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Review Article

CONTROL OF PLANT HEIGHT BY HETEROTRIMERIC G-PROTEIN ALPHA SUBUNIT IN RICE

Y. Chen[1,2], J. L. Wei[2], Y. J. Zhang[2], G. M. Li[2], B. Lü[2], and L. J. Liu[1]*

[1] Jiangsu Key Laboratory of Crop Genetics and Physiology/Jiangsu Co-Innovation Centre for Modern Production Technology of Grain Crops/Jiangsu Key Laboratory of Crop Genomics and Molecular Breeding/Key Laboratory of Plant Functional Genomics of the Ministry of Education, Yangzhou University, Yangzhou 225009, China
[2] College of Bioscience and Biotechnology, Yangzhou University, Yangzhou 225009, China
* Corresponding Author's Email: ljliu@yzu.edu.cn

ABSTRACT

Plant height is an important agronomic trait in rice that affects rice morphogenesis, apical dominance, harvest index and yield. Rice plant height is controlled by genes that lie in a complex regulatory network. At present, many plant height-related genes have been identified in rice, among which heterotrimeric G-protein α subunit, RGA1, is an important regulator. RGA1 is involved in cell division and regulates internode cell number, and in the biosynthesis and responses to phytohormones gibberellin (GA) and brassinosteroid (BR) signalling that regulates stem and internode elongation. Additionally, RGA1 affects rice plant height via the effect on nitrogen uptake and utilization and the interaction with drought stress responses. This review summarizes the progress on the regulation of rice plant height by RGA1 and proposes a focus of future research on the influence of RGA1 on rice plant height. We hope to provide a theoretical foundation for elucidating the regulatory mechanism of plant height and the application of RGA1 in the genetic improvement of plant height for a high and stable grain yield in rice production. We also propose new ideas for revealing the integral functions of G-proteins in rice.

Key words: RGA1, Plant height, Hormone, Nitrogen, Drought, Rice.

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INTRODUCTION

The first 'Green Revolution' introduced the term semi-dwarfing, effectively solved issues such as rice resistance to lodging and achieved an increase in rice yield and stable rice production (Athwal *et al*., 1971; Evenson and Gollin, 2003; Ferrero-Serrano *et al*., 2019). Plant height is an important factor that affects rice morphogenesis, apical dominance, biomass, lodging resistance, pest resistance, and harvest index (Asano *et al*., 2011; Liu *et al*., 2018). Rice plant height architecture is a result of the interactions between genes and the environment. It is determined by 2 aspects, external and internal factors. First, it is influenced by environmental factors, such as drought stress and the application of nitrogen fertilizers. Second, it is regulated via the major and minor genes controlling plant height. These genes are involved in the regulation of plant hormone signalling pathways that are tightly associated with plant height, including gibberellins (GAs) and brassinosteroids (BRs) (Asano *et al*., 2011; Liu *et al*., 2018). Through genetic analysis, scientists have obtained a large number of rice dwarf mutants, including mutants related to GA signalling (*d18*, *d35*) and BR signalling (*d2*, *d11*) and mutants with the absence of G-protein α subunit (Gα) (*d1*, *d89*) (Ashikari *et al*., 1999; Hong *et al*., 2003; Itoh *et al*., 2004; Yang *et al*., 2014).

RGA1 is the rice heterotrimeric G-protein alpha subunit and is involved in many signal transduction pathways that regulate plant height in rice (Liu *et al*., 2018; Wang *et al*., 2019). This review describes the structure and function of RGA1, with a focus on RGA1 participating in rice hormonal signal transduction, responses to nitrogen and drought stress pathways, and discusses the physiological and molecular mechanism of plant height regulation by RGA1 in rice. Our goal is to provide a reference for an in-depth understanding of the rice heterotrimeric G-protein system and the application of RGA1 in rice genetic breeding.

The structure of the RGA1 protein: Rice has a single Gα subunit, designated RGA1 or DAIKOKU DWARF1 (D1/d1). In 1990, Ma *et al*. cloned the first plant G-protein α subunit, AtGPA1, from *Arabidopsis thaliana* (Ma *et al*., 1990). In 1995, Seo *et al*. used *Arabidopsis GPA1* cDNA as a probe and cloned the G-protein α subunit (RGA1) in rice IR 36 for the first time (Seo *et al*., 1995). The full-length cDNA of *RGA1* is 1173 bp and contains 13 exons (Fig. 1a). The *RGA1* gene encodes 390 amino acids and contains many conserved sequence loci, including the N-myristoylation site, the casein kinase II phosphorylation site, the ATP/GTP-binding motif (P-loop), the tyrosine kinase phosphorylation site, the G1-5 box, the receptor binding site, the GTP/Mg^{2+} binding site, the Switch I and

II region, the GoLoco-binding site, the G-protein βγ subunit complex (Gβγ) interaction site, and the adenylyl cyclase interaction site (Fig. 1b). The RGA1 protein contains 2 domains, a C-terminal GTPase domain (Ras-like domain) and an N-terminal α-helical domain (Fig. 1c). It has a molecular weight of 45.2 kDa and an isoelectric point of 6.62 (Fujisawa *et al*., 1999; Yadav *et al*., 2013). Different from that in *Arabidopsis*, RGA1 in rice does not contain a regulator of G-protein signalling (RGS) protein interaction site, similar to that in animals. RGA1 has a self-activation/deactivation, nucleic acid-dependent regulatory mechanism. Thus, rice is an ideal model plant species to discover the regulatory mechanism of new activation (Temple and Jones, 2007; Biswal *et al*., 2019).

Function of the RGA1 protein in rice: RGA1 can function independently or coordinate with the G-protein β subunit (Gβ) and γ subunit (Gγ) to mediate the transduction of many extracellular signals to intracellular signals and regulate various physiological activities (Urano *et al*., 2013; Sun *et al*., 2018). The earliest study of RGA1 function in rice was conducted in the *d1* mutant. In 1999, Ashikari *et al*. discovered the rice dwarf mutant Daikoku, and through map-based cloning, they isolated and identified the gene associated with the dwarf phenotype. This study showed that the responsible gene was located on rice chromosome 5 and encoded RGA1, which was later named *Dwarf 1* (*d1*) (Ashikari *et al*., 1999). *RGA1* was expressed in all rice tissues tested (Izawa *et al*., 2010). Together with previous studies, it was determined that RGA1 is involved in cell division, hormonal signal transduction pathways, abiotic stress responses, resistance to rice blast, and nitrogen uptake and utilization in rice (Table 1).

RGA1 regulates signal transduction pathways related to plant height in rice: *d1*, the loss-of function mutant of the gene for rice RGA1, is the first studied Gα mutant rice, and produces a dwarf phenotype. Studies have found that RGA1 directly or indirectly regulates rice plant height through its involvement in cell division, responses to hormones and drought, and nitrogen uptake and utilization.

Involvement of RGA1 in cell division to regulate rice plant height: The discovery of and research involving plant Gα were first done in *Arabidopsis*. *Arabidopsis* G-protein α subunit, GPA1, positively regulates cell division; thus, *gpa1* mutants exhibit shorter hypocotyls and smaller seeds (Ullah *et al*., 2001). Oki *et al*. conducted a comparative analysis of 10 rice strains with *rga1* mutations and found that compared with the wild type, the absence of RGA1 resulted in a 25%-50% decrease in plant height. Additionally, the rice strains with *rga1* mutations exhibited erected panicles, darkened leaf colour, and small rounded seeds (Oki *et al*., 2009b). Compared with the wild type, *d1* decreased plant height by 52%, seed size by 25%, and leave size by 50% (Urano *et al*., 2016). *d1-5* shortened the internode length and decreased the number of cells but did not change the average cell length (Izawa *et al*., 2010). Therefore, the dwarf phenotype of the *d1* mutant is mainly caused by a reduction in the number of cells in various organs (Oki *et al*., 2005; Izawa *et al*., 2010). However, Yang *et al*. found that compared with the wild type, the *d89* mutant (*d89* represents a metastable epigenetic mutant of the D1 locus in *indica* cultivar MU101) resulted in severely shortened internodes and significant elongation of cell length in the first internode, leading to a significantly decreased cell number (Yang *et al*., 2014). Results from these studies showed that different RGA1 mutants exhibited different responses in internode cell division. RGA1 is a positive regulator of cell elongation, and the absence of RGA1 results in shortened internode length, leading to dwarfing in rice RGA1 mutants.

Involvement of RGA1 in the GA signalling pathway to regulate rice plant height: GA is an important hormone that regulates plant growth and development. It promotes seed germination, induces the activity of α-amylase, and stimulates internode and stem elongation (Ayano *et al*., 2014; Hedden and Sponsel, 2015; Binenbaum *et al*., 2018). The control of rice plant height is mostly related to the biosynthesis of and responsiveness to GA (Ashikari *et al*., 2002; Liu *et al*., 2018). *d1* was identified as a GA-insensitive mutant (Ashikari *et al*., 1999). The external GA_3 concentration for inducing internode elongation in rice *d1* mutants was 100-fold higher than that in wild-type rice plants, and *d89* did not respond to elongation of the aboveground portion induced by external GA (Ueguchi-Tanaka *et al*., 2000; Yang *et al*., 2014). This indicated that RGA1 is involved in responses to GA signals in rice, and the absence of RGA1 led to reduced sensitivity GA signals in plants, which inhibited stem elongation (Liu *et al*., 2018). The GA-GID1-DELLA pathway, which is the basic GA signal transduction pathway, has been established. The *GID1* gene encodes a soluble GA receptor, and the *SLR1* gene encodes a DELLA protein, which is a repressor of GA signalling, mediating GA signalling in rice. Until recently, the molecular mechanisms governing the repression of GA signalling by DELLA proteins were unknown. It is now revealed that DELLA proteins interact with various transcription factors, and through these interactions, regulate the transcription of genes involved in GA response. Several DELLA targets have already been identified in *Arabidopsis* and only a few in rice (Hedden and Sponsel, 2015; Daviere and Achard *et al*., 2016). The identical phenotypes in the single *slr* and double *slr/d1* mutants indicate that the D1 product functions as a member of the same GA-signalling pathway as the SLR protein (Ikeda *et al*., 2001; Ueguchi-Tanaka *et al*., 2005; Iwasaki *et al*., 2003). The DNL1 was a regulator in the GA responsiveness and signal transduction pathway, and the expression of *D1* was significantly decreased in *dnl1*, a

dwarf and narrow-leaf mutant (Wei *et al*., 2013). However, how rice perceives GA and how the GA signal is transmitted to cause GA-regulated plant growth are still not well known.

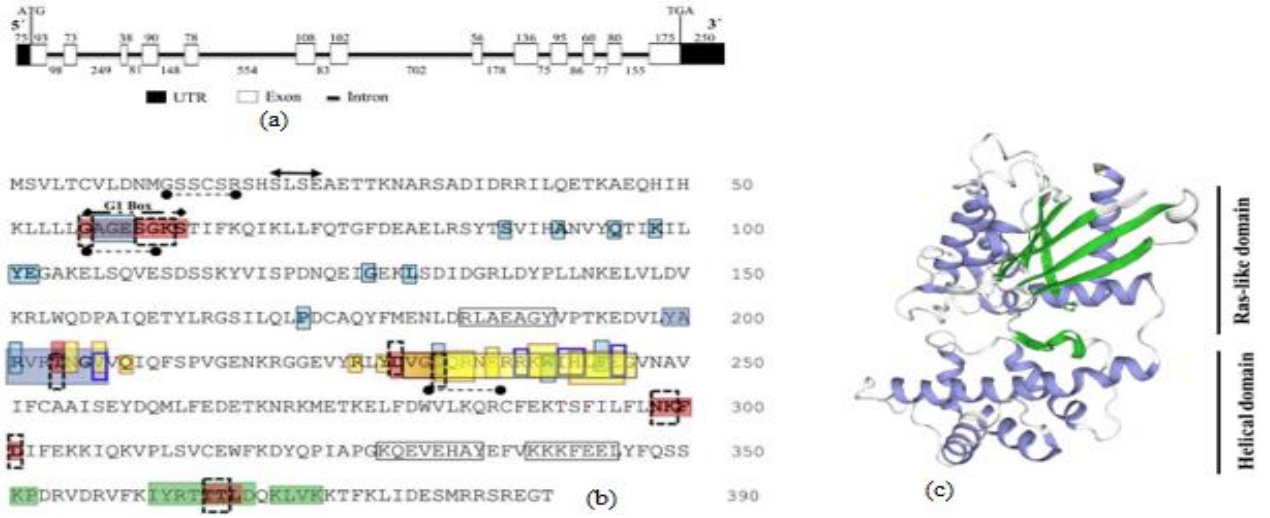

Fig. 1. Structure of RGA1. (a) The schematic representation of genomic organization (exon-intron organization) of the genomic sequence of *RGA1* (GenBank: ADU17254.1); (b) Different conservative site of RGA1: N-myristoylation site (•·····•), Casein kinase Ⅱ phosphorylation site (↔) , ATP/GTP-binding site motif A (P-loop) (←···→), Tyrosine kinase phosphorylation site (□), G1-5 box (■), Putative receptor binding site (■), GTP/Mg^{2+} binding site (⊡), Switch Ⅰ region (■), Switch Ⅱ region(■), GoLoco binding site(■), Beta-gamma complex interaction site (■), Adenylyl cyclase interaction site (□). Source: (Yadav *et al*., 2013); (c) The 3D model of RGA1 was developed using SWISS MODEL (https://swissmodel.expasy.org/interactive).

Table 1. Functions and biochemical/molecular responses of RGA1.

Physiological response	Biochemical/Molecular response	References
Cell division	Involving in cell proliferation	Oki *et al*., 2005; Izawa *et al*., 2010; Urano *et al*., 2014
GA-signalling pathway	Interaction with SLR1	Ashikari *et al*., 1999; Ueguchi-Tanaka *et al*., 2000; Yang *et al*., 2014; Ferrero-Serrano *et al*., 2019
BR-signalling pathway	Interaction with TUD1	Wang *et al*., 2006; Oki *et al*., 2009a; Tanaka *et al*., 2009; Hu *et al*., 2013; Ferrero-Serrano *et al*., 2019
Ethylene signalling pathway	ROS scavenging activities	Steffens and Sauter, 2009; 2010
Resistance to blast	*OsRac1, OsMAPK*, H_2O_2 production，*PR* and *PBL* gene expression	Suharsono *et al*., 2002; Lieberherr *et al*., 2005
Drought stress response	Photoavoidance and photoprotection	Ferrero-Serrano and Assmann, 2016; Jangam *et al*., 2016; Ferrero-Serrano *et al*., 2018
Cold stress response	*COLD1,* ROS scavenging activities	Ma *et al*., 2015; Jangam *et al*., 2016
Salt stress response	ROS scavenging activities	Urano *et al*., 2014; Peng *et al*., 2019
Nitrogen uptake and utilization	Interaction with DEP1	Sun *et al*., 2014

In addition to components in GA signalling, endogenous GA levels regulated by the GA metabolism also have an important role in the control of plant height. Many GA-related genes are feedback or feedforward regulated by bioactive GAs, where GA20ox and GA3ox function in GA biosynthesis with feedback regulation, and GA2ox functions in GA catabolism with feedforward regulation by bioactive GAs (Zhang *et al*., 2008). The dwarf phenotype of *d1* mainly presents severely shortened second and third internodes, especially the second

internode. However, in the second and third internodes of rice *d1* mutants, the expression of Os20ox was 6- and 4.5-fold higher than that in wild-type rice plants, respectively. Ueguchi-Tanaka *et al*. indicated that the feedback inhibitory effect of active GA on Os20ox was absent in RGA1-absent internodes (Ueguchi-Tanaka *et al*., 2000). The mechanism of RGA1 function involving in GA signalling to regulate rice height is showed in Fig. 2a.

Involvement of RGA1 in the BR signalling pathway to regulate rice plant height: BR is also proven to be an important hormone that regulate plant height (Nagai *et al*., 2018). Rice mutants insensitive to BR or defective in BR signalling also exhibit a dwarf phenotype (Mori *et al*., 2002; Hong *et al*., 2003; Tanaka *et al*., 2009; Nakagawa *et al*., 2012; Hu *et al*., 2013; Castorina and Consonni, 2020). Compared with the wild type, mutant *d1* and *d61-1* were insensitive to 24-epiBL (24-epibrassinolide, external BR analogue) in the stimulation of coleoptile elongation (Wang *et al*., 2006). Compared with wild-type T65, mutant *T65d1* exhibited lower sensitivity to 24-epiBL (Oki *et al*., 2009a). This indicates that RGA1 is involved in the responses to BR signals in rice and that the absence of RGA1 causes insensitivity to BR and inhibits coleoptile elongation.

The levels of mRNAs for BR-biosynthetic genes *D2*, *D11*, and *DWARF* were all reduced in rice *d1* mutants and wild-type rice plants T65d1 by application of 24-epiBL. Since the feedback regulation with 24-epiBL in the T65d1 mutant is not impaired, RGA1-mediated internode elongation seems not be connected directly with the BR cascade via rice BR receptor, BRI1 (Oki *et al*., 2009a; Tanaka *et al*., 2009). TUD1, a U-box E3 ubiquitin ligase, can directly downregulate D1, thereby mediating the BR signalling pathway. In rice *tud1-2* mutants, the dwarf phenotype in the second internode was the same as that in BR-defective mutants *d61* and *brd1*; *BRD1*, *DWARF4*, and *D61*, genes related to BRI1-mediated BR signalling, had significantly higher expression levels in the second internode than in the first internode. Thus, BR signal transduction mediated by D1-TUD1-BU1 pathway may parallel or partially overlapped with the canonical BRI1-mediated BR signal transduction and its regulation of plant height (Hu *et al*., 2013; Tong *et al*., 2014). The relationship among RGA1, TUD1, BU1and BRI1 is shown in Fig. 2b.

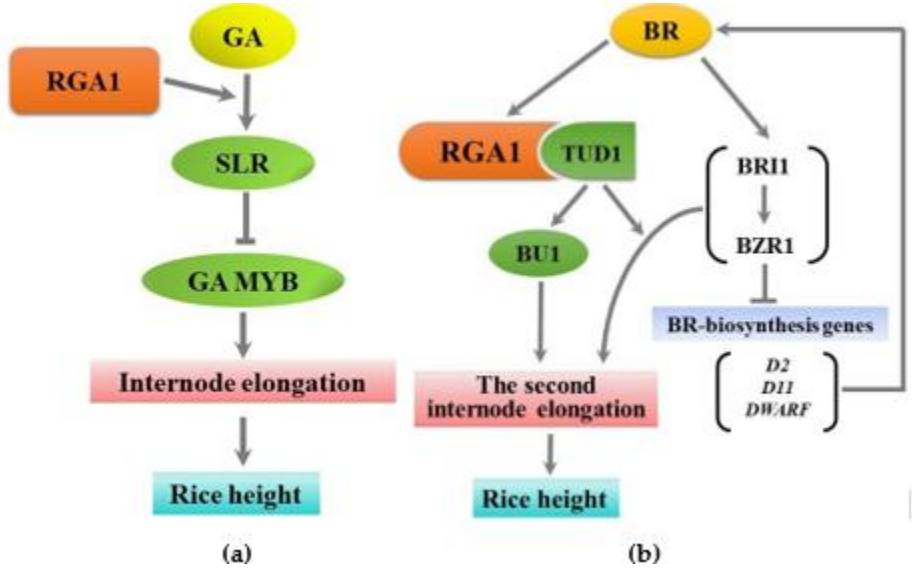

Fig. 2. The model of RGA1 involving in GA signalling (a) and BR signalling pathways (b) in rice height formation (Ueguchi-Tanaka *et al*., 2000; Oki *et al*., 2009a; Zhang *et al*., 2014; Ferrero-Serrano *et al*., 2019).

Involvement of RGA1 in the regulation of nitrogen to affect plant height: Nitrogen is one of the macronutrients necessary for the growth and development of crops. It is an important component for maintaining normal metabolism and the cycling and distribution of substances in crops. Additionally, nitrogen fertilizer is a crucial factor that influences plant height (Ali *et al*., 2018; Yang *et al*., 2020). Sun *et al*. constructed a series of near-isogenic lines carrying *DEP1* (encoding Gγ and regulating seed development) as well as single and double *DEP1* and *D1* mutants. They found that different *DEP1* alleles exhibited different responses to nitrogen. The vegetative growth of rice RGA1 mutants was insensitive to nitrogen, and nitrogen content increased. Rice *dep1-d1* double mutants exhibited a severe dwarf phenotype (Sun *et al*., 2014). The molecular mechanism of the interaction between RGA1 and DEP1 is still unclear; therefore, an in-depth investigation of the coordination between DEP1 in seed development and RGA1 in the formation of plant height can provide new ideas for increasing nitrogen utilization efficiency and rice yield.

Involvement of RGA1 in the influence of drought stress on rice plant height: The interaction between genes and the environment is ubiquitous phenomenon. Genetic and physiological traits often change with the interaction with environmental variables. Drought is an important stress for rice. A limited water supply often inhibits height development, consequently affecting yield (Zhuang *et al*. 1997; Oladosu *et al*., 2019). Lots of studies performed on the gene × environment interaction of agronomic traits, as grain filling, panicle size, root growth and plant height, most of which focusing on the genetic effects of QTLs (Zhuang *et al*., 1997; Pandey and Shukla, 2015; Oladosu *et al*., 2019). So far, few reports have documented the RGA1 function for rice height combined with drought stress. Droughted *d1* plants showed a significantly higher root to shoot ratio than the wild-type rice under the identical drought conditions, while this ratio did not differ between genotypes in the absence of drought. *d1* had a lower leaf temperature, higher stomatal conductance, and higher photochemical reflectance index, resulting in lower sensitivity to drought stress (Ferrero-Serrano and Assmann, 2016; Ferrero-Serrano *et al*., 2018). Jangam *et al*. performed microarray analysis in combination with the STIFDB 2.0 database and obtained 106 differentially expressed genes related to drought stress between wild-type rice plants and *d1* mutants. Among them, 13 genes were significantly associated with drought, including heat shock protein, MAP kinase and transcription factors, etc (Jangam *et al*., 2016). This indicated that the absence of RGA1 led to an increase in the photochemical reflectance index, disrupted the expression of drought stress-related genes, and increased drought resistance in rice *d1* mutants. These results deepen the understanding of the mechanism of RGA1 in response to drought stress and provide references for plant type improvement and drought resistance breeding in rice.

Future prospective: Early studies on RGA1 in rice mostly focused on the phenotype and physiological characteristics of mutants. In recent years, substantial progress has been made in the molecular mechanisms of RGA1 in regulating plant height by participating in hormone signalling and nitrogen utilization. For the regulation of plant height by RGA1 in rice, future studies should address the following areas:

Strengthen research on the mechanism of how RGA1 affects plant height by regulating hormones: Hormones that affect the formation of plant height include GA, BR, IAA (an auxin), abscisic acid (ABA), and strigolactones. Past studies have described, in depth, the mechanism of RGA1 regulation of rice plant height through the GA and BR signal transduction pathways. Very few reports have addressed the role of RGA1 in the regulation of plant height by other hormones. Thus, is RGA1 involved in the signal transduction pathway of other hormones to regulate plant height in rice? The mechanism of the interaction between RGA1 and various hormones in the regulation of plant height needs to be further studied.

Improve the G-protein signalling network and further elucidate plant height regulation mechanisms in rice: RGA1 is a membrane protein. It can function alone or interact with Gβ and Gγ to regulate intracellular signal transduction. Clarification of the associations between G protein and each signalling pathway is necessary for constructing and improving the enormous G-protein signalling network. Additionally, to reveal the detailed mechanism of RGA1 regulation of rice plant height, it is urgent and necessary to utilize the massive genetic resources (new genes, mapping populations, near-isogenic lines, introgression lines, recombinant inbred lines, double haploids, etc.) and advanced 'omic' technologies to analyse the upstream regulatory proteins and downstream effectors and their functions. It is also necessary to discuss the functions of RGA1 in rice stem development under different environmental conditions and growth stages.

Strengthen research on rice plant height regulation by RGA1 under abiotic stresses: In recent years, extreme abiotic stresses (such as drought and heat) have occurred frequently and are posing significant impacts on the growth, development, and yield of rice. However, there is a lack of research on how RGA1 is expressed and how it affects rice plant height under these abiotic stresses. In the future, it is necessary to strengthen research on the expression patterns of RGA1 under extreme drought, high temperature, and multiple stresses during the rice vegetative growth period and to determine how RGA1 regulates plant height plant to adaptation to the environment, with a goal of providing a reference for achieving a high and stable rice yield.

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REFERENCES

Ali, J., Z. A. Jewel, A. Mahender, A. Anandan, J. Hernandez, and Z. Li (2018). Molecular genetics

and breeding for nutrient use efficiency in rice. Int. J. Mol. Sci. 19(6): 1762.

Asano, K., M. Yamasaki, S. Takuno, K. Miura, S. Katagiri, T. Ito, K. Doi, J. Wu, K. Ebana, T. Matsumoto, H. Innan, H. Kitano, M. Ashikari, and M. Matsuoka (2011). Artificial selection for a green revolution gene during *japonica* rice domestication. Proc. Natl. Acad. Sci. USA. 108(27): 11034–11039.

Ashikari, M., J. Wu, M. Yano, T. Sasaki, and A. Yoshimura (1999). Rice gibberellin-insensitive dwarf mutant gene *Dwarf 1* encodes the α-subunit of GTP-binding protein. Proc. Natl. Acad. Sci. USA. 96(18): 10284–10289.

Ashikari, M., A. Sasaki, M. Ueguchi-Tanaka, H. Itoh, A. Nishimura, S. Datta, K. Ishiyama, T. Saito, M. Kobayashi, G. S. Khush, H. Kitano, and M. Matsuoka (2002). Loss-of-function of a rice gibberellin biosynthetic gene, *GA20 oxidase (GA20ox-2)*, led to the rice 'Green Revolution'. Breed. Sci. 52(2): 143–150.

Athwal, D. S. (1971). Semidwarf rice and wheat in global food needs. Q. Rev. Biol. 46(1): 1–34.

Ayano, M., T. Kani, M. Kojima, H. Sakakibara, T. Kitaoka, T. Kuroha, R. B. Angeles-Shim, H. Kitano, K. Nagai, and M. Ashikari (2014). Gibberellin biosynthesis and signal transduction is essential for internode elongation in deepwater rice. Plant Cell Environ. 37(10): 2313–2324.

Binenbaum, J., R. Weinstain, and E. Shani (2018). Gibberellin localization and transport in plants. Trends Plant Sci. 23(5): 410–421.

Biswal, A. K., E. W. McConnell, E. G. Werth, S. F. Lo, S. M. Yu, L. M. Hicks, and A. M. Jones (2019). The nucleotide-dependent interactome of rice heterotrimeric G-Protein α-subunit. Proteomics. 19(9): e1800385.

Castorina, G., and G. Consonni (2020). The role of brassinosteroids in controlling plant height in *Poaceae*: A genetic perspective. Int. J. Mol. Sci. 21(4): 16.

Daviere, J. M., and P. Achard (2016). A pivotal role of DELLAs in regulating multiple hormone signals. Mol. Plant. 9(1): 10–20.

Evenson, R. E., and D. Gollin (2003). Assessing the impact of the green revolution, 1960 to 2000. Science. 300(5620): 758–762.

Ferrero-Serrano, Á., and S. M. Assmann (2016). The α-subunit of the rice heterotrimeric G protein, RGA1, regulates drought tolerance during the vegetative phase in the dwarf rice mutant *d1*. J. Exp. Bot. 67(11): 3433–3443.

Ferrero-Serrano, Á., Z. Su, and S. M. Assmann (2018). Illuminating the role of the Gα heterotrimeric G protein subunit, RGA1, in regulating photoprotection and photoavoidance in rice. Plant Cell Environ. 41(2): 451–468.

Ferrero-Serrano, Á., C. Cantos, and S. M. Assmann (2019).The role of dwarfing traits in historical and modern agriculture with a focus on rice. Cold Spring Harbor Perspect. Biol. 11(11): 30.

Fujisawa, Y., T. Kato, S. Ohki, A. Ishikawa, H. Kitano, T. Sasakt, T. Asahi, and Y. Iwasaki (1999). Suppression of the heterotrimeric G protein causes abnormal morphology, including dwarfism, in rice. Proc. Natl. Acad. Sci. USA. 96(13): 7575–7580.

Hedden, P., and V. Sponsel (2015). A Century of gibberellin research. J. Plant Growth Regul. 34(4):740–760.

Hong, Z., M. Ueguchi-Tanaka, K. Umemura, S. Uozu, S. Fujioka, S. Takatsuto, S. Yoshida, M. Ashikari, H. Kitano, and M. Matsuoka (2003). A rice brassinosteroid-deficient mutant, *ebisu dwarf (d2)*, is caused by a loss of function of a new member of cytochrome P450. Plant Cell. 15(12): 2900–2910.

Hu, X. M., Q. Qian, T. Xu, Y. Zhang, G. J. Dong, T. Gao, Q. Xie, and Y. B. Xue (2013). The U-box E3 ubiquitin ligase TUD1 functions with a heterotrimeric Gα subunit to regulate brassinosteroid-mediated growth in rice. PLoS Genet. 9(3): e1003391.

Ikeda, A., M. Ueguchi-Tanaka., Y. Sonoda, H. Kitano, M. Koshioka, Y. Futsuhara, M. Matsuoka, and J. Yamaguchi (2001). Slender rice, a constitutive gibberellin response mutant, is caused by a null mutation of the *SLR1* gene, an ortholog of the height-regulating gene *GAI/RGA/RHT/D8*. Plant Cell. 13(5): 999–1010.

Itoh, H., T. Tatsumi, T. Sakamoto, K. Otomo, T. Toyomasu, H. Kitano, M. Ashikari, S. Ichihara, and M. Matsuoka (2004). A rice semi-dwarf gene, *Tan-Ginbozu (D35)*, encodes the gibberellin biosynthesis enzyme, ent-kaurene oxidase. Plant Mol. Biol. 54(4): 533–547.

Iwasaki, Y., Y. Fujisawa, and H. Kato (2003). Function of heterotrimeric G protein in gibberellin signaling. J. Plant Growth Regul. 22: 126–133.

Izawa, Y., Y. Takayanagi, N. Inaba, Y. Abe, M. Minami, Y. Fujisawa, H. Kato, S. Ohki, H. Kitano, and Y. Iwasaki (2010). Function and expression pattern of the α subunit of the heterotrimeric G protein in rice. Plant Cell Physiol. 51(2): 271–281.

Jangam, A. P., R. R. Pathak, and N. Raghuram (2016). Microarray analysis of rice d1 (RGA1) mutant reveals the potential role of G-protein alpha subunit in regulating multiple abiotic stresses such as drought, salinity, heat, and cold. Front. Plant Sci. 7: 11.

Lieberherr, D., N. P. Thao, A. Nakashima, K. Umemura, T. Kawasaki, and K. Shimamoto (2005). A sphingolipid elicitor-inducible mitogen-activated

protein kinase is regulated by the small GTPase OsRac1 and heterotrimeric G-protein in rice. Plant Physiol. 138(3): 1644–1652.

Liu, F., P. D. Wang, X. B. Zhang, X. F. Li, X. H. Yan, D. H. Fu, and G. Wu (2018). The genetic and molecular basis of crop height based on a rice model. Planta. 247(1): 1–26.

Ma, H., M. F. Yanofsky, and E. M. Meyerowitz (1990). Molecular cloning and characterization of *GPA1,* a G protein α subunit gene from *Arabidopsis thaliana.* Proc. Natl. Acad. Sci. USA. 87(10): 3821–3825.

Ma, Y., X. Y. Dai, Y. Y. Xu, W. Luo, X. M. Zheng, D. L. Zeng, Y. J. Pan, X. L. Lin, H. H. Liu, D. J. Zhang, J. Xiao, X. Y. Guo, S. J. Xu, Y. D. Niu, J. B. Jin, H. Zhang, X. Xu, L. G. Li, W. Wang, Q. Qian, S. Ge, and K. Chong (2015). *COLD1* Confers chilling tolerance in rice. Cell. 160(6): 1209–1211.

Mori, M., T. Nomura, H. Ooka, M. Ishizaka, T. Yokota, K. Sugimoto, K. Okabe, H. Kajiwara, K. Satoh, K. Yamamoto, H. Hirochika, and S. Kikuchi (2002). Isolation and characterization of a rice dwarf mutant with a defect in brassinosteroid biosynthesis. Plant Physiol. 130(3): 1152–1161.

Nagai, K., K. Hirano, R. B. Angeles-Shim, and M. Ashikari (2018). Breeding applications and molecular basis of semi-dwarfism in rice. In: Sasaki, T., and M. Ashikari (eds) Rice genomics, genetics and breeding. Springer (Singapore). 155–176.

Nakagawa, H., A. Tanaka, T. Tanabata, M. Ohtake, S. Fujioka, H. Nakamura, H. Ichikawa, and M. Mori (2012). *SHORT GRAIN1* decreases organ elongation and brassinosteroid response in rice. Plant Physiol. 158(3): 1208–1219.

Oki, K., Y. Fujisawa, H. Kato, and Y. Iwasaki (2005). Study of the constitutively active form of the α subunit of rice heterotrimeric G proteins. Plant Cell Physiol. 46(2): 381–386.

Oki, K., N. Inaba, K. Kitagawa, S. Fujioka, H. Kitano, Y. Fujisawa, H. Kato, and Y. Iwasaki (2009a). Function of the α subunit of rice heterotrimeric G protein in brassinosteroid signaling. Plant Cell Physiol. 50(1): 161–172.

Oki, K., N. Inaba, , H. Kitano, S.Takahashi, Y. Fujisawa, H. Kato, and Y. Iwasaki (2009b). Study of novel *d1* alleles, defective mutants of the α subunit of heterotrimeric G-protein in rice. Genes Genet. Syst. 84(1): 35–42.

Oladosu, Y., M. Y. Rafii, C. Samuel, A. Fatai, U. Magaji, I. Kareem, Z. S. Kamarudin, I. Muhammad, and K. Kolapo (2019). Drought resistance in rice from conventional to molecular breeding: A review. Int. J. Mol. Sci. 20(14): 3519–3540.

Pandey, V., and A. Shukla (2015). Acclimation and tolerance strategies of rice under drought stress. Rice Sci. 22(4): 147–161.

Peng, P., Y. D. Gao, Z. Li, Y. W. Yu, H. Qin, Y. Guo, R. F. Huang, and J. Wang (2019). Proteomic analysis of a rice mutant *sd58* possessing a novel *d1* allele of heterotrimeric G protein α subunit (RGA1) in salt stress with a focus on ROS scavenging. Int. J. Mol. Sci. 20(1): 167.

Seo, H. S., H. Y. Kim, J. Y. Jeong, S. Y. Lee, M. J. Cho, and J. D. Bahk (1995). Molecular cloning and characterization of *RGA1* encoding a G protein α subunit from rice *Oryza sativa* L. Plant Mol. Biol. 27(6): 1119–1131.

Steffens, B., and M. Sauter (2009). Heterotrimeric G protein signaling is required for epidermal cell death in rice. Plant Physiol. 151(2): 732–740.

Steffens, B., and M. Sauter (2010). G proteins as regulators in ethylene-mediated hypoxia signaling. Plant Signal. Behav. 5(4): 375–378.

Suharsono, U., Y. Fujisawa, T. Kawasaki, Y. Iwasaki, H. Satoh, and K. Shimamoto (2002). The heterotrimeric G protein α subunit acts upstream of the small GTPase rac in disease resistance of rice. Proc. Natl. Acad. Sci. USA. 99(20): 13307–13312.

Sun, H., Q. Qian, K. Wu, J. Luo, S. Wang, C. Zhang, Y. Ma, Q. Liu, X. Huang, Q. Yuan, R. Han, M. Zhao, G. Dong, L. Guo, X. Zhu, Z. Gou, W. Wang, Y. Wu, H. Lin, and X. Fu (2014). Heterotrimeric G proteins regulate nitrogen-use efficiency in rice. Nat. Genet. 46(6): 652–656.

Sun, S., L. Wang, H. Mao, L. Shao, X. Li, J. Xiao, Y. Ouyang, and Q. Zhang (2018). A G-protein pathway determines grain size in rice. Nat. Commun. 9: 851.

Tanaka, A., H. Nakagawa, C. Tomita, Z. Shimatani, M. Ohtake, T. Nomura, C. J. Jiang, J. G. Dubouzet, S. Kikuchi, H. Sekimoto, T. Yokota, T. Asami, T. Kamakura, and M. Mori (2009). *BRASSINOSTEROID UPREGULATED1*, encoding a helix-loop-helix protein, is a novel gene involved in brassinosteroid signaling and controls bending of the lamina joint in rice. Plant Physiol. 151(2):669–680.

Temple, B. R. S., and A. M. Jones (2007).The plant heterotrimeric G-Protein complex. Annu. Rev. Plant Biol. 58: 249–266.

Tong, H., Y. Xiao, D. Liu, S. Gao, L. Liu, Y. Yin, Y. Jin, Q. Qian, and C. Chu (2014). Brassinosteroid regulates cell elongation by modulating gibberellin metabolism in rice. Plant Cell. 26(11): 4376–4393.

Ueguchi-Tanaka, M., Y. Fujisawa, M. Kobayashi, M. Ashikari, Y. Iwasaki, H. Kitano, and M. Matsuoka (2000). Rice dwarf mutant *d1*, which is

defective in the α subunit of the heterotrimeric G protein, affects gibberellin signal transduction. Proc. Natl. Acad. Sci. USA. 97(21): 11638–11643.

Ueguchi-Tanaka, M., M. Ashikari, M. Nakajima, H. Itoh, E. Katoh, M. Kobayashi, T. Y. Chow, Y. I. C. Hsing, H. Kitano, I. Yamaguchi, and M. Matsuoka (2005). *GIBBERELLIN INSENSITIVE DWARF1* encodes a soluble receptor for gibberellin. Nature. 437(7059): 693–698.

Ullah, H., J. G. Chen, J. C. Young, K. H. Im, M. R. Sussman, and A. M. Jones (2001). Modulation of cell proliferation by heterotrimeric G protein in *Arabidopsis*. Science. 292(5524): 2066–2069.

Urano, D., J. G. Chen, J. R. Botella, and A. M. Jones (2013). Heterotrimeric G protein signalling in the plant kingdom. Open Biol. 3(3): 120186.

Urano, D., A. Colaneri, and A. M. Jones (2014). Gα modulates salt-induced cellular senescence and cell division in rice and maize. J. Exp. Bot. 65(22): 6553–6561.

Urano, D., K. Miura, Q. Wu, Y. Iwasaki, D. Jackson, and A. M. Jones (2016). Plant morphology of heterotrimeric G protein mutants. Plant Cell Physiol. 57(3): 437–445.

Wang, L., Y. Xu,, Q. Ma, D. Li,, Z. Xu, and K. Chong (2006). Heterotrimeric G protein α subunit is involved in rice brassinosteroid response. Cell Res. 16: 916–922.

Wang, Y., Y. Wang, and D. Deng (2019). Multifaceted plant G protein: interaction network, agronomic potential, and beyond. Planta. 249: 1259–1266.

Wei, X., S. Tang, G. Shao, M. Chen, Y. Hu, and P. Hu (2013). Fine mapping and characterization of a novel dwarf and narrow-leaf mutant *dnl1* in rice. Genet. Mol. Res. 12(3): 3845–3855.

Yadav, D. K., D. Shukla, and N. Tuteja (2013). Rice heterotrimeric G-protein α subunit (RGA1): In silico analysis of the gene and promoter and its upregulation under abiotic stress. Plant Physiol. Biochem. 63: 262–271.

Yang, D., X. Zheng, C. Cheng, W. Wang, D. Xing, L. Lu, C. Liu, N. Ye, M. Zeng, and X. Ye (2014). A dwarfing mutant caused by deactivation function of α subunit of the heterotrimeric G-protein in rice. Euphytica. 197(1): 145–159.

Yang, Y., J. Xiong, L. Tao, Z. Cao, W. Tang, J. Zhang, X. Yu, G. Fu, X. Zhang, and Y. Lu (2020). Regulatory mechanisms of nitrogen (N) on cadmium (Cd) uptake and accumulation in plants: A review. Sci. Total Environ. 708: 135186.

Zhang, C., M. Bai, and K. Chong (2014). Brassinosteroid-mediated regulation of agronomic traits in rice. Plant Cell Rep. 33(5): 683–696.

Zhang, Y., Y. Zhu, Y. Peng, D. Yan, Q. Li, J. Wang, L. Wang, and Z. He (2008). Gibberellin homeostasis and plant height control by EUI and a role for gibberellin in root gravity responses in rice. Cell Res. 18(3): 412–421.

Zhuang, J., H. Lin, J. Lu, H. Qian, S. Hittalmani, N. Huang, and K. Zheng (1997). Analysis of QTL×environment interaction for yield components and plant height in rice. Theor. Appl. Genet. 95(5–6): 799–808.