

The fundamental role of DELLA protein and regulatory mechanism during plant growth and development

Qianyu ZHAO^{1,2,a}, Ali ANWAR^{1,b}, Huimin ZHANG^{1,3}, Shu ZHANG¹,
Lilong HE¹, Fengde WANG^{1*}, Jianwei GAO^{1*}

¹Shandong Academy of Agricultural Sciences, Institute of Vegetables, Shandong Branch of National Vegetable Improvement Center, Jinan, Shandong, China; zhaoy1224@163.com; dr.ali_ivf@hotmail.com; zhm1625532906@163.com; shuzhang2013@126.com;

hllong1984@163.com; wfengde@163.com (*corresponding author); scsgaojianwei@shandong.cn

²Qufu Normal University, College of Life Science, Qufu, Jinan, Shandong, China

³Shandong Normal University, College of Life Science, Jinan, Shandong, China

^{a,b}These authors contributed equally to the work.

Abstract

Gibberellins (GAs) play a major role in a variety of key plant development processes, especially in promoting seed germination, stem and root growth, and fruit development. DELLA proteins are the core elements in GA signal transduction pathway, which exist in the plant nucleus and belong to the GRAS protein family. DELLA proteins negatively regulate the GA signaling pathway and biosynthesis, inhibiting plant growth. DELLA proteins can also interact with F-box, PIFS, ROS, SCL3 and other proteins to enhance plant response to various adverse environmental influences such as drought, low and high temperature, heavy metal stresses. In addition, DELLA proteins can also partially regulate plant growth and development through interacting plant hormones such as ABA (abscisic acid), CK (cytokinin), ET (ethylene), BR (brassinosteroid) and JA (jasmine). This review summarized the basic characteristics of DELLA proteins, the transduction of hormone and environmental signals, as well as the regulation of plant growth and developments. DELLA proteins have broad application prospects in modern agricultural production in the future, but the molecular mechanism of DELLA proteins regulating plant growth and development are still unclear, and needs further study.

Keywords: abiotic stress; DELLA proteins; GA; growth; plant hormone

Introduction

Plants are regulated by a variety of environmental factors and hormones in the process of growth and development. Gibberellin (GA) is a central regulator in the process of plant growth and development, including seed germination, seedling growth, leaf development, root and stem growth, flower organ development and fruit ripening (Bolle, 2004). DELLA proteins are a subfamily of the GRAS family. In early studies, several DELLA genes have been found in many plant species, such as *GAI*, *RGA*, *RGL1*, *RGL2* and *RGL3* genes of *Arabidopsis*, *d8* gene of maize, *RHT* gene of wheat, *L1* gene of grape, *SLR1* gene of rice and *sln1* gene of barley, etc. (Phokas and Coates, 2021). Recent physiological and biochemical studies of DELLA proteins have enabled

Received: 05 Nov 2021. Received in revised form: 08 Dec 2021. Accepted: 09 Dec 2021. Published online: 15 Dec 2021.

From Volume 49, Issue 1, 2021, Notulae Botanicae Horti Agrobotanici Cluj-Napoca journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

us to construct a model of GA signaling: GA perception is mediated by *GID1*, and GA promotes plant growth by GID1-mediated destabilization of the DELLA protein via the 26S proteasome pathway (Jiang and Fu, 2007). DELLA proteins are important regulatory elements in the GA signal pathway and play a negative regulatory role in the GA signal transduction pathway (Figure 1). A recent study reported that DELLA proteins not only participate in GA signal transduction but also play a vital role in hormonal biosynthesis and signaling pathways, such as abscisic acid (ABA), ethylene (ET) and jasmonic acid (JA) (Binenbaum *et al.*, 2018). The interaction of DELLA with various plant hormones enhanced plant tolerance to various environmental influences, such as temperature, drought, salinity and heavy metal stresses (Asier *et al.*, 2017). The DELLA proteins are highly conserved among different species, but the number and function of DELLA members in different species are different. In the “Green revolution” during the 1950s to 1960s, the introduction of wheat mutant dwarfing alleles at Reduced height-1 (Rht-B1 and Rht-D1) loci led to significant increases in worldwide grain yields during the 1960s, owing to improvements in both harvest index and lodging resistance (Hedden, 2003). Since then, Rht-1 dwarfing alleles were still widely used in modern wheat cultivars. The wheat Rht-B1b and Rht-D1b alleles encoded a mutant DELLA protein that conferred semi-dominant GA insensitive dwarfism (Peng *et al.*, 1999). At present, the expression level of DELLA proteins can be regulated by transgenic technology in various crops to dwarf plants, enhance resistance and increase yield (Jutarou, 2014). In addition, DELLA proteins also played an important role in relieving seed dormancy, early flowering, prolonging the flowering period, improving fruit quality, delaying plant senescence and regulating the synthesis of secondary metabolites (Jutarou, 2014; Asier *et al.*, 2017).

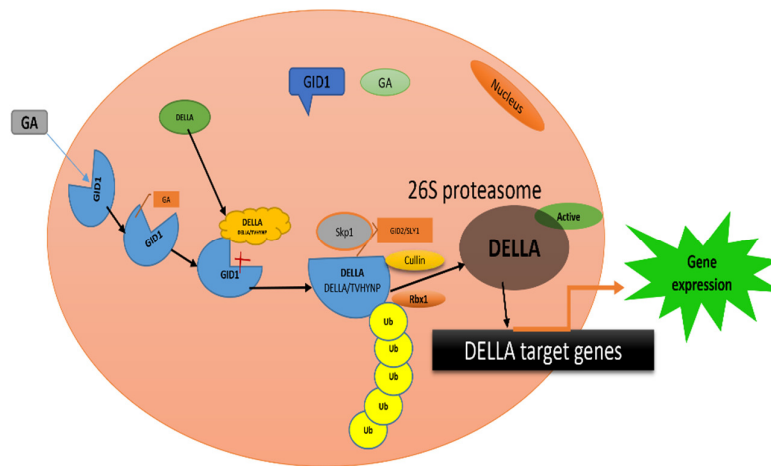


Figure 1. DELLA signaling pathway and biosynthesis in plants

In the absence of GA, DELLA proteins are repressed by GA action, but in presence of GA, GID1 receptor binds GA, and then GID1-GA complex interact with DELLA and TVHYNP protein of DELLA motifs. The DELLA/TVHYNP proteins are integrated with SCFGID2/SLY1 complex (consisting of Skp1, Cullin, F-box protein, and Rbx1), and then polyubiquitinated by SCFGID2/SLY1 complex, and degrade DELLA proteins through 26s proteasome pathway, hence DELLA are activated.

DELLA negatively regulate the GAs metabolic pathway and integrated factors of plant response to environmental signals (light, temperature, drought, salt, etc.) and hormone signals (GAs, IAA, ABA, BR, JA, etc.). The inhibitory effect of DELLA proteins on plants growth is beneficial when plants are subjected to stress. To a certain extent, the higher the content of DELLA proteins, enhanced tolerance of plants to the environmental influences (Jutarou, 2014). Therefore, the function of DELLA proteins has become the focus of the plant signal transduction pathway. Under adverse conditions, DELLA proteins enable plants to survive adverse conditions by integrating adverse environmental conditions and hormones in plants (Zhou *et al.*, 2017). When the contents of GA in plants were low but the DELLA contents were higher, and the tolerance

to stress would become stronger (Vera-Sirera *et al.*, 2016). *SLRI*, the only one DELLA gene in rice, which was highly induced by *OsMYB91* overexpression, had been proved to integrate the signals of endogenous developmental genes under environmental conditions (Zhu *et al.*, 2015). DELLA proteins and SCL protein were integrated into ABA and GA reaction pathway to increase plant tolerance to abiotic stress (Golldack *et al.*, 2013). Therefore, the research results of DELLA proteins are very important for regulating plant growth and development, stress resistance and disease resistance, which has a broad application prospect.

DELLA proteins

DELLA protein's structure

The DELLA proteins are located in the nucleus of plants, and the conserved C-terminal GRAS domain is mainly involved in the interaction between proteins and the process of transcriptional regulation which includes two leucine heptapeptide repeats (LHRI and LHRII) and three conserved motifs (VHIID, PFYRE and SAW) as shown on Figure 2. Compared with other GRAS proteins, DELLA proteins have DELLA and TVHYNP at the N-terminal, and their mutations interfered with the binding of DELLA proteins to GA receptor GID1, resulting in a GA-insensitive dwarf phenotype (Cheng *et al.*, 2019). GA stimulates the formation of GA-GID1-DELLA complex when GA concentration increases, and the complex is subsequently targeted for degradation in the 26S proteasome. (Ito *et al.*, 2018). The amino acid sequence of DELLA proteins is also divided into different domains. The N-terminal is a highly conserved DELLA sequence, and its adjacent domain is a highly conserved TVHYNP sequence, which participates in the binding of DELLA proteins and GIDI proteins. In addition, the C-terminal has conserved SAW, SH2 and VHID domains, which can regulate DELLA proteins activity during GA biosynthesis and signaling pathways (Phokas and Coates, 2021). In addition, the number of amino acids between the DELLA and TVHYNP domain is very important for the acceptance of the GA signal, but this amino acid sequence is not conservative.

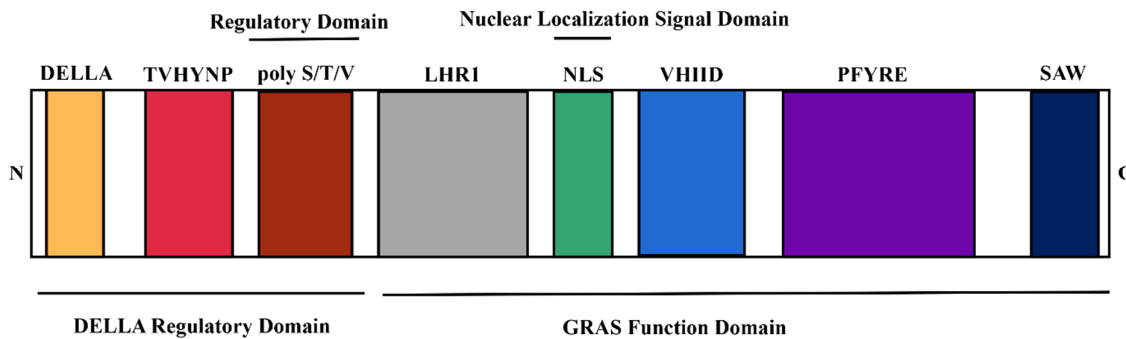


Figure 2. The DELLA protein's structure

N terminal of DELLA regulatory domain contains DELLA, VHYNP and Poly S/T/V (polymeric Ser and Thr and Val) region, which DELLA and VHYNP are highly conserved. While C terminal region is GRAS function domain, which contains two LHR (Leu heptad repeat), one NLS (nuclear localization signal), and three conserved motifs, VHIID, PFYRE, and SAW.

DELLA genes expression levels

DELLA proteins showed varied expression in different plant tissues and also changed with the external environment. The *DELLA* genes in *Arabidopsis* included *AtRGL1*, *AtGAI*, *AtRGA*, *AtRGL2* and *AtGRL3* (Javier *et al.*, 2010), of which *AtRGL1*, *AtRGL2* and *AtRGL3* were differentially expressed in different tissues and had high expression in flowers, fruits and seeds (Tyler *et al.*, 2004). There were 4 *DELLA* genes in cucumber, including *CsGAI1*, *CsGAI2*, *CsGAI3* and *CsGAIP*, which were expressed in distinct level in

different plant tissue. The expression of *CsGAI2* and *CsGAI3* were higher, but the expression of the others was lower. The *CsGAI1* was expressed at low levels in all tissues, and the transcription of *CsGAI3* was mainly concentrated in the root (Yan *et al.*, 2014). In peanut, the *AhDELLA1* and *AhDELLA2* genes were expressed ubiquitously in different tissues, while *AhDELLA3* and *AhDELLA4* showed much higher expression level in flowers and seeds as compared with other organs (An *et al.*, 2015). These findings suggested that DELLA proteins are available in all tissue of plants, and the expression levels of DELLA proteins were distinct in different tissues, among these DELLA proteins were mainly high expressed in flowers, fruits and growth sites.

Table 1. DELLA genes known at present

Species	Gene name	References
<i>Arabidopsis thaliana</i>	<i>GAI, RGA, RGL1, RGL2 and RGL3</i>	Tyler <i>et al.</i> , 2004
<i>Malus domestica</i> Borkh	<i>MdRGL1a/b, MdRGL2a/b and MdRGL3a/b</i>	Foster <i>et al.</i> , 2007
<i>Malus hupehensis</i> (Pamp.) Rehd	<i>MhGAI1, MhGAI2</i>	Wang <i>et al.</i> , 2012
<i>Pyrus bretschneideri</i> Rehd	<i>GAI</i>	Zhang <i>et al.</i> , 2012c
<i>Vitis vinifera</i> L.	<i>VvGAI1</i>	Vargas <i>et al.</i> , 2013
<i>Glycine max</i> (L.) Merr.	<i>GAI1</i>	Wang <i>et al.</i> , 2021
<i>Medicago truncatula</i> Gaertn.	<i>MtDELLA</i>	Floss <i>et al.</i> , 2021
<i>Phaseolus vulgaris</i> L.	<i>PvGAI1, PvGAI2</i>	Yamauchi <i>et al.</i> , 2007
<i>Populus trichocarpa</i> Torrey & A.Gray	<i>PtGAI1, PtGAI2, PtRGL1 and PtRGL2</i>	Liu <i>et al.</i> , 2016
<i>Gossypium barbadense</i> L.	<i>GbGAI, GbSLR1a and GbSLR1b</i>	Liao <i>et al.</i> , 2009
<i>Solanum lycopersicum</i> L.	<i>LeGAI</i>	Jasinski <i>et al.</i> , 2008
<i>Oryza sativa</i> L.	<i>OsGAI/SLR1</i>	Gomi <i>et al.</i> , 2010; Ueguchi-Tanaka <i>et al.</i> , 2007
<i>Zea mays</i> L.	<i>D8, D9</i>	Peng <i>et al.</i> , 1999; Cassani <i>et al.</i> , 2009
<i>Hordeum vulgare</i> L.	<i>SLN1</i>	Fu and Harberd, 2002
<i>Triticum aestivum</i> L.	<i>Rht</i>	Ikeda <i>et al.</i> , 2001
<i>Artemisia annua</i>	<i>AaDELLA1, AaDELLA2</i>	Shen <i>et al.</i> , 2015
<i>Populus alba</i>	<i>PeRGAI, PeRGAI2, PeGAI1, PeGAI2</i>	Liu <i>et al.</i> , 2016
<i>Artocarpus incisa</i>	<i>AaDELLA1, AaDELLA2</i>	Zhou and Underhill, 2017

DELLA protein's interaction

DELLA proteins can interact with many proteins to deal with complex environments and ensure the survival and reproduction of species. Interaction between F-box and DELLA proteins consolidated the function of DELLA. F-box protein is a subunit of SKP1-CUL1-F-box complex, which can mediate the recognition of specific substrates by the SCF complex. The SCF /SLY of GA receptor *GID1* and E3 ligase could regulate the degradation of DELLA proteins by the 26S proteasome (Wang *et al.*, 2016). DELLA proteins interacted with PIFs (Phytochrome Interacting Factors) to prevent its binding to the target gene promoter and inhibit growth (Karel *et al.*, 2017). However, exogenous GA application would degrade DELLA proteins, accumulating PIFs and promoting plant development (Li *et al.*, 2016). *SCL3* (SCARECROW-LIKE3) promoted gibberellin signal transduction by antagonizing DELLA proteins (Zhang *et al.*, 2011). The DELLA proteins family member *GAI* regulated plant apical growth by interacting with the ERF (Ethylene Response factor) family member *RAP2.3* (Marín-de la Rosa *et al.*, 2014).

DELLA proteins mediate plant hormone signal transduction

The growth and development of plants are regulated by many hormones. DELLA proteins are the key factors for coordinating many hormone signals, and most hormones regulate DELLA proteins by affecting the signal transduction of GAs.

Gibberellin (GA)

GA is a hormone widely present in higher plants and plays an important role in plant growth and development. At present, the basic path and molecular mechanism in the process of GA signal transduction have been clarified (Figure 1). When the gibberellin receptor protein GID1 does not bind to GA, the structure of its N-terminal extension (N-Ex) is more flexible; but when the GA signal is present, the conformation of N-Ex begins to change, and GA binds tightly to the GID1 protein, which are closely bound to form GA-GID1 complex (Peng and Harberd, 1997). The phosphorylation of *EL1* (*Earlier Flowering 1*) protein and SPY (Spindly) protein can activate the activity of DELLA protein, making it easy to combine with GA-GID1 complex to form a more stable GA-GID1-DELLA complex (Murase *et al.*, 2008). This complex can be polyubiquitinated by a specific ubiquitin E3 ligase complex (SCFSLY1/GID2) and then degraded by 26S protease to produce GA effect, promoting plant growth (Sun, 2010). Plants can coordinate with the external environment by regulating GA content and signal transduction during development, which has become an important research direction.

Auxin (IAA)

Auxin is an important signal molecule mainly used to promote the stem and coleoptile growth of the plant. Auxin also plays a significant role in abiotic stress tolerance (Kirungu *et al.*, 2019). The previous studies in *Arabidopsis* provided direct evidence of auxin and gibberellin signal crosstalk mediated by RGA (Eunkyoo *et al.*, 2014). The signal crosstalk between auxin and gibberellin significance for plant growth regulation and fruit germination was mediated by SIDELLA in tomato and SLARF7/SLIAA9 complexes. DELLA proteins could directly inhibit the transcriptional activity of PIF proteins, which could promote auxin biosynthesis (Junbo *et al.*, 2018). A study showed that the promoting effect of GA on plant growth required the synergistic action of IAA, and the polar transport of IAA was related to the content of DELLA proteins in the root tip (Fu and Harberd, 2003). Inhibiting the polar transport of IAA or removing the apical growth point can delay the degradation process of DELLA proteins and then restrain root growth. DELLA proteins can interact with PIN protein to regulate the formation of apical hook and plant gravitropism (Gallego-Bartolomé *et al.*, 2011; Javier *et al.*, 2011). In addition, In the presence of GAs, DELLA proteins were inactivated, the function of *PIF5* was released, increasing the expression of downstream *WAG2* and the activity of PIN protein, which affected the transport and distribution of IAA and promoted the formation of hooks (Willige *et al.*, 2012). Therefore, IAA affects plant growth and development by regulating the degradation of DELLA proteins mediated by GA. These findings suggest that DELLA proteins and IAA signal are interconnected and lead to control various kinds of molecular mechanisms during plant growth.

Table 2. The interaction of DELLA genes in plant hormones

Hormone	Related gene	Function	References
GA	<i>GID1</i>	Promote the formation of GA-GID1-DELLA complex and inhibit the function of DELLA proteins.	Murase <i>et al.</i> , 2008
Auxin	<i>RGA</i>	Mediate auxin and gibberellin signal crosstalk.	Eunkyoo <i>et al.</i> , 2014
Auxin	<i>SIDELLA</i>	Interact with SLARF7/SLIAA9 to regulate plant growth and fruit germination.	Junbo <i>et al.</i> , 2018
IAA	<i>IAA</i>	Degrade DELLA proteins and then restrain root growth.	Gallego-Bartolomé <i>et al.</i> , 2011
IAA	<i>IAA</i>	Related to the content of DELLA proteins in root tip.	Fu and Harberd 2003
CK	<i>GA3ox</i>	Promote the expression of <i>GAI</i> and <i>RGA</i> by inhibiting the expression of <i>GA3ox</i> .	Dai and Xue 2010
CK	<i>RGA</i> and <i>GAI</i>	Regulate the expression of CK response genes.	Marín-de la Rosa <i>et al.</i> , 2014
ABA	<i>OsAP2-39</i>	Regulate the expression of ABA and gas key synthase.	Yaish <i>et al.</i> , 2010
ABA	<i>ABI3</i> and <i>ABI5</i>	Interact with DELLA proteins to jointly induce the expression of SOMNUS (SOM) gene to mediate the inhibition of high temperature on seed germination.	Lim <i>et al.</i> , 2013
ABA	<i>ABI5</i>	Participate in PIF1 / SOM / ABI5 / DELLA regulation mode participated, inhibiting seed germination.	Vaistij <i>et al.</i> , 2018
ABA	<i>NF-YC</i>	Interact with DELLA proteins, and induced <i>ABI5</i> expression affecting the expression of a series of GA and ABA response genes.	Liu <i>et al.</i> , 2016
ABA	<i>ICE1</i>	Interact with DELLA proteins and <i>ABI5</i> to fine-tune Abscisic Acid Signaling during Seed Germination in Arabidopsis.	Hu <i>et al.</i> , 2019
ET	<i>ACS5</i> and <i>ACS8</i>	Are regulated by DELLA proteins and affect the development of top hook together with PIN vector.	An <i>et al.</i> , 2012
ET	<i>EIN3 / EIL1</i>	Interact with the DNA binding domain to affect the development of vertex hook.	An <i>et al.</i> , 2012
ET	<i>EIN3</i>	Regulate <i>rhgail</i> to control the growth of rose petal cells.	Luo <i>et al.</i> , 2013
ET	<i>AtERF11</i>	Enhance GA signaling by antagonizing the function of DELLA proteins.	Zhou <i>et al.</i> , 2016
JA	<i>JAZs</i>	Interact with DELLA proteins to wake their inhibitory effect on their respective downstream transcription factors.	Ye <i>et al.</i> , 2016
JA	<i>PIF3</i>	Interact with the DNA and hinder its regulation of downstream target gene expression, inhibiting hypocotyl elongation.	Hou <i>et al.</i> , 2010
JA	<i>OSJAZ8</i> and <i>OSJAZ9</i>	Mediate the antagonistic regulation of GA and JA on plant height traits.	Um <i>et al.</i> , 2018
JA	<i>WD repeat / bHLH / MYB complex</i>	Interact directly with DELLA and <i>jazs</i> to jointly regulate the development of trichrome	Qi <i>et al.</i> , 2014
JA	<i>HbGAI</i>	Regulate latex formation by mediating JA or ET signal transduction	Shaohua <i>et al.</i> , 2015
BR	<i>BZR1</i>	Interact with DELLA to mediate the cross dialogue between GA and BR, so as to realize the joint regulation of cell elongation and plant growth.	Bai <i>et al.</i> , 2012; Li <i>et al.</i> , 2012
BR	<i>SPY (SPINDLY)</i>	Enhance the interaction between DELLA proteins and <i>BZR1</i> transcription factors, resulting in different physiological effects on plants.	Zentella <i>et al.</i> , 2017

Cytokinin (CK)

CK is involved in plant development regulation, including apical dominance, taproot elongation and vascular bundle formation. DELLA proteins are also related to the signal transduction pathway and biosynthesis of CK, thus leading to induce its mechanism in plant growth and development. CK promotes the expression of *GAI* and *RGA* by inhibiting the expression of *GA3ox* (Dai and Xue, 2010). There is an

antagonistic effect between GA and CK. When CK and GA were used alone, they could promote and inhibit the accumulation of anthocyanin, but GA inhibited the effect of CK when they were used together. Similarly, GA and CK exhibited antagonistic effects on various processes in tomato (Fleishon *et al.*, 2011). Likewise, when plants were responded to abiotic stress, the expression of the GA response gene and CK metabolism gene were up-regulated (Qin *et al.*, 2011). Previous studies reported that CK and GA played an antagonistic role in regulating various physiological processes of plants. *SPINLY* (*SPY*), as the coding gene of *O-GlcNAc* transferase in *Arabidopsis*, functionally inhibited GA signal transduction and promoted CK response. The earlier studies have shown that *SPY* can enhance its interaction with other transcription factors by mono-O-fucosylated DELLA proteins (Zentella *et al.*, 2017). DELLA proteins RGA and GAI interacted directly with Type-B ARR response regulators in the CK signaling pathway to form a transcriptional activator complex to jointly regulate the expression of CK response genes (Marín-de la Rosa *et al.*, 2014). This molecular mechanism can well explain that DELLA proteins regulate the CK signaling pathway and enhance growth and development.

Abscisic acid (ABA)

ABA, as a major hormone regulating plant response to stress, is also involved in the regulation of seed dormancy and germination, cell division and elongation, stomatal closure and fruit abscission (Liu *et al.*, 2016). During rice seed germination, AP2-like transcription factor mediated their antagonistic effects. *OsAP2-39* maintained the balance of ABA and GAs in plants by regulating the expression of ABA and GAs key synthase (Yaish *et al.*, 2010). In *Arabidopsis*, ABA treatment increased the expression of *GA2ox6* by reducing the expression of *GA2ox1*. To affect the GAs synthesis, ABA inhibited root growth by regulating the stability of DELLA proteins and acted on the downstream of *DELLA* genes (Achar *et al.*, 2006). Meanwhile, DELLA proteins promoted ABA synthesis by enhancing the expression of its target gene *XERICO* and eliminating the impact of GAs so as to improve plant drought resistance (Ko *et al.*, 2006; Zentella *et al.*, 2007). In addition, ABA and JA affected leaf and flower development by jointly regulating the expression of DELLA proteins. In the process of rice seed germination, the balance of GA and ABA *in vivo* were maintained by the transcription factor AP2-like (Yaish *et al.*, 2010). DELLA proteins could promote E3 ligase gene expression in response to abiotic stress so as to reduce GA content, increase ABA content and reduce the harm caused by abiotic stress (Zhang *et al.*, 2011). DELLA proteins in *Arabidopsis* were known to promote ABA biosynthesis in seeds and enhance ABA signaling under stress conditions. *ABI3* (*Abscisic acid insensitive3*) and *ABI5* transcription factors, as core regulatory proteins in the ABA signal transduction pathway, could interact with DELLA proteins to jointly induce the expression of *SOMNUS* (*SOM*) gene to mediate the inhibition of high temperature on seed germination (Lim *et al.*, 2013). Previous studies have found that PIF1, a key transcription factor in the light signaling pathway, inhibited seed germination by promoting the expression of *ABI5* and *DELLA* genes. Studies have further proved that the expression of *MOTHER-OF-FT-AND-TFL1* (*MFT*) gene was induced by far-infrared light, which depended on the PIF1 / SOM / ABI5 / DELLA regulation mode participated by ABI5 and DELLA proteins, thereby inhibiting seed germination (Vaistij *et al.*, 2018). It was found that three members of *NF-YC* (*NUCLEAR FACTOR-YC*) in *Arabidopsis*, were involved in the regulation of seed germination mediated by GA and ABA. This process depended on the interaction between NF-YC and DELLA proteins and induced *ABI5* expression by directly targeting the *ABI5* promoter, thereby affecting the expression of a series of GA and ABA response genes (Liu *et al.*, 2016). Recently, a breakthrough has been made in the further analysis of the regulation mechanism. It was found that *ABI5* protein could interact with the low-temperature responsive protein ICE1 (INDUCER OF CBF EXPRESSION 1) to form a complex. *ICE1* negatively regulated ABA signal transduction by antagonizing the transcriptional activity of *ABI5*, thereby regulating the expression of downstream ABA response genes. In addition, DELLA proteins could also interact with *ICE1* to form a transcriptional complex so as to inhibit the transcriptional activity of *ICE1* and its regulation of *ABI5*. This study further enriched the molecular mechanism of GA-ABA co-

regulating plant seed germination mediated by the *DELLA-ABI5* interaction motif (Hu *et al.*, 2019). Therefore, ABA can improve plant resistance and yield by regulating DELLA proteins levels.

Ethylene (ET)

The activation of the ET signal can delay the degradation of DELLA proteins and inhibit the growth of roots. At the same time, ET relied on the CTR1 (Constitutive Triple Response1) signal transduction pathway to delay the degradation of DELLA proteins; ET could also maintain the apical hook by regulating the downstream GAs signal and regulating the expression of *DELLA* genes (Achard *et al.*, 2003). The key genes *ACS5* and *ACS8* of ethylene synthesis were also regulated by DELLA proteins and affected the development of apical hook together with PIN vector (An *et al.*, 2012). DELLA proteins interacted with the DNA binding domain of the ET signal pathway component *EIN3 / EIL1* protein to inhibit its regulation of the expression of downstream *HLS1* gene and affected the development of vertex hook (An *et al.*, 2012). The expression of *RhGAIL* gene in rose was regulated by *EIN3*, and *RhGAIL* protein could bind to the promoter of downstream gene *RhCesA2*, controlling the growth of rose petal cells (Luo *et al.*, 2013). ET pathway gene *AtERF11* also participated in GAs signal transduction. *AtERF11* enhanced GA signaling by antagonizing the function of DELLA proteins (Zhou *et al.*, 2016). ET increased DELLA proteins accumulation by reducing GAs biological activity, thus inhibiting the expression of *LFY* and *SOCI* to delay flowering (Chappie *et al.*, 2007). ET could inhibit the biological activity of gibberellin and increase the concentration of DELLA proteins in the nucleus so as to inhibit flowering gene and delay flowering (Achard and Harberd, 2007). Therefore, rational use of ET to regulate DELLA proteins is conducive in the improvement of plant stress resistance and productivity.

Jasmonic acid (JA)

As a kind of hormone widely existing in plants, JA plays an important role in regulating plant response to environmental stress and pathogen invasion. JA and GA can synergistically or antagonistically regulate plant development. Studies have shown that in the defense response of plants, JA antagonized the effect of GA mainly by regulating the stability of DELLA inhibitor and interfering with its interaction with PIF growth promoting factors (Navarro *et al.*, 2008). For example, the interaction between DELLA and JAZs (JA ZIM-domain) woke their inhibitory effect on their respective downstream transcription factors, while GA signal could induce DELLA degradation to eliminate the interaction between DELLA and JAZ. The released JAZs combined with downstream MYC2 transcription factors to weaken their activity and finally inhibited root growth. DELLA could interact with downstream PIF3 transcription factor and hinder its regulation of downstream target gene expression, inhibiting hypocotyl elongation (Hou *et al.*, 2010). Studies had shown that DELLA protein SLR1 in rice also interacted directly with *OsJAZ8* and *OsJAZ9* of JAZ family, mediating the antagonistic regulation of GA and JA on plant height traits (Um *et al.*, 2018). In addition to antagonism, GA and JA could also synergistically regulate stamen development and induce the initiation of trichomes. WD repeat / bHLH / MYB complex was a direct target of DELLA and JAZ interaction, and its activation required GA and JA signal transduction. At the same time, the essential components of WD repeat / bHLH / MYB complex interacted directly with DELLA and JAZs to jointly regulate the development of trichomes (Qi *et al.*, 2014). It was also found that *HbGAI* gene of rubber regulated latex formation by mediating JA or ET signal transduction (Wu *et al.*, 2015). In addition, DELLA proteins also resisted biological stress by regulating the balance of JA and salicylic acid (SA) in plants (Navarro *et al.*, 2008).

Brassinolide (BR)

BR is a kind of plant steroid hormone, which is widely involved in the regulation of a series of plant growth and development processes, including cell elongation, vascular bundle development and seed germination (Anwar *et al.*, 2018). Early physiological studies explored the interaction between BR and GA from the aspects of plant hypocotyl elongation, seed germination and plant flowering. The main regulatory mechanism of *Arabidopsis* hypocotyl elongation is that DELLA proteins affect BR signal transduction by

reducing BZR1 stability and inhibiting BZR1 DNA binding ability, while GA induce DELLA proteins degradation will enhance BR signal accordingly. Therefore, the direct interaction between DELLA and BZR1 mediated the cross dialogue between GA and BR, so as to realize the joint regulation of cell elongation and plant growth (Bai *et al.*, 2012; Li *et al.*, 2012). Further studies showed that the post-translational modification of DELLA proteins would affect the intensity of its interaction with BZR1. Fucosylation modification mediated by SPY (SPINDLY) enhanced the interaction between DELLA proteins and BZR1 transcription factors, resulting in different physiological effects on plants (Zentella *et al.*, 2017). In addition to the interaction model based on the core elements of signal pathway, the researchers also proposed an interaction model based on hormone synthesis regulation that BR could co-regulate plant growth by regulating GA level in plants (Tong *et al.*, 2014). Both BR and GAs promoted hypocotyl elongation in *Arabidopsis*, but when BR signal was absent, GAs had little effect on hypocotyl elongation, indicating that GAs regulated hypocotyl elongation dependent on BR (Bai *et al.*, 2012). In the presence of exogenous GAs, DELLA proteins was degraded, but BZR1 transcription factor was released, activating downstream response gene expression (Li *et al.*, 2012). Only in the dephosphorylated state, the transcription factors BZR1 and BES1 in BR signal transduction activated the expression of BR response genes, but DELLA proteins could specifically interact with dephosphorylated *BZR1* and *BES1* to inhibit BR signal transduction (Gallego-Bartolomé *et al.*, 2012).

DELLA proteins respond to environmental signals

Environmental stress hinders the normal growth and development of plants. At this time, the higher the content of DELLA proteins, the stronger the resistance of plants to stress, as presented in Figure 3.

Salt stress

High salt will inhibit root water intake, destroy root physiological function, affect upward transportation of root water and reduce plant growth rate (Zhu, 2002). When plants are subjected to salt stress, the survival rate of DELLA proteins function deficient mutants is low (Figure 3) (Achard *et al.*, 2006). In *Arabidopsis* the higher the content of DELLA proteins, the stronger its salt tolerance, and vice versa (Fuentes *et al.*, 2012). Salt stress promotes the accumulation of DELLA proteins by inhibiting GAs signal transduction, thus inhibiting plant growth and improving plant salt tolerance (Magome *et al.*, 2010). In soybean, salt stress forced the accumulation of DELLA proteins, and when exogenous GAs was applied to degrade DELLA proteins, the growth inhibition of soybean under salt stress would be offset (Zhang *et al.*, 2011). High salt stress mainly promoted the accumulation of DELLA proteins by activating ABA signal transduction, resulting in the increase of plant ACS expression and ET content, which enhanced plant tolerance to stress (Figure 3) (Wang *et al.*, 2002). DELLA proteins and SCL protein were integrated into ABA pathway through GA reaction to increase plant tolerance of abiotic stress (Gollmack *et al.*, 2013). In addition, in *Arabidopsis* (Zhu, 2002) and wheat (Wang *et al.*, 2016), DELLA proteins enhanced the ability of scavenging reactive oxygen by increasing the activities of catalase (CAT) and superoxide dismutase (SOD) under salt stress, so as to improve the salt resistance of plants.

Drought stress

During drought stress, ABA signal transduction pathway in plants is activated. ABA positively regulated *SnRK2s* to promote stomatal closure and reduce water loss of plants under drought stress (Acharya *et al.*, 2013; Pantin *et al.*, 2013), but GAs inhibited ABA signal transduction by reducing *SnRK2s* activity (Figure 3) (Lin *et al.*, 2015). Osmotic stress can inhibit GAs synthesis and stabilize DELLA proteins level. In soybean, DELLA could interact with ABA, IAA, PYRIPL, SAUR, GID2, CYCD3 in GAs and BR signal transduction pathways, which also enhanced the expression of *MYC2* in JA signal transduction pathway (Colebrook *et al.*, 2014). In tomato guard cells, DELLA proteins promoted stomatal closure and reduced water loss by improving the

sensitivity of plants to ABA, enhancing drought resistance (Nir *et al.*, 2017). In *Medicago sativa*, *MsGAI* gene participated in the stress response of drought by cooperating with ABA (Zhang *et al.*, 2019). Therefore, DELLA proteins improve plant drought resistance by mediating the transduction of various hormones and environmental signals, which needs further research.

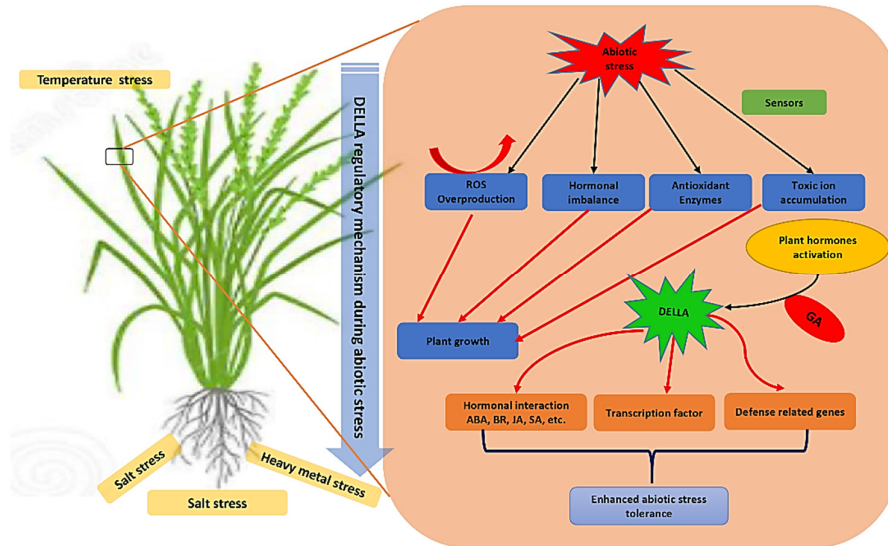


Figure 3. The regulatory mechanism of DELLA proteins in abiotic stress tolerance. DELLA interact with plant hormones to activate plant stress responses

Low temperature stress

Low temperature stress leads to differences in plant gene expression, changes in cell morphology and function, which in turn leads to plant damage and even death at the physiological and metabolic levels (Figure 3). It was found that low temperature stress increased the expression of *CBF1* gene and promoted the expression of *GA2ox3* and *GA2ox6* genes, resulting in the decrease of GA contents (Zhou *et al.*, 2017). Some studies indicated that after GA3 treatment, the expression of *GAI* gene decreased and the expression of *CBF1* gene increased, thus improving the cold resistance of tomato (Achard *et al.*, 2008a). In summary, the accumulation of DELLA proteins inhibited plant growth and development, but the cold resistance was enhanced.

Reactive oxygen species (ROS)

DELLA proteins regulates the adaptability of plants to stress environment by regulating the contents of ROS (Achard *et al.*, 2008b). As a second messenger, ROS played a pivotal role in stress response. Under stress, DELLA proteins reduced the content of ROS by up-regulating the expression and activity of ROS detoxifying enzyme, which delayed cell programmed death and enhanced plant stress resistance (Achard *et al.*, 2007; Gapper and Dolan, 2006). DELLA proteins inhibited root cell expansion and regulated root growth by regulating the content of ROS as shown on Figure 3 (Gapper and Dolan, 2006). ROS can also improve plant stress resistance by regulating ABA and GAs signals (Tsukagoshi, 2016). In short, DELLA proteins can inhibit plant growth and enhance its resistance by regulating ROS contents and activating plant defense.

Table 3. The responses of DELLA genes to different kind of abiotic stresses

Stress	Related gene	Function	References
Salt stress	<i>GA2ox7</i>	Promote the accumulation of DELLA proteins by inhibiting GAs signal transduction.	Magome <i>et al.</i> , 2010
Salt stress	<i>ACS</i>	Promote the accumulation of DELLA proteins by activating ABA signal transduction, resulting in the increase of plant ABA expression and ET contents.	Wang <i>et al.</i> , 2002
Salt stress	<i>SCL</i>	DELLA proteins and SCL protein were integrated into ABA pathway through GA reaction to increase plant tolerance of abiotic stress.	Golldack <i>et al.</i> , 2013
Salt stress	<i>OsMYB91</i>	DELLA proteins enhance the ability of scavenging reactive oxygen species by increasing the activities of CAT and SOD under salt stress, so as to improve the salt resistance of plants.	Zhu, 2002; Wang <i>et al.</i> , 2016
Drought stress	<i>SnRK2s</i>	SnRK2s can be inhibited by GA from reducing water loss of plants under drought stress.	Lin <i>et al.</i> , 2015
Drought stress	<i>MYC</i>	DELLA can interact with <i>phytochrome interaction</i> factors (<i>PIFS</i>), which can also enhance the expression of <i>MYC2</i> in JA signal transduction pathway.	Colebrook <i>et al.</i> , 2014
Drought stress	<i>DELLA</i>	DELLA proteins promote stomatal closure and reduced water loss by improving the sensitivity of plants to ABA, enhancing drought resistance.	Nir <i>et al.</i> , 2017
Drought stress	<i>MsGAI</i>	Participate in the stress response of drought by cooperating with ABA.	Zhang <i>et al.</i> , 2019
Low temperature stress	<i>GAI</i>	Interact with <i>CBF1</i> , thus improving the cold resistance of tomato.	Achard <i>et al.</i> , 2008a
Reactive oxygen species	<i>DELLA</i>	Reduce the content of ROS to enhance plant stress resistance.	Achard <i>et al.</i> , 2007
Reactive oxygen species	<i>DELLA</i>	Inhibit root cell expansion and regulate root growth by regulating the content of ROS.	Tsukagoshi, 2016
Phosphorus stress	<i>SPY</i>	Overexpression of DELLA protein will strengthen plant phosphorus starvation.	Hauvermale <i>et al.</i> , 2012
Phosphorus stress	<i>GA20ox</i> and <i>GA3ox</i>	Accumulate DELLA proteins by reducing the transcription of <i>GA20ox</i> and <i>GA3ox</i> , and inhibit plant growth and improve phosphorus stress tolerance.	Morcillo <i>et al.</i> , 2020

Phosphorus stress

Phosphorus is a necessary element for plant growth. In order to maintain normal growth, plants have evolved various response measures to adapt to low phosphorus, in which the typical response mechanism is to change the root state and anthocyanin accumulation (Caifu and Fu, 2007). The low phosphorus response of *Arabidopsis* depends on the signal transduction regulated by DELLA proteins. Reducing the content of DELLA proteins or exogenous spraying GAs could inhibit phosphorus starvation. Quadruple-DELLA mutant could inhibit the flowering delay caused by phosphorus deficiency, and the overexpression of DELLA proteins would strengthen plant phosphorus starvation (Hauvermale *et al.*, 2012). In fact, phosphorus starvation accumulated DELLA proteins by reducing the transcription of *GA20ox* and *GA3ox*, so as to inhibit plant growth and development and improve its tolerance to phosphorus stress (Morcillo *et al.*, 2020).

DELLA proteins regulate plant growth and development

Plant growth and development will be affected by external environment and hormones, and DELLA proteins are integrated factors in the response of a variety of hormone signals and environmental signal systems as presented in Figure 4.

Seed germination

Seed germination is not only related to external environmental factors such as light, temperature and water, but also closely related to the regulation of internal hormones. Studies have shown that GA releases its inhibition of seed germination through the degradation of DELLA proteins. The loss of function of the 4 *DELLA* genes (*RGL2*, *RGL1*, *RGA* and *GAI*) could make seeds germinate in the absence of light and GA. The loss-of-function DELLA-mutants such as *gai-t6* showed enhanced germination (Kucera *et al.*, 2005). Under

light, light degraded *PIL5* through phytochrome and induced the accumulation of GA, so as to degrade *DELLA* proteins and start seed germination. Studies in *Arabidopsis* showed that *PIL5* activated the expression of DELLA proteins by binding to the promoter of DELLA proteins in the dark. Under a suitable environment, the GA level increased, but *RGL2* was degraded and seeds germinated. In *Arabidopsis*, *RGL2* protein inhibited seed germination by promoting the expression of *XERICICO* gene, which promoted ABA synthesis and then inhibited seed germination (Lee *et al.*, 2002; Lim *et al.*, 2013). DELLA proteins can also directly interact with *ABI3* and *ABI5* to up-regulate the expression of downstream gene *SOM*, and then regulate seed germination as presented in Figure 4 (Cao and Peng, 2006). The loss-of-function DELLA-mutants of *gai-t6* showed enhanced germination (Kucera *et al.*, 2005) It can be concluded that DELLA proteins inhibit seed germination by mediating hormone and light signal transduction.

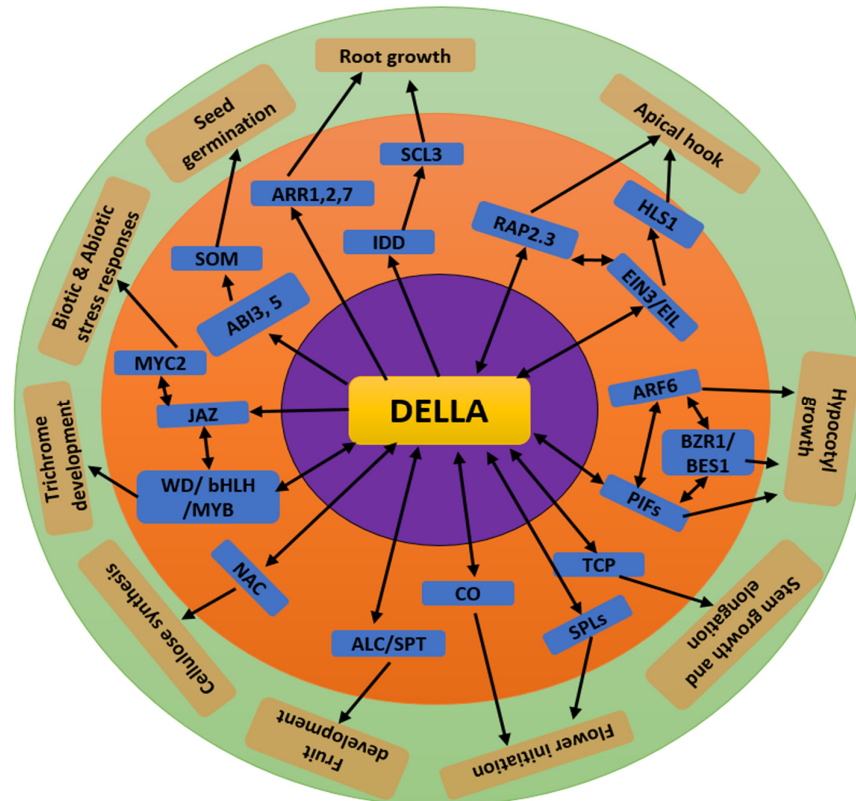


Figure 4. The interaction and correlation of transcription factor with DELLA during plant growth and developments including biotic and abiotic stress, plant growth to flower initiation and seed developments

Development of apical hook

GAs and ET regulate the development of apical hook by regulating the IAA biosynthesis. DELLA proteins played a very important role in regulation early apical hook developmental process. Previous study reported that, the deletion of DELLA proteins could increase the bending degree of apical hook developments (Gallego-Bartolomé *et al.*, 2011). The DELLA proteins affected the gravitational reorientation and apical hook of plants by regulating the gene *PIN7* related to IAA transport (Gallego-Bartolomé *et al.*, 2011). DELLA can also affect the concave growth of the apical hook by regulating the *WAG2* gene. The growth of the apical hook and the establishment of the IAA gradient of dark-growing *wag2* mutants are affected (Willige *et al.*, 2012). In addition, ET synthesis key genes *ACS5* (*ACC SYNTHASE5*) and *ACS8* have also been shown to be regulated and expressed by the DELLA proteins in the development of apical hook (Gallego-Bartolomé *et al.*, 2011; An *et al.*, 2012). ET plays an important role in the formation and maintenance of apical hooks by regulating the

downstream GA signal and the expression of DELLA proteins. The *gai* mutant could only form small apical hook in the presence of exogenous ET (Achard *et al.*, 2003). As shown in Figure 4, DELLA proteins regulated the effect of ET on plant apical bending growth by inhibiting the activity of *EIN3* (*Ethylene Insensitive 3*) (An *et al.*, 2012). In addition, *GAI* and *RAP2-3* transcription factors jointly mediated the regulation of GAs and ET on apical bending growth of *Arabidopsis*. The interaction between DELLA proteins and *EIN3/EILs* complex could counteract the promotion of ET on apical hook development (Marín-de la Rosa *et al.*, 2014). DELLA proteins inhibited the formation of hook structure of etiolated seedlings, and this inhibition was reversed by GA (Achard *et al.*, 2003). The etiolated seedlings of GA deficient type (*gai-3*) insensitive to GA did not show hook structure, but showed hook structure in etiolated seedlings of *GAI* and RGA deficient type: *gai-3gai-t6rga-24* (Cheng *et al.*, 2019).

Hypocotyl elongation

The elongation of seedling hypocotyl depends on the joint regulation of BR, IAA, GAs, light and temperature. DELLA proteins, as the node of the cross-action of these signals, are very important for hypocotyl elongation. DELLA deficient mutants were hypersensitive to exogenous BR, but the mutants with *GAI* function had a weak response to exogenous BR (Stewart Lilley *et al.*, 2013). Light promoted DELLA accumulation by inhibiting GAs synthesis. Further, it prevented PIF3 from binding to its target gene promoter and inhibited hypocotyl elongation (Feng *et al.*, 2008). *PIF4*, *BZR* and *ARF6* interacted to form a functional complex and stimulated the expression of gene *PRE* related to cell elongation (Figure 4). DELLA could bind to this complex, inhibiting its transcriptional activity and hypocotyl elongation of bamboo nodes (Eunkyoo *et al.*, 2014).

Plant dwarfing

DELLA mutant plants usually have two forms: GAs insensitive dwarfing phenotype and GAs sensitive slender phenotype. Mutation of DELLA domain at the N-terminal of DELLA proteins would cause plant dwarfing, because the mutation of DELLA domain couldn't sense GAs signal, thus affecting downstream response and plant dwarfing and exogenous spraying of GAs could not restore the wild phenotype of plants (Ito *et al.*, 2018). *SLEEPY1* (*SLY1*) encoded an F-box-containing protein, and the loss-of-function *slY1* mutant of RGA had a GA-insensitive dwarf phenotype (Dill *et al.*, 2004). In rice, DELLA could interact with *HD2* protein and participate in the regulation of rice plant height (Li *et al.*, 2015). *Brassica napus* transformed with *BnaA6. rga-ds* obtained dwarfing phenotype, and it showed that *BnaA6. rga-ds* gene had the ability to control the plant height of *Brassica napus* (Wu *et al.*, 2020). When *FveRGA1* gene was transferred into wild-type strawberries, plants would produce stolons (Li *et al.*, 2018). For example, *DS-3* in rape encoded a DELLA protein, negatively regulated the elongation of rape stems (Zhao *et al.*, 2017). At the same time, the structural integrity of DELLA proteins itself is very important for normal plant growth. It was reported that the deletion of 17 amino acids in the DELLA domain of *Arabidopsis* DELLA proteins led to the dwarf phenotype of *Arabidopsis* (Peng and Harberd, 1997). A missense mutation in the VHYNP motif of DELLA proteins caused a semi-dwarf mutant phenotype in *Brassica napus* (Liu *et al.*, 2010). However, mutations at the C-terminal of DELLA proteins often make plants show an overgrowth phenotype, which is called invisible mutations, such as *rga* and *rgl* of *Arabidopsis thaliana*, *slr1* of rice, *sln1c* of barley and *tht* of wheat (Chandler *et al.*, 2002; Dai and Xue 2010; Itoh *et al.*, 2002). It was found that DELLA proteins mutants in plants often change plant morphology, inhibit the elongation of plant stems, and then cause plant dwarf growth. Therefore, in agricultural production, the expression level of DELLA proteins can be regulated by gene transfer to realize plant dwarfing.

Root elongation

Plants jointly regulate their growth rate through cell proliferation and expansion. GAs eliminated the inhibition of DELLA proteins on taproot growth by promoting DELLA proteins degradation, and the

weakening of IAA transport or signal pathway would also slow down DELLA proteins degradation (Figure 4) (Chandler *et al.*, 2002). The density and length of lateral roots of poplar GA synthesis deficient plants and GA insensitive plants were larger than those of wild type, because GA negatively regulated lateral root formation by inhibiting the initiation of LRP (Gou *et al.*, 2010). In the legume *Centaurus* root, DELLA interacted with *IPN2*, *NSP2* and *CYPs*, which formed protein complexes to regulate the spatial expression of initial nodulation genes and affect the production of rhizobia (Fan *et al.*, 2019). It shows that DELLA proteins are very important for the growth and development of plant roots.

Flower development

DELLA proteins are very important for plant flower bud development and morphogenesis. ET promoted DELLA proteins accumulation by down regulating GA synthesis and metabolism genes, resulting in late flowering (Figure 4) (Achar *et al.*, 2003). The DELLA proteins RGA and GAI in *Arabidopsis* induced flower formation (King *et al.*, 2001), while RGL1 and RGL2 jointly regulated flower development (Cheng *et al.*, 2004; Tyler *et al.*, 2004). In the GA signaling pathway, there are two key genes to promote flowering: *SOC1* (*Suppressor Overexpression of Co 1*) and *AGL24* (*Agamouslike 24*). Under the condition of short sunlight, the expression of *SOC1* could hardly be detected in *ga1-3* mutant, indicating that GA played a key role in regulating the expression of *SOC1*. Exogenous application of GA would induce the increase of *AGL24* transcription level, and this signal response depended on *SOC1* (Moon *et al.*, 2003). Some studies compared transcriptomes in developing flowers of *ga1-3*, *ga1-3/gai-t6/rga-t1/rgl1-1/rgl2-1*, and wild-type plants, which revealed that GA could regulate downstream genes during flower development in a DELLA relevant manner (Cao *et al.*, 2006). In the process of releasing flower bud dormancy at low temperatures, the expression of *PsGRAS1* gene of peony was down-regulated, which was consistent with that of plum blossom (Wu *et al.*, 2019). DELLA proteins can not only release flower bud dormancy, but also delay flowering period. Therefore, by regulating the expression of *DELLA* genes, plants could bloom in advance and prolong flowering period, so as to increase economic value.

Conclusions

DELLA proteins are key repressors of GA signaling, acting as a negative regulator involved in plant growth and developments. In the past decade, numerous studies have been carried out to explore the molecular mechanism and interaction of GA and DELLA proteins. DELLA proteins are potentially involved in contribution plant growth and developmental process through correlation with hormone signaling pathway. Additionally, GA stimulate DELLA proteins interaction to control/overcome on dynamic character and abiotic stress tolerance in plants. The understanding DELLA proteins and its regularity network are not fully understood; we need to focus on following points. A) identification of downstream genes of DELLA proteins that regulate abiotic stress tolerance. B) Characterization of DELLA posttranscriptional regulatory network under abiotic stress C) The interaction of DELLA proteins and hormones are not fully understood. D) The co-activator roles for transcription factors and gene expression need to be explored, which can be helpful for future genetic improvement and enhanced crop production.

Authors' Contributions

Conceptualization: QYZ, AA and FDW; Data curation: HMZ and SZ; Funding acquisition: JWG and FDW; Project administration: JWG, FW and LLH; Supervision: FDW; Writing original draft: QYZ, AA; Writing review and editing: SZ, LLH, FDW and HMZ.

All authors read and approved the final manuscript.

Acknowledgements

This study was supported by the Taishan Scholars Program of Shandong Province, China (tsqn201909167); Key R & D Program of Shandong Province, China (2019GHZ014); Shandong Upgraded Project of “Bohai Granary” Science and Technology Demonstration Engineering in 2019; Prospect of Shandong Seed Project, China (2019LZGC0060101); Agricultural Science and Technology, Innovation Project of SAAS (CXGC2021A10); Jinan City Agricultural Application Technology 334Innovation Plan Project (202009).

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

References

- Achard P, Baghour M, Chapple A, Hedden P, Van Der Straeten D, Genschik P, ... Harberd NP (2007). The plant stress hormone ethylene controls floral transition via DELLA-dependent regulation of floral meristem-identity genes. *Proceedings of the National Academy of Science, USA* 104:6484-6489. <https://doi.org/10.1073/pnas.0610717104>
- Achard P, Baghour M, Chapple A, Hedden P, Van Der Straeten D, Genschik P, ... Harberd NP (2007). The plant stress hormone ethylene controls floral transition via DELLA-dependent regulation of floral meristem-identity genes. *Proceedings of the National Academy of Sciences* 104(15):6484-6489. <https://doi.org/10.1073/pnas.0610717104>
- Achard P, Cheng H, De Grauwe L, Decat J, Schoutteten H, Moritz T, ... Harberd NP (2006). Integration of plant responses to environmentally activated phytohormonal signals. *Science* 311(5757):91-94. <http://dx.doi.org/10.1126/science.1118642>
- Achard P, Gong F, Cheminant S, Alioua M, Hedden P, Genschik P (2008a). The cold-inducible CBF1 factor-dependent signaling pathway modulates the accumulation of the growth-repressing DELLA proteins via its effect on gibberellin metabolism. *The Plant Cell* 20:2117-2129. <https://doi.org/10.1105/tpc.108.058941>
- Achard P, Renou JP, Berthomé R, Harberd NP, Genschik P (2008b). Plant DELLAs restrain growth and promote survival of adversity by reducing the levels of reactive oxygen species. *Current Biology* 18:656-660. <https://doi.org/10.1016/j.cub.2008.04.034>
- Achard P, Vriezen WH, Van Der Straeten D, Harberd NP (2003). Ethylene regulates *Arabidopsis* development via the modulation of DELLA proteins growth repressor function. *The Plant Cell* 15:2816-2825. <https://doi.org/10.1105/tpc.015685>
- Acharya BR, Jeon BW, Zhang W, Assmann SM (2013). Open Stomata 1 (OST1) is limiting in abscisic acid responses of *Arabidopsis* guard cells. *New Phytologist* 200:1049-1063. <http://dx.doi.org/10.1111/nph.12469>
- An F, Zhang X, Zhu Z, Ji Y, He W, Jiang Z, Li M, Guo H (2012). Coordinated regulation of apical hook development by gibberellins and ethylene in etiolated *Arabidopsis* seedlings. *Cell Research* 22:915-927. <https://doi.org/10.1038/cr.2012.29>
- Anwar A, Liu Y, Dong R, Bai L, Yu X, Li Y (2018). The physiological and molecular mechanism of brassinosteroid in response to stress: a review. *Biological Research* 51. <https://doi.org/10.1186/s40659-018-0195-2>
- Asier BM, Jorge HG, Carlos VC, Romero-Campero FJ, Romero JM, Federico V, Blázquez M (2017). Evolutionary analysis of DELLA-associated transcriptional networks. *Frontiers in Plant Science* 8:626. <https://doi.org/10.3389/fpls.2017.00626>
- Bai MY, Shang JX, Oh E, Fan M, Bai Y, Zentella R, Sun TP, Wang ZY (2012). Brassinosteroid, gibberellin and phytochrome impinge on a common transcription module in *Arabidopsis*. *Nature Cell Biology* 14:810-817. <https://doi.org/10.1038/ncb2546>

- Binenbaum J, Weinstain R, Shani E (2018). Gibberellin localization and transport in plants. *Trends in Plant Science* 23:410-421. <https://doi.org/10.1016/j.tplants.2018.02.005>
- Bolle C (2004). The role of GRAS proteins in plant signal transduction and development. *Planta* 218:683-692. <https://doi.org/10.1007/s00425-004-1203-z>
- Cao D, Cheng H, Wu W, Soo HM, Peng J (2006) Gibberellin mobilizes distinct DELLA-dependent transcriptomes to regulate seed germination and floral development in *Arabidopsis*. *Plant Physiology* 142(2):509-525. <https://doi.org/10.1104/pp.106.082289>
- Cassani E, Bertolini E, Badone FC, Landoni M, Gavina D, Sirizzotti A, Pilu R (2009). Characterization of the first dominant dwarf maize mutant carrying a single amino acid insertion in the VHYNP domain of the dwarf8 gene. *Molecular Breeding* 24:375-385. <https://doi.org/10.1007/s11032-009-9298-3>
- Chandler PM, Marion-Poll A, Ellis M, Gubler F (2002). Mutants at the Slender1 locus of barley cv Himalaya. Molecular and physiological characterization. *Plant Physiology* 129:181-190. <https://doi.org/10.1104/pp.010917>
- Cheng H, Qin L, Lee S, Fu X, Richards DE, Cao D, ... Peng J (2004). Gibberellin regulates *Arabidopsis* floral development via suppression of DELLA protein function. *Development* 131:1055. <https://doi.org/10.1242/dev.00992>
- Cheng J, Zhang M, Tan B, Jiang Y, Zheng X, Ye X, ... Li J (2019). A single nucleotide mutation in GID1c disrupts its interaction with DELLA1 and causes a GA-insensitive dwarf phenotype in peach. *Plant Biotechnology Journal* 17:1723-1735. <https://doi.org/10.1111/pbi.13094>
- Colebrook EH, Thomas SG, Phillips AL, Hedden P (2014). The role of gibberellin signalling in plant responses to abiotic stress. *Journal of Experimental Biology* 217:67-75. <https://doi.org/10.1242/jeb.089938>
- Dai C, Xue HW (2010). Rice early flowering1, a CKI, phosphorylates DELLA proteins SLR1 to negatively regulate gibberellin signalling. *Embo Journal* 29:1916-1927. <https://doi.org/10.1038/emboj.2010.75>
- Dill A, Thomas SG, Hu J, Steber CM, Sun TP (2004). The *Arabidopsis* F-box protein SLEEPY1 targets gibberellin signaling repressors for gibberellin-induced degradation. *Plant Cell* 16:1392-1405. <https://doi.org/10.1105/tpc.020958>
- Du J, Jiang H, Sun X, Li Y, Liu Y, Sun M, ... Yang W (2018). Auxin and gibberellins are required for the receptor-like kinase ERECTA regulated hypocotyl elongation in shade avoidance in *Arabidopsis*. *Frontiers in Plant Science* 9:124. <https://doi.org/10.3389/fpls.2018.00124>
- Eunkyo O, Zhu JY, Bai MY, Augusto AR, Yu S, Wang ZY (2014). Cell elongation is regulated through a central circuit of interacting transcription factors in the *Arabidopsis* hypocotyl. *eLife* 3:e03031. <https://doi.org/10.7554/eLife.03031>
- Fan Y, Xiao A, Zhang Z (2019). Identification of interaction between transcription factors involved in initiation of nodulation in *Lotus japonicus*. *Journal of Huazhong Agricultural University* 38:10-15
- Feng S, Martinez C, Gusmaroli G, Wang Y, Zhou J, Wang F, ... Deng XW (2008). Coordinated regulation of *Arabidopsis thaliana* development by light and gibberellins. *Nature* 451:475-479. <https://doi.org/10.1038/nature06448>
- Fleishon S, Shani E, Ori N, Weiss D (2011). Negative reciprocal interactions between gibberellin and cytokinin in tomato. *New Phytologist* 190:609-617. <https://doi.org/10.1111/j.1469-8137.2010.03616.x>
- Floss DS, Lévesque-Tremblay V, Park HJ, Harrison MJ (2016). DELLA proteins regulate expression of a subset of AM symbiosis-induced genes in *Medicago truncatula*. *Plant Signaling and Behavior* 11(4):e1162369.. <https://doi.org/10.1080/15592324.2016.1162369>
- Foster T, Kirk C, Jones WT, Allan A, Espley R, Karunairetnam S, Rakonjac J (2007). Characterization of the DELLA subfamily in apple (*Malus x domestica* Borkh.). *Tree Genetics and Genomes* 3:187-197. <https://doi.org/10.1007/s11295-006-0047-z>
- Fu X, Harberd NP (2003). Auxin promotes *Arabidopsis* root growth by modulating gibberellin response. *Nature* 421:740. <https://doi.org/10.1038/nature01387>
- Fuentes S, Ljung K, Sorefan K, Alvey E, Harberd NP, Ostergaard L (2012). Fruit growth in *Arabidopsis* occurs via DELLA-dependent and DELLA-independent gibberellin responses. *Plant Cell* 24:3982-3996. <https://doi.org/10.1105/tpc.112.103192>
- Gallego-Bartolomé J, Arana MV, Vandenbussche F, Ádníková P, Minguet EG, Guardiola V, ... Blázquez M (2011). Hierarchy of hormone action controlling apical hook development in *Arabidopsis*. *The Plant Journal* 67:622-634. <https://doi.org/10.1111/j.1365-313X.2011.04621.x>
- Gallego-Bartolomé J, Minguet EG, Grau-Enguix F, Abbas M, Locascio A, Thomas SG, Alabadi D, Blázquez MA (2012). Molecular mechanism for the interaction between gibberellin and brassinosteroid signaling pathways in

- Arabidopsis*. Proceedings of the National Academy of Science USA 109:13446-13451. <https://doi.org/10.1073/pnas.1119992109>
- Gallego-Bartolomé J, Minguet EG, Marín JA, Prat S, Blázquez MA, Alabadí D (2010). Transcriptional diversification and functional conservation between DELLA proteins in *Arabidopsis*. *Molecular Biology and Evolution* 27(6):1247-1256. <https://doi.org/10.1093/molbev/msq012>
- Gapper C, Dolan L (2006). Control of plant development by reactive oxygen species. *Plant Physiology* 141:341-345. <https://doi.org/10.2307/20205751>
- Golldack D, Li C, Mohan H, Probst N (2013). Gibberellins and abscisic acid signal crosstalk: living and developing under unfavorable conditions. *Plant Cell Reports* 32:1007-1016. <https://doi.org/10.1007/s00299-013-1409-2>
- Gomi K, Sasaki A, Itoh H, Ueguchi-Tanaka M, Ashikari M, Kitano H, Matsuoka M (2010). *GID2*, an F-box subunit of the SCF E3 complex, specifically interacts with phosphorylated SLR1 protein and regulates the gibberellin-dependent degradation of SLR1 in rice. *Plant Journal* 37:626-634. <https://doi.org/10.1111/j.1365-313X.2003.01990.x>
- Gou J, Strauss SH, Tsai CJ, Fang K, Chen Y, Jiang X, Busov VB (2010). Gibberellins regulate lateral root formation in *Populus* through interactions with auxin and other hormones. *Plant Cell* 22:623-639. <https://doi.org/10.1105/tpc.109.073239>
- Hauvermale AL, Ariizumi T, Steber CM (2012). Gibberellin signaling: a theme and variations on DELLA repression. *Plant Physiology* 160:83-92. <https://doi.org/10.1104/pp.112.200956>
- Hedden P (2003). The genes of the Green Revolution. *Trends in Genetic* 19:5-9. [https://doi.org/10.1016/s0168-9525\(02\)00009-4](https://doi.org/10.1016/s0168-9525(02)00009-4)
- Hou SW (2016). Prokaryotic Expression and Polyclonal Antibodies Preparation of the DELLA proteins-coding gene, RGA and GAI, in *Arabidopsis*. *Journal of Lanzhou University*.
- Hou X, Li Y, Xia K, Yan Y, Hao Y (2010). DELLAs modulate jasmonate signaling via competitive binding to JAZs. *Developmental Cell* 19:884-894. <https://doi.org/10.1016/j.devcel.2010.10.024>
- Hu Y, Han X, Yang M, Zhang M, Pan J, Yu D (2019). The transcription factor INDUCER OF CBF EXPRESSION1 interacts with abscisic acid Insensitive5 and DELLA proteins to fine-tune abscisic acid signaling during seed germination in *Arabidopsis*. *Plant Cell* 31:1520-1538. <https://doi.org/10.1105/tpc.18.00825>
- Ikeda A, Ueguchi-Tanaka M, Sonoda Y, Kitano H, Koshioka M, Futsuhara Y, Matsuoka M, Yamaguchi J (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* 13:999-1010. <https://doi.org/10.1105/tpc.13.5.999>
- Ito T, Okada K, Fukazawa J, Takahashi Y (2018). DELLA-dependent and -independent gibberellin signaling. *Plant Signaling and Behaviour* 13:e1445933. <https://doi.org/10.1080/15592324.2018.1445933>
- Itoh H, Ueguchi-Tanaka M, Sato Y, Ashikari M, Matsuoka M (2002). The gibberellin signaling pathway is regulated by the appearance and disappearance of SLENDER RICE1 in nuclei. *Plant Cell* 14:57-70. <https://doi.org/10.1105/tpc.010319>
- Jasinski S, Tattersall A, Piazza P, Hay A, Tsiantis M (2010). PROCERA encodes a DELLA protein that mediates control of dissected leaf form in tomato. *The Plant Journal* 56:603-612. <https://doi.org/10.1111/j.1365-313X.2008.03628.x>
- Javier GB, David A, Blázquez M, Mohammed B (2011). DELLA-induced early transcriptional changes during etiolated development in *Arabidopsis thaliana*. *Plos One* 6:e23918. <https://doi.org/10.1371/journal.pone.0023918>
- Jiang C, Gao X, Liao L, Harberd NP, Fu X (2007). Phosphate starvation root architecture and anthocyanin accumulation responses are modulated by the gibberellin-DELLA signaling pathway in *Arabidopsis*. *Plant physiology* 145(4):1460-1470. <https://doi.org/10.1104/pp.107.103788>
- Jutarou F (2014). DELLAs function as coactivators of GAI-ASSOCIATED FACTOR1 in regulation of gibberellin homeostasis and signaling in *Arabidopsis*. *The Plant Cell* 26:2920-2938. <https://doi.org/10.1105/tpc.114.125690>
- King KE, Moritz T, Harber DNP (2001). Gibberellins are not required for normal stem growth in *Arabidopsis thaliana* in the absence of GAI and RGA. *Genetics* 159:767-776.
- Kirungu JN, Magwanga RO, Lu P, Cai X, Liu F (2019). Functional characterization of Gh_A08G1120 (GH3.5) gene reveal their significant role in enhancing drought and salt stress tolerance in cotton. *BMC Genetics* 20:62. <https://doi.org/10.1186/s12863-019-0756-6>
- Kucera B, Cohn MA, Leubner-Metzger G (2005). Plant hormone interactions during seed dormancy release and germination. *Seed Science Research* 15:281-307. <https://doi.org/10.1079/SSR2005218>

- Lee S, Cheng H, King KE, Wang W, He Y, Hussain A, Lo J, Harberd NP, Peng J (2002). Gibberellin regulates *Arabidopsis* seed germination via RGL2, a GAI/RGA-like gene whose expression is up-regulated following imbibition. *Genes and Development* 16:646-658. <https://doi.org/10.1101/gad.969002>
- Li K, Yu R, Fan LM, Wei N, Chen H, Deng XW (2016). DELLA-mediated PIF degradation contributes to coordination of light and gibberellin signalling in *Arabidopsis*. *Nature Communications* 7:11868. <https://doi.org/10.1038/ncomms11868>
- Li QF, Wang C, Jiang L, Li S, Sun S, He JX (2012). An interaction between BZR1 and DELLAs mediates direct signaling crosstalk between brassinosteroids and gibberellins in *Arabidopsis*. *Science Signaling* 5:ra72. <https://doi.org/10.1126/scisignal.2002908>
- Li X, Liu H, Wang M, Liu H, Tian X, Zhou W, ... Bu Q (2015). Combinations of Hd2 and Hd4 genes determine rice adaptability to Heilongjiang Province, northern limit of China. *Journal of Integrative Plant Biology* 57:698-707. <https://doi.org/10.1111/jipb.12326>
- Liao WB, Ruan MB, Cui BM, Xu NF, Lu JJ, Ming P (2009). Isolation and characterization of a GAI/RGA-like gene from *Gossypium hirsutum*. *Plant Growth Regulation* 58:35-45. <https://doi.org/10.1007/s10725-008-9350-z>
- Lim S, Park J, Lee N, Jeong J, Toh S, Watanabe A, ... Choi G (2013). ABA-insensitive3, ABA-insensitive5, and DELLAs interact to activate the expression of SOMNUS and other high-temperature-inducible genes in imbibed seeds in *Arabidopsis*. *Plant Cell* 25:4863-4878. <https://doi.org/10.1105/tpc.113.118604>
- Lin Q, Wu F, Sheng P, Zhang Z, Zhang X, Guo X, ... Wan J (2015). The SnRK2-APC/C(TE) regulatory module mediates the antagonistic action of gibberellic acid and abscisic acid pathways. *Nature Communications* 6:7981. <https://doi.org/10.1038/ncomms8981>
- Liu C, Wang J, Huang T, Wang F, Liu K (2010). A missense mutation in the VHYNP motif of a DELLA proteins causes a semi-dwarf mutant phenotype in *Brassica napus*. *Theoretical and Applied Genetics* 121:249. <https://doi.org/10.1007/s00122-010-1306-9>
- Liu S, Xuan L, Xu LA, Huang M, Xu M (2016). Molecular cloning, expression analysis and subcellular localization of four DELLA genes from hybrid poplar. *SpringerPlus* 5:1-8. <https://doi.org/10.1186/s40064-016-2728-x>
- Luo J, Ma N, Pei H, Chen J, Li J, Gao J (2013). A DELLA gene, RhGAI1, is a direct target of EIN3 and mediates ethylene-regulated rose petal cell expansion via repressing the expression of RhCesA2. *Journal of Experimental Botany* 64:5075-5084. <https://doi.org/10.1093/jxb/ert296>
- Magome H, Yamaguchi S, Hanada A, Kamiya Y, Oda K (2010). The DDF1 transcriptional activator upregulates expression of a gibberellin-deactivating gene, GA2ox7, under high-salinity stress in *Arabidopsis*. *Plant Journal* 56:613-626. <https://doi.org/10.1111/j.1365-313X.2008.03627.x>
- Marín-de la Rosa N, Sotillo B, Miskolczi P, Gibbs DJ, Vicente J, Carbonero P, ... Blázquez MA (2014). Large-scale identification of gibberellin-related transcription factors defines group VII ETHYLENE RESPONSE FACTORS as functional DELLA partners. *Plant Physiology* 166:1022-1032. <https://doi.org/10.1104/pp.114.244723>
- Moon J, Suh SS, Lee H, Choi KR, Lee I (2003). The SOC1 MADS-box gene integrates vernalization and gibberellin signals for flowering in *Arabidopsis*. *Plant Journal* 35:613-623. <https://doi.org/10.1046/j.1365-313X.2003.01833.x>
- Morcillo RJL, Singh SK, He D, Vilchez JI, Kaushal R, Wang W, ... Zhang H (2020). Bacteria-derived diacetyl enhances *Arabidopsis* phosphate starvation responses partially through the DELLA-dependent gibberellin signaling pathway. *Plant Signaling and Behavior* 15:1740872. <https://doi.org/10.1080/15592324.2020.1740872>
- Murase K, Hlirano Y, Sun TP, *Hakoshima* T (2008). Gibberellin-induced DELLA recognition by the gibberellin receptor GID1. *Nature* 456:459-463. <https://doi.org/10.1038/nature07519>
- Navarro L, Bari R, Achard P, Lisón P, Nemri A, Harberd NP, Jones JDG (2008). DELLAs control plant immune responses by modulating the balance of jasmonic acid and salicylic acid signaling. *Current Biology* 18:650-655. <https://doi.org/10.1016/j.cub.2008.03.060>
- Nir I, Shohat H, Panizel I, Olszewski NE, Aharoni A, Weiss D (2017). The Tomato DELLA proteins PROCERA acts in guard cells to promote stomatal closure. *Plant Cell* 29:3186-3197. <https://doi.org/10.1105/tpc.17.00542>
- Pantin F, Monnet F, Jannaud D, Costa JM, Renaud J, Muller B, Simonneau T, Genty B (2013). The dual effect of abscisic acid on stomata. *New Phytologist* 197:65-72. <https://doi.org/10.1111/nph.12013>
- Peng J, Harberd NP (1997). Gibberellin deficiency and response mutations suppress the stem elongation phenotype of phytochrome-deficient mutants of *Arabidopsis*. *Plant Physiology* 113:1051-1058. <https://doi.org/10.1104/pp.113.4.1051>

- Peng J, Richards DE, Hartley NM, Murphy GP, Devos KM, Flintham JE, ... Pelica F (1999). 'Green revolution' genes encode mutant gibberellin response modulators. *Nature* 400:256-261. <https://doi.org/10.1038/22307>
- Phokas A, Coates JC (2021). Evolution of DELLA function and signaling in land plants. *Evolution and Development* 23:137-154. <https://doi.org/10.1111/ede.12365>
- Qin F, Kodaira KS, Maruyama K, Mizoi J, Tran LS, Fujita Y, ... Yamaguchi-Shinozaki K (2011). SPINDLY, a negative regulator of gibberellic acid signaling, is involved in the plant abiotic stress response. *Plant Physiology* 157:1900-1913. <https://doi.org/10.1104/pp.111.187302>
- Shen Q, Cui J, Fu XQ, Yan TX, Tang KX (2015). Cloning and characterization of DELLA genes in *Artemisia annua*. *Genetic and Molecular Research* 14:10037-10049. <https://doi.org/10.4238/2015>
- Stewart Lilley JL, Gan Y, Graham IA, Nemhauser JL (2013). The effects of DELLAs on growth change with developmental stage and brassinosteroid levels. *The Plant Journal* 76:165-173. <https://doi.org/10.1111/tpj.12280>
- Sun, T (2010). Gibberellin-GID1-DELLA: a pivotal regulatory module for plant growth and development. *Plant Physiology* 154:567. <https://doi.org/10.1104/pp.110.161554>
- Tong H, Xiao Y, Liu D, Gao S, Liu L, Yin Y, Jin Y, Qian Q, Chu C (2014). Brassinosteroid regulates cell elongation by modulating gibberellin metabolism in rice. *Plant Cell* 26:4376-4393. <https://doi.org/10.1105/tpc.114.132092>
- Tsukagoshi H (2016). Control of root growth and development by reactive oxygen species. *Current Opinion in Plant Biology* 29:57-63. <https://doi.org/10.1016/j.pbi.2015.10.012>
- Tyler L, Thomas SG, Hu J, Dill A, Alonso JM, Ecker JR, Sun T-P (2004). DELLA proteins and gibberellin-regulated seed germination and floral development in *Arabidopsis*. *Plant Physiology* 135(2):1008-1019. <https://doi.org/10.1104/pp.104.039578>
- Ueguchi-Tanaka M, Nakajima M, Karoh E, Ohmiya H, Matsuoka M (2007). Molecular interactions of a soluble gibberellin receptor, GID1, with a rice DELLA protein, SLR1, and gibberellin. *The Plant Cell* 19:2140-2155. <https://doi.org/10.1105/tpc.106.043729>
- Um TY, Han YL, Lee S, Sun HC, Chung PJ, Oh KB, ... Yang DC (2018). Jasmonate Zim-Domain Protein 9 interacts with Slender Rice 1 to mediate the antagonistic interaction between jasmonic and gibberellic acid signals in rice. *Frontiers in Plant Science* 9:1866. <https://doi.org/10.3389/fpls.2018.01866>
- Vaistij FE, Barros-Galvão T, Cole AF, Gilday AD, He Z, Li Y, Harvey D, Larson TR, Graham IA (2018). MOTHER-OF-FT-AND-TFL1 represses seed germination under far-red light by modulating phytohormone responses in *Arabidopsis thaliana*. *Proceedings of the National Academy of Science USA* 115:8442-8447. <https://doi.org/10.1073/pnas.1806460115>
- Van De Velde K, Ruelens P, Geuten K, Rohde A, Van Der Straeten D (2017). Exploiting DELLA signaling in cereals. *Trends in Plant Science* 22(10):880-893. <https://doi.org/10.1016/j.tplants.2017.07.010>
- Vargas AM, Le Cunff L, This P, Ibáñez J, de Andrés MT (2013). VvGAI1 polymorphisms associate with variation for berry traits in grapevine. *Euphytica* 191(1):85-98. <https://doi.org/10.1007/s10681-013-0866-6>
- Vera-Sirera F, Gomez M, Perez-Amador MA (2016). DELLA proteins, a group of GRAS transcription regulators that mediate gibberellin signaling. *Plant Transcription Factors* 313-328. <https://doi.org/10.1016/B978-0-12-800854-6.00020-8>
- Wang H, Pan J, Li Y, Lou D, Hu Y, Yu D (2016). The DELLA-CONSTANS transcription factor cascade integrates gibberellic acid and photoperiod signaling to regulate flowering. *Plant Physiology* 172:479-488. <https://doi.org/10.1104/pp.16.00891>
- Wang LC, Hai L, Ecker JR (2002). Ethylene biosynthesis and signaling networks. *The Plant Cell* 4:S131-S151. <https://doi.org/10.1105/tpc.001768>
- Wang SS, Liu ZZ, Chao S, Shi QH, Yao YX, You CX, Hao YJ (2012). Functional characterization of the apple MhGAI1 gene through ectopic expression and grafting experiments in tomatoes. *Journal of Plant Physiology* 169:303-310. <https://doi.org/10.1016/j.jplph.2011.09.012>
- Wang W, Wang Z, Hou W, Chen L, Wu C (2021). GmNMHC5 may promote nodulation via interaction with GmGAI in soybean. *The Crop Journal*. <https://doi.org/10.1016/j.cj.2021.03.019>
- Willige BC, Ogiso-Tanaka E, Zourelidou M, Schwechheimer C (2012). WAG2 represses apical hook opening downstream from gibberellin and PHYTOCHROME INTERACTING FACTOR 5. *Development* 139:4020-4028. <https://doi.org/10.1242/dev.081240>
- Wu H, Liu C, Fu X, Gai S, Zhang Y (2019). Screening, cloning and expression patterns analysis of PsGRASs associated with dormancy release in tree peony (*Paeonia suffruticosa*). <https://doi.org/10.16420/j.issn.0513-353x.2018-0207>

- Wu J, Yan G, Duan Z, Wang Z, Dai C (2020). Roles of the *Brassica napus* DELLA proteins BnaA6.RGA, in modulating drought tolerance by interacting with the ABA signaling component BnaA10.ABF2. *Frontiers in Plant Science* 11. <https://doi.org/10.3389/fpls.2020.00577>
- Wu S, Zhang S, Chen Y, Tian W (2015). Cloning and expression analysis of HbGAI gene in rubber tree (*Hevea brasiliensis* Muell. Arg.). *Acta Botanica Boreali-Occidentalia Sinica* 35(11):2157-2163.
- Yaish MW, El-Kereamy A, Zhu T, Beatty PH, Good AG, Bi YM, Rothstein SJ (2010). The APETALA-2-like transcription factor OsAP2-39 controls key interactions between abscisic acid and gibberellin in rice. *PLoS Genetics* 6:e1001098. <https://doi.org/10.1371/journal.pgen.1001098>
- Yamauchi D, Kobayashi M, Nakai T, Kou K (2007). Cloning of cDNAs for DELLA proteins suppressing cysteine proteinase genes in germinated cotyledons of common bean seeds. *Plant Biotechnology* 24:513-517. <https://doi.org/10.5511/plantbiotechnology.24.513>
- Zentella R, Sui N, Barnhill B, Hsieh WP, Hu J, Shabanowitz J, ... Sun TP (2017). The *Arabidopsis* O-fucosyltransferase SPINDLY activates nuclear growth repressor DELLA. *Nature Chemical Biology* 13:479-485. <https://doi.org/10.1038/nchembio.2320>
- Zentella R, Zhang ZL, Park M, Thomas SG, Endo A, Murase K, ... Sun TP (2007). Global analysis of DELLA direct targets in early gibberellin signaling in *Arabidopsis*. *The Plant Cell* 19:3037-3057. <https://doi.org/10.1105/tpc.107.054999>
- Zhang H, Wang XM, Liu XQ, Lin MA, Wen HY, Wang Z (2019). Cloning expression analysis and transformation of MsGAI gene from *Medicago sativa* L. *Scientia Agricultura Sinica*. <https://doi.org/10.3864/j.issn.0578-1752.2019.02.002>
- Zhang T, Zhao L, Jian-Gang Z, Wen-Bin LI (2011 a). Function of Plant DELLA proteins and its research advancement in soybean. *Soybean Science* 88:171-178. [https://doi.org/10.1002/1098-2337\(1991\)17:3<171::AID-AB2480170305>3.0.CO;2-G](https://doi.org/10.1002/1098-2337(1991)17:3<171::AID-AB2480170305>3.0.CO;2-G)
- Zhang WN, Gong L, Ma C, Xu HY, Li TZ (2011 c). Gibberellic acid-insensitive mRNA transport in *Pyrus*. *Plant Molecular Biology Reporter* 30:614-623. <https://doi.org/10.1007/s11105-011-0365-7>
- Zhang Y, Liu B, Yang S, An J, Chen C, Zhang X, Ren H (2014). A cucumber DELLA homolog CsGAIP may inhibit staminate development through transcriptional repression of B class floral homeotic genes. *PLoS One* 9(3):e91804. <https://doi.org/10.1371/journal.pone.0091804>
- Zhang ZL, Ogawa M, Fleet CM, Zentella R, Hu J, Heo JO, ... Sun TP (2011 b). Scarecrow-like 3 promotes gibberellin signaling by antagonizing master growth repressor DELLA in *Arabidopsis*. *Proceedings of the National Academy of Sciences* 108:2160-2165. <https://doi.org/10.1073/pnas.1012232108>
- Zhao B, Li H, Li J, Wang B, Dai C, Wang J, Liu K (2017). *Brassica napus* DS-3, encoding a DELLA proteins, negatively regulates stem elongation through gibberellin signaling pathway. *Theoretical and Applied Genetics* 130:727-741. <https://doi.org/10.1007/s00122-016-2846-4>
- Zhou M, Chen H, Wei D, Ma H, Lin J (2017). *Arabidopsis* CBF3 and DELLAs positively regulate each other in response to low temperature. *Scientific Reports* 7:39819. <https://doi.org/10.1038/srep39819>
- Zhou X, Zhang ZL, Park J, Tyler L, Yusuke J, Qiu K, ... Mccourt P (2016). The ERF11 transcription factor promotes internode elongation by activating gibberellin biosynthesis and signaling. *Plant Physiology* 171:2760. <https://doi.org/10.1104/pp.16.00154>
- Zhou Y, Underhill S (2017). Breadfruit (*Artocarpus altilis*) DELLA genes: gibberellin-regulated stem elongation and response to high salinity and drought. *Plant Growth Regulation* 83:375-383. <https://doi.org/10.1007/s10725-017-0302-3>
- Zhu JK (2002). Salt and drought stress signal transduction in plants. *Annual Reviews in Plant Biology* 53:247-273. <https://doi.org/10.1146/annurev.arplant.53.091401.143329>
- Zhu N, Cheng S, Liu X, Du H, Dai M, Zhou DX, ... Zhao Y (2015). The R2R3-type MYB gene OsMYB91 has a function in coordinating plant growth and salt stress tolerance in rice. *Plant Science* 236:146-156. <https://doi.org/10.1016/j.plantsci.2015.03.023>



The journal offers free, immediate, and unrestricted access to peer-reviewed research and scholarly work. Users are allowed to read, download, copy, distribute, print, search, or link to the full texts of the articles, or use them for any other lawful purpose, without asking prior permission from the publisher or the author.



License - Articles published in *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* are Open-Access, distributed under the terms and conditions of the Creative Commons Attribution (CC BY 4.0) License.

© Articles by the authors; UASVM, Cluj-Napoca, Romania. The journal allows the author(s) to hold the copyright/to retain publishing rights without restriction.