calcium-independent ways is demonstrated for ion channels involved in ABA-dependent closing of stomata [65—68]. In the first case, the ion channels are controlled with protein kinase OST1, whereas in the second case, it is controlled with calcium/calmodulin-dependent kinases. In case of the absence of ABA, OST1 is under negative control of protein phosphatase 2C (PP2C), which suppresses the activity of this protein kinase [69]. When ABA interacts with receptor, the activity of PP2C is suppressed, which results in the activation of OST1. Recently, it has been detected that protein phosphatase PP2C interacts with the β-subunits of heterotrimeric G-protein [70]. Besides direct regulation of the ion channels, protein kinase OST1 and calcium/calmodulin-dependent kinases stimulate the NADPH-oxidase controlled synthesis of ROS, which influences the functioning of the ion channels [71].

REGULATION OF BIOTIC INTERACTIONS OF PLANTS AND MICROORGANISMS

Heterotrimeric G-proteins are involved in controlling the biotic interaction of plants, namely, plant immune response react upon the recognition of phytopathogenes as well as in the formation of symbiotic relations with rhizobia.

The mode of operation of *At*FLS2/*At*BAK1 complex was discussed above for flagellin in Arabidopsis, which activates the intracellular kinase of *At*BIK1 directly phosphorylating the atypical subunit of G-protein *At*XLG2, which results in signal transfer in the cell (Fig. 1, *c*) [24]. Tunc-Ozdemir and Jones [72], using Förster Resonance Energy Transfer (FRET) method, investigated the operation of negative regulator of the immune response of receptor-like kinase *At*BIR1, which interacts with receptors to flagellin *At*FLS2 and *At*BAK1 in Arabidopsis. It was demonstrated that in the inactive state, separate from *At*FLS2/*At*BAK1 complex, there is *At*RGS1 complex with definitive α-, β-, and γ-subunits of heterotrimeric G-protein associated with *At*BIR1. Following treatment with peptide flg22, the activation of receptors *At*FLS2/*At*BAK1, signal transfer with *At*BIK1 involvement, and interaction with receptors with receptor-like kinase *At*BIR1 occurs after some time [72]. This further stimulates *At*RGS1 and causes the dissociation of canonical G-protein and activation of β-subunit. ROS is formed in the process of signal transfer with β-subunit involvement via NADPH-oxidase. These processes ultimately result in the ubiquitination and degradation of *At*FLS2, which allows finely regulating the content and activity of receptors to flagellin.

One of the first studies that demonstrated the involvement of heterotrimeric G-proteins in development of symbiotic relations was conducted by Pingret et al. [15], who treated the roots of *Medicago truncatula* with agonist G-protein (mastoparan) and demonstrated the activation of gene *MtENOD12*, which is marker of nodules formation. For example, when plant roots are treated with G-protein and pertussis toxin antagonists, a reduced expression of *MtENOD12* induced by mastoparan occurs.

Thereafter, Choudhury et al. [73] experimenting with soy (*Glycine max*) presented data demonstrating the involvement of heterotrimeric G-proteins in signal transfer during the reception of Nod-factors by receptor NFR1. It was detected that the activated receptor interacts with RGS and G-protein, which is required for signal transmission during the recognition of Nod-factors and further nodule development.

Heterotrimeric G-proteins are involved in establishing symbiotic relations with fungi. The role of heterotrimeric G-proteins in signal transmission upon the recognition of molecules emitted by fungi of ectomycorrhizas was investigated [18]. The authors demonstrated an association between the activation of heterotrimeric G-proteins and operation of calcium channels as well as the formation of ROS and increase of pH values around the cells in the research on the suspension culture of fir-tree *Picea abies*.

INVOLVEMENT OF G-PROTEINS IN PLANTS RESPONSE TO ABIOTIC FACTORS

Owing to the research about the loci responsible for agronomically valuable indicators of cultivated plants, it was detected that a sufficient amount of genes coding the subunits of heterotrimeric G-proteins is available among them [74].

Further, the expression of appropriate genes depends on environmental conditions. For example, effect of salinity, drought, and cold and thermal stress was studied in addition to the effect of ABA on the changes in gene expression of γ-subunits *OsRGG1* and *OsRGG2* of rice *Oryza sativa* [75]. The experiments showed that an increase in gene expression level of *OsRGG1* and *OsRGG2* occurs in response to most of these factors.

Further experiments for searching the components of signal pathway interacting with the γ-subunit *OsRGG1* of rice via yeast two-hybrid system and BiFC allowed detecting 10 potential proteins of γ-subunits [76]. Analysis of these proteins demonstrated that most of them play a role in plant resistance to abiotic stresses. However, the mechanisms on the basis of signal transmission during plant reaction to abiotic factors are insufficiently studied.

Another environmental abiotic factor that is important for plants is lighting as it affects plant growth and development. Negative effect of the α- and β-subunits of heterotrimeric G-proteins on photomorphogenesis was demonstrated in Arabidopsis [77, 78]. Such effect can be based on interaction of the β-subunit *AtAGB1* with the major regulators of photomorphogenesis—cryptochrome CRY1 and transcriptional factor HY5 [79].

This data states that G-proteins play a the key role in the plant response on the effect of several factors of environment, which renders the examination of G-proteins rather perspective in terms of using the obtained knowledge for regulation of these processes in plants.

CONTROL OF PROLIFERATION AND DIFFERENTIATION OF PLANT CELLS WITH INVOLVEMENT OF G-PROTEINS

Heterotrimeric G-proteins are involved in controlling the proliferation and differentiation of plant cells. Positive effect of the α-subunit of heterotrimeric G-protein on cell proliferation was detected in Arabidopsis [80]. During the transformation of cultivated cells of Arabidopsis with the structure for the overexpression of gene *AtGPA1* coding the α-subunit of G-protein, the stimulation of the

cell cycle of cells in synchronous culture were demonstrated [80].

Stimulation of cell division and development of lateral roots in Arabidopsis were observed under effect of auxin, whereas a negative effect of β- and γ-subunits of heterotrimeric G-protein *AtAGB1* and *AtAGG1* was detected [38]. Mutants in gene *agb1* were characterized with elevated sensitivity to auxin and increase in the amount of primordia of lateral roots. The authors demonstrated that elevated sensitivity to auxin with the stimulation of cells division of *agb1*-mutants can be compensated by the overexpression of gene *AtGPA1*. Therefore, it was determined that G-proteins could affect cell proliferation indirectly via hormones.

Regulation of cell division in the roots of *A. thaliana* was examined using the mutants *gpa1* and *agb1*, as well as of plants with overexpression of appropriate genes [81]. The authors characterized the phenotypes of these mutants from the point of view of roots development. Plants with genotype *gpa1* had less lateral roots in comparison with the wild-growing plants. On the contrary, the mutant *agb1* had more lateral roots and longer main root. Data obtained using such mutants facilitate inferring G-proteins as the important regulators of plant cell proliferation; however, the possible molecular mechanisms of such processes have not yet been elucidated.

Complex of receptors CLAVATA (CLV), CORYNE (CRN), RECEPTOR-LIKE PROTEIN KINASE2 (RPK2), and regulatory peptide CLE (CLV3/ENDOSPERM SURROUNDING REGION, ESR) are involved in controlling cell proliferation in plants meristems [82]. In *Arabidopsis*, the transcriptional factor WUSHEL (WUS) containing homeodomain in the shoot apical meristem regulates the stem cell pool supporting their activity [83]. Association of regulatory peptide CLE/CLV3 with complexes of receptors CLV1–CLV1, CLV2–CRN, or RPK2–RPK2 activates the signal pathways, which suppress the expression of gene *WUSHEL* (*WUS*). Subsequently, WUS induces the expression of gene *CLV3* acting according to the mechanism of the negative feedback [84].

When studying features of functioning of the system CLV–WUS, it was detected that receptors CLV2/CRN and RPK2/RPK2 could form complexes with heterotrimeric G-protein, following which the MAP-kinase cascade is activated [85]. Indeed, the *Arabidopsis* mutants in gene *agb1* coding the β-subunit of G-protein *AtAGB1* has an enlarged zone of stem cells. This phenomenon was detected in mutants in gene *clv2*, *crn*, and *rpk2* [86]. Ishida et al. [87] studied *in vitro* interaction of RPK2 and the β-subunits of G-protein, which probably is responsible for the activation of MAP-kinase pathway that resulted in regulation of the stem cells pool.

Therefore, the interaction of receptors CLV, CRN, and RPK2 and heterotrimeric G-proteins is a required condition of signal transmission to transcriptional factor WUS involved in controlling plant cell proliferation.

CONCLUSION

Despite the currently available knowledge about the structure and principles of activation and function of heterotrimeric G-proteins in some processes in plants, the complete picture of their functioning remains to be elucidated. Considering the little diversity of the subunit composition of the complexes of heterotrimeric G-proteins and significant amount of processes that are controlled by them, it can be assumed that G-proteins play the role of master-regulators accepting signals from many signals simultaneously and modulating development and functioning in accordance with such signals. However, additional examinations are required for understanding the mechanism underlying the signal regulation in plants with involvement of heterotrimeric G-proteins.

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REFERENCES

1. Urano D, Jones AM. Heterotrimeric G protein-coupled signaling in plants. *Annu Rev Plant Biol*. 2014;65:365-384. https://doi.org/10.1146/annurev-arplant-050213-040133.
2. Scherer GF. Stimulation of growth and phospholipase A, by the peptides mastoparan and melittin and by the auxin 2, 4-dichlorophenoxyacetic acid. *Plant Growth Regulation*. 1992;11(2):153-157. https://doi.org/10.1007/bf00024069.
3. White I, Wise A, Millner P. Evidence for G-protein-linked receptors in higher plants: stimulation of GTP-gamma-S binding to membrane fractions by the mastoparan analogue mas 7. *Planta*. 1993;191(2):285-288. https://doi.org/10.1007/bf00199762.
4. Legendre L, Yueh YG, Crain R, et al. Phospholipase C activation during elicitation of the oxidative burst in cultured plant cells. *J Biol Chem*. 1993;268(33):24559-24563.
5. Aharon GS, Gelli A, Snedden WA, Blumwald E. Activation of a plant plasma membrane Ca^{2+} channel by TGα1, a heterotrimeric G protein α-subunit homologue. *FEBS Lett*. 1998;424(1-2):17-21. https://doi.org/10.1016/s0014-5793(98)00129-x.
6. Zaina S, Reggiani R, Bertani A. Preliminary evidence for involvement of GTP-binding protein(s) in auxin signal transduction in rice (*Oryza sativa* L.) coleoptile. *J Plant Physiol*. 1990;136(6):653-658. https://doi.org/10.1016/s0176-1617(11)81339-8.

7. Warpeha KM, Hamm HE, Rasenick MM, Kaufman LS. A blue-light-activated GTP-binding protein in the plasma membranes of etiolated peas. *Proc Natl Acad Sci USA*. 1991;88(20):8925-9. https://doi.org/10.1073/pnas.88.20.8925.
8. Warpeha KM, Kaufman LS, Briggs WR. A flavoprotein may mediate the blue light-activated binding of guanosine 5'-triphosphate to isolated plasma membranes of *Pisum sativum* L. *Photochem Photobiol*. 1992;55(4):595-603. https://doi.org/10.1111/j.1751-1097.1992.tb04282.x.
9. Romero LC, Sommer D, Gotor C, Song PS. G-proteins in etiolated Avena seedlings. Possible phytochrome regulation. *FEBS Lett*. 1991;282(2):341-346. https://doi.org/10.1016/0014-5793(91)80509-2.
10. Perfus-Barbeoch L, Jones AM, Assmann SM. Plant heterotrimeric G protein function: Insights from Arabidopsis and rice mutants. *Curr Opin Plant Biol*. 2004;7(6):719-31. https://doi.org/10.1016/j.pbi.2004.09.013.
11. Lease KA, Wen J, Li J, et al. A mutant Arabidopsis heterotrimeric G-protein beta subunit affects leaf, flower, and fruit development. *Plant Cell*. 2001;13(12):2631-41. https://doi.org/10.1105/tpc.010315.
12. Liang X, Ding P, Lian K, et al. Arabidopsis heterotrimeric G proteins regulate immunity by directly coupling to the FLS2 receptor. *Elife*. 2016;5:e13568. https://doi.org/10.7554/eLife.13568.
13. Ishikawa A. The Arabidopsis G-protein beta-subunit is required for defense response against Agrobacterium tumefaciens. *Biosci Biotechnol Biochem*. 2009;73(1):47-52. https://doi.org/10.1271/bbb.80449.
14. Maruta N, Trusov Y, Brenya E, et al. Membrane-localized extra-large G proteins and Gβγ of the heterotrimeric G proteins form functional complexes engaged in plant immunity in Arabidopsis. *Plant Physiol*. 2015;167(3):1004-1016. https://doi.org/10.1104/pp.114.255703.
15. Pingret J-L. Rhizobium nod factor signaling: evidence for a G protein mediated transduction mechanism. *Plant Cell*. 1998;10(5):659-672. https://doi.org/10.1105/tpc.10.5.659.
16. Rogato A, Valkov VT, Alves LM, et al. Down-regulated Lotus japonicus GCR1 plants exhibit nodulation signalling pathways alteration. *Plant Sci*. 2016;247:71-82. https://doi.org/10.1016/j.plantsci.2016.03.007.
17. Choudhury SR, Pandey S. Phosphorylation-dependent regulation of G-protein cycle during nodule formation in soybean. *Plant Cell*. 2015;27(11):3260-3276. https://doi.org/10.1105/tpc.15.00517.
18. Hebe G, Hager A, Salzer P. Initial signalling processes induced by elicitors of ectomycorrhiza-forming fungi in spruce cells can also be triggered by G-protein-activating mastoparan and protein phosphatase-inhibiting cantharidin. *Planta*. 1999;207(3):418-425. https://doi.org/10.1007/s004250050500.
19. Aranda-Sicilia MN, Trusov Y, Maruta N, et al. Heterotrimeric G proteins interact with defense-related receptor-like kinases in Arabidopsis. *J Plant Physiol*. 2015;188:44-48. https://doi.org/10.1016/j.jplph.2015.09.005.
20. Neer EJ. G proteins: critical control points for transmembrane signals. *Protein Sci*. 2008;3(1):3-14. https://doi.org/10.1002/pro.5560030102.
21. Iismaa TP, Biden TJ, Shine J. G protein-coupled receptors. Berlin, Heidelberg: Springer Berlin Heidelberg; 1995. P. 135-136.
22. Oldham WM, Hamm HE. Heterotrimeric G protein activation by G-protein-coupled receptors. *Nat Rev Mol Cell Biol*. 2008;9(1):60-71. https://doi.org/10.1038/nrm2299.
23. Siderovski DP, Willard FS. The GAPs, GEFs, and GDIs of heterotrimeric G-protein alpha subunits. *Int J Biol Sci*. 2005;1(2):51-66. https://doi.org/10.7150/ijbs.1.51.
24. Stateczny D, Oppenheimer J, Bommert P. G-protein signaling in plants: minus times minus equals plus. *Curr Opin Plant Biol*. 2016;34:127-135. https://doi.org/ 10.1016/j.pbi.2016.11.001.
25. Brown NA, Schrevens S, van Dijck P, Goldman GH. Fungal G-protein-coupled receptors: Mediators of pathogenesis and targets for disease control. *Nat Microbiol*. 2018;3(4):402-414. https://doi.org/10.1038/s41564-018-0127-5.
26. Li L, Wright SJ, Krystofova S, et al. Heterotrimeric G protein signaling in filamentous fungi. *Annu Rev Microbiol*. 2007;61:423-452. https://doi.org/10.1146/annurev.micro.61.080706.093432.
27. Hoffman CS. Except in every detail: comparing and contrasting G-protein signaling in *Saccharomyces cerevisiae* and Schizosaccharomyces pombe. *Eukaryot Cell*. 2005;4(3):495-503. https://doi.org/10.1128/EC.4.3.495-503.2005.
28. Moretti M, Wang L, Grognet P, et al. Three regulators of G protein signaling differentially affect mating, morphology and virulence in the smut fungus Ustilago maydis. *Mol Microbiol*. 2017;105(6):901-921. https://doi.org/ 10.1111/mmi.13745.
29. Xue C, Hsueh Y-P, Heitman J. Magnificent seven: roles of G protein-coupled receptors in extracellular sensing in fungi. *FEMS Microbiol Rev*. 2008;32(6):1010-1032. https://doi.org/10.1111/j.1574-6976.2008.00131.x.
30. Krishnan A, Almén MS, Fredriksson R, Schiöth HB. The origin of GPCRs: identification of mammalian like Rhodopsin, Adhesion, Glutamate and Frizzled GPCRs in fungi. *PLoS One*. 2012;7(1):e29817. https://doi.org/10.1371/journal.pone.0029817.
31. Lafon A, Han K, Seo J, et al. G-protein and cAMP-mediated signaling in aspergilli: a genomic perspec-

tive. *Fungal Genet Biol*. 2006;43(7):490-502. https://doi.org/10.1016/j.fgb.2006.02.001.
32. Chen J-G, Willard FS, Huang J, et al. A seven-transmembrane RGS protein that modulates plant cell proliferation. *Science*. 2003;301(5640):1728-1731. https://doi.org/10.1126/science.1087790.
33. Trusov Y, Botella JR. Plant G-proteins come of age: breaking the bond with animal models. *Front Chem*. 2016;4:24. https://doi.org/10.3389/fchem.2016.00024.
34. Urano D, Jones JC, Wang H, et al. G protein activation without a GEF in the plant kingdom. *PLoS Genet*. 2012;8(6):e1002756. https://doi.org/10.1371/journal.pgen.1002756.
35. Johnston CA, Taylor JP, Gao Y, et al. GTPase acceleration as the rate-limiting step in Arabidopsis G protein-coupled sugar signaling. *Proc Natl Acad Sci USA*. 2007;104(44):17317-17322. https://doi.org/10.1073/pnas.0704751104.
36. Urano D, Phan N, Jones JC, et al. Endocytosis of the seven-transmembrane RGS1 protein activates G-protein-coupled signalling in Arabidopsis. *Nat Cell Biol*. 2012;14(10):1079-1088. https://doi.org/10.1038/ncb2568.
37. Hackenberg D, McKain MR, Lee SG, et al. Gα and regulator of G-protein signaling (RGS) protein pairs maintain functional compatibility and conserved interaction interfaces throughout evolution despite frequent loss of RGS proteins in plants. *New Phytol*. 2017;216(2):562-75. https://doi.org/10.1111/nph.14180.
38. Ullah H, Chen J, Temple B, et al. The beta-subunit of the Arabidopsis G protein negatively regulates auxin-induced cell division and affects multiple developmental processes. *Plant Cell*. 2003;15(2):393-409. https://doi.org/10.1105/tpc.006148.
39. Pfeuffer T, Helmreich EJ. Activation of pigeon erythrocyte membrane adenylate cyclase by guanylnucleotide analogues and separation of a nucleotide binding protein. *J Biol Chem*. 1975;250(3):867-876.
40. Sunahara RK. Isoforms of mammalian adenylyl cyclase: multiplicities of signaling. *Mol Interv*. 2002;2(3):168-184. https://doi.org/10.1124/mi.2.3.168.
41. McCudden CR, Hains MD, Kimple RJ, et al. G-protein signaling: back to the future. *Cell Mol Life Sci*. 2005;62(5):551-577. https://doi.org/10.1007/s00018-004-4462-3.
42. Kadamur G, Ross EM. Mammalian phospholipase C. *Annu Rev Physiol*. 2013;75(1):127-154. https://doi.org/10.1146/annurev-physiol-030212-183750.
43. Berridge MJ. The inositol trisphosphate/calcium signaling pathway in health and disease. *Physiol Rev*. 2016;96(4):1261-1296. https://doi.org/10.1152/physrev.00006.2016.
44. Dhanasekaran DN, Kashef K, Lee CM, et al. Scaffold proteins of MAP-kinase modules. *Oncogene*. 2007;26(22):3185-3202. https://doi.org/10.1038/sj.onc.1210411.
45. Liu R, Wong W, IJzerman AP. Human G protein-coupled receptor studies in *Saccharomyces cerevisiae*. *Biochem Pharmacol*. 2016;114:103-115. https://doi.org/10.1016/j.bcp.2016.02.010.
46. Lomovatskaya LA, Kuzakova OV, Romanenko AS, Goncharova AM. Activities of adenylate cyclase and changes in camp concentration in root cells of pea seedlings infected with Mutualists and Phytopathogens. *Russ J Plant Physiol*. 2018;65(4):588-597. https://doi.org/10.1134/S1021443718030056.
47. Chatukuta P, Dikobe TB, Kawadza DT, et al. An arabidopsis clathrin assembly protein with a predicted role in plant defense can function as an adenylate cyclase. *Biomolecules*. 2018;8(2). pii: E15. https://doi.org/10.3390/biom8020015.
48. Isner JC, Maathuis FJ. cGMP signalling in plants: from enigma to main stream. *Funct Plant Biol*. 2018;45(1-2):93-101. https://doi.org/10.1071/fp16337.
49. den Hartog M, Musgrave A, Munnik T. Nod factor-induced phosphatidic acid and diacylglycerol pyrophosphate formation: a role for phospholipase C and D in root hair deformation. *Plant J*. 2001;25(1):55-65. https://doi.org/10.1046/j.1365-313x.2001.00931.x.
50. Sun J, Liu X, Pan Y. The physical interaction between LdPLCs and Arabidopsis G beta in a yeast two-hybrid system. *Front Agric China*. 2011;5(1):64-71. https://doi.org/10.1007/s11703-011-1063-9.
51. Zhao J, Wang X. Arabidopsis phospholipase dalpha 1 interacts with the heterotrimeric G-protein α-subunit through a motif analogous to the DRY motif in G-protein-coupled receptors. *J Biol Chem*. 2004;279(3):1794-1800. https://doi.org/10.1074/jbc.M309529200.
52. Zheng L, Krishnamoorthi R, Zolkiewski M, Wang X. Distinct Ca^{2+} binding properties of novel C2 domains of plant phospholipase dalpha and β. *J Biol Chem*. 2000;275(26):19700-19706.
53. Cheng Z, Li JF, Niu Y, et al. Pathogen-secreted proteases activate a novel plant immune pathway. *Nature*. 2015;521(7551):213-216. https://doi.org/10.1038/nature14243.
54. Yuan GL, Li HJ, Yang WC. The integration of Gβ and MAPK signaling cascade in zygote development. *Sci Rep*. 2017;7(1):8732. https://doi.org/10.1038/s41598-017-08230-4.
55. Nakashima A, Chen L, Thao NP, et al. RACK1 Functions in rice innate immunity by interacting with the Rac1 immune complex. *Plant Cell*. 2008;20(8):2265-79. https://doi.org/10.1105/tpc.107.054395.
56. Suharsono U, Fujisawa Y, Kawasaki T, et al. The heterotrimeric G protein alpha subunit acts upstream of the small GTPase Rac in disease resistance of rice. *Proc*

Natl Acad Sci. 2002;99(20):13307-13312. https://doi.org/10.1073/pnas.192244099.
57. Petry A, Görlach A. Regulation of NADPH oxidases by G protein-coupled receptors. *Antioxid Redox Signal*. 2019;30(1):74-94. https://doi.org/10.1089/ars.2018.7525.
58. Wrzaczek M, Brosché M, Kangasjärvi J. ROS signaling loops – production, perception, regulation. *Curr Opin Plant Biol*. 2013;16(5):575-582. https://doi.org/10.1016/j.pbi.2013.07.002.
59. Wong HL, Pinontoan R, Hayashi K, et al. Regulation of rice NADPH oxidase by binding of rac GTPase to its N-terminal extension. *Plant Cell*. 2007;19(12):4022-34. https://doi.org/10.1105/tpc.107.055624.
60. Sirichandra C, Gu D, Hu HC, et al. Phosphorylation of the Arabidopsis AtrbohF NADPH oxidase by OST1 protein kinase. *FEBS Lett*. 2009;583(18):2982-2986. https://doi.org/10.1016/j.febslet.2009.08.033.
61. Suzuki N, Miller G, Morales J, et al. Respiratory burst oxidases: the engines of ROS signaling. *Curr Opin Plant Biol*. 2011;14(6):691-699. https://doi.org/10.1016/j.pbi.2011.07.014.
62. Zeevaart JA, Creelman RA. Metabolism and physiology of abscisic acid. *Annu Rev Plant Physiol Plant Mol Biol*. 1988;39(1):439-473. https://doi.org/10.1146/annurev.pp.39.060188.002255.
63. Wang XQ, Ullah H, Jones AM, Assmann SM. G protein regulation of ion channels and abscisic acid signaling in Arabidopsis guard cells. *Science*. 2001;292(5524):2070-2072. https://doi.org/10.1126/science.1059046.
64. Fan L-M, Zhang W, Chen J-G, et al. Abscisic acid regulation of guard-cell K+ and anion channels in Gβ- and RGS-deficient Arabidopsis lines. *Proc Natl Acad Sci*. 2008;105(24):8476-8481. https://doi.org/10.1073/pnas.0800980105.
65. Mori IC, Murata Y, Yang Y, et al. CDPKs CPK6 and CPK3 function in ABA regulation of guard cell S-type anion- and Ca^{2+}-permeable channels and stomatal closure. *PLoS Biol*. 2006;4(10):e327. https://doi.org/10.1371/journal.pbio.0040327.
66. Lee SC, Lan W, Buchanan BB, Luan S. A protein kinase-phosphatase pair interacts with an ion channel to regulate ABA signaling in plant guard cells. *Proc Natl Acad Sci*. 2009;106(50):21419-21424. https://doi.org/10.1073/pnas.0910601106.
67. Geiger D, Scherzer S, Mumm P, et al. Activity of guard cell anion channel SLAC1 is controlled by drought-stress signaling kinase-phosphatase pair. *Proc Natl Acad Sci*. 2009;106(50):21425-21430. https://doi.org/10.1073/pnas.0912021106.
68. Geiger D, Scherzer S, Mumm P, et al. Guard cell anion channel SLAC1 is regulated by CDPK protein kinases with distinct Ca^{2+} affinities. *Proc Natl Acad Sci*. 2010;107(17):8023-8028. https://doi.org/10.1073/pnas.0912030107.
69. Vlad F, Rubio S, Rodrigues A, et al. Protein phosphatases 2C regulate the activation of the Snf1-related kinase OST1 by abscisic acid in Arabidopsis. *Plant Cell*. 2009;21(10):3170-3184. https://doi.org/10.1105/tpc.109.069179.
70. Tsugama D, Liu H, Liu S, Takano T. Arabidopsis heterotrimeric G protein β subunit interacts with a plasma membrane 2C-type protein phosphatase, PP2C52. *Biochim Biophys Acta*. 2012;1823(12):2254-60. https://doi.org/10.1016/j.bbamcr.2012.10.001.
71. Hauser F, Li Z, Waadt R, Schroeder JI. SnapShot: abscisic acid signaling. *Cell*. 2017;171(7):1708-1708.e0. https://doi.org/10.1016/j.cell.2017.11.045.
72. Tunc-Ozdemir M, Jones AM. Ligand-induced dynamics of heterotrimeric G protein-coupled receptor-like kinase complexes. *PLoS One*. 2017;12(2):e0171854. https://doi.org/10.1371/journal.pone.0171854.
73. Choudhury SR, Pandey S. Heterotrimeric G-protein complex and its role in regulation of nodule development. *Exocytosis Cell Res*. 2016;27(2):29-35.
74. Botella JR. Can heterotrimeric G proteins help to feed the world? *Trends Plant Sci*. 2012;17(10):563-568. https://doi.org/10.1016/j.tplants.2012.06.002.
75. Yadav DK, Islam SM, Tuteja N. Rice heterotrimeric G-protein gamma subunits (RGG1 and RGG2) are differentially regulated under abiotic stress. *Plant Signal Behav*. 2012;7(7):733-40. https://doi.org/10.4161/psb.20356.
76. Swain DM, Sahoo RK, Srivastava VK, et al. Function of heterotrimeric G-protein γ subunit RGG1 in providing salinity stress tolerance in rice by elevating detoxification of ROS. *Planta*. 2017;245(2):367-383. https://doi.org/10.1007/s00425-016-2614-3.
77. Ullah H, Chen J-G, Temple B, et al. The beta-subunit of the Arabidopsis G protein negatively regulates auxin-induced cell division and affects multiple developmental processes. *Plant Cell*. 2003;15(2):393-409. https://doi.org/10.1105/tpc.006148.
78. Jones AM. A reevaluation of the role of the heterotrimeric G protein in coupling light responses in Arabidopsis. *Plant Physiol*. 2003;131(4):1623-1627. https://doi.org/10.1104/pp.102.017624.
79. Lian H, Xu P, He S, et al. Photoexcited CRYPTOCHROME 1 interacts directly with G protein β subunit AGB1 to regulate the DNA-binding activity of HY5 and photomorphogenesis in Arabidopsis. *Mol Plant*. 2018;11(10):1248-1263. https://doi.org/10.1016/j.molp.2018.08.004.
80. Ullah H, Chen JG, Young JC, et al. Modulation of cell proliferation by heterotrimeric G protein in Arabidopsis. *Science*. 2001;292(5524):2066-2069. https://doi.org/10.1126/science.1059040.

81. Chen JG, Gao Y, Jones AM. Differential roles of Arabidopsis heterotrimeric G-protein subunits in modulating cell division in roots. *Plant Physiol*. 2006;141(3):887-897. https://doi.org/10.1104/pp.106.079202.
82. Betsuyaku S, Takahashi F, Kinoshita A, et al. Mitogen-activated protein kinase regulated by the CLAVATA receptors contributes to shoot apical meristem homeostasis. *Plant Cell Physiol*. 2011;52(1):14-29. https://doi.org/10.1093/pcp/pcq157.
83. Laux T, Mayer KF, Berger J, et al. The *WUSCHEL* gene is required for shoot and floral meristem integrity in Arabidopsis. *Development*. 1996;122(1):87-96.
84. Fletcher JC, Brand U, Running MP, et al. Signaling of cell fate decisions by CLAVATA3 in Arabidopsis shoot meristems. *Science*. 1999;283(5409):1911-1914. https://doi.org/10.1126/science.283.5409.1911.
85. Somssich M, Je BI, Simon R, Jackson D. CLAVATA-WUSCHEL signaling in the shoot meristem. *Development*. 2016;143(18):3238-48. https://doi.org/10.1242/dev.133645.
86. Kinoshita A, Betsuyaku S, Osakabe Y, et al. RPK2 is an essential receptor-like kinase that transmits the CLV3 signal in Arabidopsis. *Development*. 2010;137(22):3911-20. https://doi.org/10.1242/dev.048199.
87. Ishida T, Tabata R, Yamada M, et al. Heterotrimeric G proteins control stem cell proliferation through CLAVATA signaling in Arabidopsis. *EMBO Rep*. 2016;17(8):1236. https://doi.org/10.15252/embr.201678010.

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