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

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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, SCL13 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 \textit{GAI}, \textit{RGA}, \textit{RGL1}, \textit{RGL2} and \textit{RGL3} genes of \textit{Arabidopsis}, \textit{d8} gene of maize, \textit{RHT} gene of wheat, \textit{L1} gene of grape, \textit{SLR1} gene of rice and \textit{sln1} gene of barley, etc. (Phokas and Coates, 2021). Recent physiological and biochemical studies of DELLA proteins have enabled
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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 DALLA and TVHYNP protein of DALLA motifs. The DALLA/TVHYNP proteins are integrated with SCFGID2/SY1 complex (consisting of Skp1, Cullin, F-box protein, and Rbx1), and then polyubiquitinated by SCFGID2/SY1 complex, and degrade DALLA 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). \textit{SLR1}, the only one DELLA gene in rice, which was highly induced by \textit{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 VHIID 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](image)

DELLA genes expression levels

DELLA proteins showed varied expression in different plant tissues and also changed with the external environment. The DELLA genes in \textit{Arabidopsis} included \textit{AtRGL1}, \textit{AtGAI}, \textit{AtRGA}, \textit{AtRGL2} and \textit{AtGRL3} (Javier et al., 2010), of which \textit{AtRGL1}, \textit{AtRGL2} and \textit{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 \textit{CsGAI1}, \textit{CsGAI2}, \textit{CsGAI3} and \textit{CsGAIP}, which were expressed in distinct level in
different plant tissue. The expression of \( \text{CsGAI2} \) and \( \text{CsGAIP} \) were higher, but the expression of the others was lower. The \( \text{CsGAI1} \) was expressed at low levels in all tissues, and the transcription of \( \text{CsGAI3} \) was mainly concentrated in the root (Yan et al., 2014). In peanut, the \( \text{AhDELLA1} \) and \( \text{AhDELLA2} \) genes were expressed ubiquitously in different tissues, while \( \text{AhDELLA3} \) and \( \text{AhDELLA4} \) 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                  |
|----------------------------------|------------------------------|-----------------------------|
| Arabidopsis thaliana             | \( \text{GAI, RGA, RGL1, RGL2 and RGL3} \) | Tyler et al., 2004          |
| Malus domestics Borkh            | \( \text{MdRGL1a/b, MdRGL2a/b and MdRGL3a/b} \) | Foster et al., 2007         |
| Malus hupehensis (Pamp.) Rehd    | \( \text{MbGAI1, MbGAI2} \)   | Wang et al., 2012           |
| Pyrus bretschneideri Rehd        | \( \text{GAI} \)             | Zhang et al., 2012c          |
| Vitis vinifera L.                | \( \text{VvGAII} \)          | Vargas et al., 2013          |
| Glycine max (L.) Merr.           | \( \text{GAI1} \)            | Wang et al., 2021            |
| Medicago truncatula Gaertn.      | \( \text{MtDELLA} \)         | Floss et al., 2021           |
| Phaseolus vulgaris L.            | \( \text{PvGAI1, PvGAI2} \)   | Yamauchi et al., 2007        |
| Populus trichocarpa Torrey & A.Gray | \( \text{PtGAI1, PtGAI2, PtRGL1 and PtRGL2} \) | Liu et al., 2016             |
| Gossypium barbadense L.          | \( \text{GbGAI, GbSLR1a and GbSLR1b} \) | Liao et al., 2009          |
| Solanum lycopersicum L.          | \( \text{LeGAI} \)           | Jasinski et al., 2008        |
| Oryza sativa L.                  | \( \text{OsGAI/SLR1} \)       | Gomi et al., 2010; Ueguchi-Tanaka et al., 2007 |
| Zea mays L.                      | \( \text{D8, D9} \)           | Peng et al., 1999; Cassani et al., 2009 |
| Hordeum vulgare L.               | \( \text{SLN1} \)            | Fu and Harberd, 2002         |
| Triticum aestivum L.             | \( \text{Rht} \)             | Ikeda et al., 2001           |
| Artemisia annua                   | \( \text{AaDELLA1, AaDELLA2} \) | Shen et al., 2015            |
| Populus alba                      | \( \text{PeRGA1, PeRGA2, PeGAI1, PeGAI2} \) | Liu et al., 2016            |
| Artocarpus incisa                 | \( \text{AaDELLA1, AaDELLA2} \) | 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 \( \text{RAP2.3} \) (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-GID 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      | GID1         | Promote the formation of GA-GID1-DELLA complex and inhibit the function of DELLA proteins. | Murase et al., 2008 |
| Auxin   | RGA          | Mediate auxin and gibberellin signal crosstalk. | Eunkyoo et al., 2014 |
| Auxin   | SIDELLA      | Interact with SLARF7/SLIAA9 to regulate plant growth and fruit germination. | Junbo et al., 2018 |
| IAA     | IAA          | Degrade DELLA proteins and then restrain root growth. | Gallego-Bartolomé et al., 2011 |
| IAA     | IAA          | Related to the content of DELLA proteins in root tip. | Fu and Haferd 2003 |
| CK      | GA3ox        | Promote the expression of GAI and RGA by inhibiting the expression of GA3ox. | Dai and Xue 2010 |
| CK      | RGA and GAI  | Regulate the expression of CK response genes. | Marin-de-la Rosa et al., 2014 |
| ABA     | OsAP2-39     | Regulate the expression of ABA and gas key synthase. | Yaish et al., 2010 |
| ABA     | ABI3 and ABI5| 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 |
| ABA     | ABI5         | Participate in PIF1 / SOM / ABI5 / DELLA regulation mode participated, inhibiting seed germination. | Vaistij et al., 2018 |
| ABA     | NF-YC        | Interact with DELLA proteins, and induced ABI5 expression affecting the expression of a series of GA and ABA response genes. | Liu et al., 2016 |
| ABA     | ICE1         | Interact with DELLA proteins and ABI5 to fine-tune Abscisic Acid Signaling during Seed Germination in Arabidopsis. | Hu et al., 2019 |
| ET      | ACS5 and ACS8| Are regulated by DELLA proteins and affect the development of top hook together with PIN vector. | An et al., 2012 |
| ET      | EIN3 / EIL1  | Interact with the DNA binding domain to affect the development of vertex hook. | An et al., 2012 |
| ET      | EIN3         | Regulate rhgai1 to control the growth of rose petal cells. | Luo et al., 2013 |
| ET      | AtERF11      | Enhance GA signaling by antagonizing the function of DELLA proteins. | Zhou et al., 2016 |
| JA      | JAZs         | Interact with DELLA proteins to wake their inhibitory effect on their respective downstream transcription factors. | Ye et al., 2016 |
| JA      | PIF3         | Interact with the DNA and hinder its regulation of downstream target gene expression, inhibiting hypocotyl elongation. | Hou et al., 2010 |
| JA      | OSJAZ8 and OSJAZ9 | Mediate the antagonistic regulation of GA and JA on plant height traits. | Um et al., 2018 |
| JA      | WD repeat / bHLH / MYB complex | Interact directly with DELLA and jazs to jointly regulate the development of trichome | Qi et al., 2014 |
| JA      | HbGAI        | Regulate latex formation by mediating JA or ET signal transduction | Shaohua et al., 2015 |
| BR      | BZR1         | 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 et al., 2012; Li et al., 2012 |
| BR      | SPY (SPINDLY) | Enhance the interaction between DELLA proteins and BZR1 transcription factors, resulting in different physiological effects on plants. | Zentella et al., 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 ARRs 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 GA20ox1. To affect the GAs synthesis, ABA inhibited root growth by regulating the stability of DELLA proteins and acted on the downstream of DELLA genes (Achard 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 \textit{DELLA-ABI5} interaction motif (Hu \textit{et al.}, 2019). Therefore, ABA can improve plant resistance and yield by regulating DELLA proteins levels.

\textit{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 \textit{DELLA} genes (Achard \textit{et al.}, 2003). The key genes \textit{ACSS} and \textit{ACS8} of ethylene synthesis were also regulated by DELLA proteins and affected the development of apical hook together with PIN vector (An \textit{et al.}, 2012). DELLA proteins interacted with the DNA binding domain of the ET signal pathway component \textit{EIN3/EIL1} protein to inhibit its regulation of the expression of downstream \textit{HLS1} gene and affected the development of vertex hook (An \textit{et al.}, 2012). The expression of \textit{RhGAI1} gene in rose was regulated by \textit{EIN3}, and \textit{RhGAI1} protein could bind to the promoter of downstream gene \textit{RhCesA2}, controlling the growth of rose petal cells (Luo \textit{et al.}, 2013). ET pathway gene \textit{AtERF11} also participated in GAs signal transduction. \textit{AtERF11} enhanced GA signaling by antagonizing the function of DELLA proteins (Zhou \textit{et al.}, 2016). ET increased DELLA proteins accumulation by reducing GAs biological activity, thus inhibiting the expression of \textit{LFY} and \textit{SOCI} to delay flowering (Chappie \textit{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.

\textit{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 \textit{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 \textit{et al.}, 2010). Studies had shown that DELLA protein SLR1 in rice also interacted directly with \textit{OgJAZ8} and \textit{OgJAZ9} of JAZ family, mediating the antagonistic regulation of GA and JA on plant height traits (Um \textit{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 \textit{et al.}, 2014). It was also found that \textit{HbGAI} gene of rubber regulated latex formation by mediating JA or ET signal transduction (Wu \textit{et al.}, 2015). In addition, DELLA proteins also resisted biological stress by regulating the balance of JA and salicylic acid (SA) in plants (Navarro \textit{et al.}, 2008).

\textit{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 \textit{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 \textit{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 (Goldack 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.
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Table 3. The responses of DELLA genes to different kind of abiotic stresses

| Stress               | Related gene | Function                                                                 | References                                      |
|----------------------|--------------|--------------------------------------------------------------------------|-------------------------------------------------|
| Salt stress          | GA2ox7       | Promote the accumulation of DELLA proteins by inhibiting GAs signal transduction. | Magome et al., 2010                             |
| Salt stress          | ACS          | Promote the accumulation of DELLA proteins by activating ABA signal transduction, resulting in the increase of plant ABS expression and ET contents. | Wang et al., 2002                                |
| Salt stress          | SCL          | DELLA proteins and SCL protein were integrated into ABA pathway through GA reaction to increase plant tolerance of abiotic stress. | Golldack et al., 2013                           |
| Salt stress          | OsMYB91      | 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 et al., 2016                     |
| Drought stress       | SnRK2s       | SnRK2s can be inhibited by GA from reducing water loss of plants under drought stress. | Lin et al., 2015                                 |
| Drought stress       | MYC          | DELLA can interact with phytochrome interaction factors (PIFs), which can also enhance the expression of MYC2 in JA signal transduction pathway. | Colebrook et al., 2014                          |
| Drought stress       | DELLA        | DELLA proteins promote stomatal closure and reduced water loss by improving the sensitivity of plants to ABA, enhancing drought resistance. | Nir et al., 2017                                 |
| Drought stress       | MsGAI        | Participate in the stress response of drought by cooperating with ABA. | Zhang et al., 2019                               |
| Low temperature stress| GAI          | Interact with CBF2, thus improving the cold resistance of tomato. | Achar et al., 2008a                              |
| Reactive oxygen species| DELLA       | Reduce the content of ROS to enhance plant stress resistance. | Achar et al., 2007                               |
| Reactive oxygen species| DELLA       | Inhibit root cell expansion and regulate root growth by regulating the content of ROS. | Tsukagoshi, 2016                                 |
| Phosphorus stress    | SPY          | Overexpression of DELLA protein will strengthen plant phosphorus starvation. | Hauvermale et al., 2012                          |
| Phosphorus stress    | GA2ox and GA3ox | Accumulate DELLA proteins by reducing the transcription of GA2ox and GA3ox, and inhibit plant growth and improve phosphorus stress tolerance. | Morcillo et al., 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 GA2ox 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 XERICO 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 DELLLA 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, DELLLA 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, GA1 and RAP2.3 transcription factors jointly mediated the regulation of GAs and ET on apical bending growth of Arabidopsis. The interaction between DELLLA proteins and EIN3/EILs complex could counteract the promotion of ET on apical hook development (Marín-de la Rosa et al., 2014). DELLLA 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 (ga1-3) insensitive to GA did not show hook structure, but showed hook structure in etiolated seedlings of GA1 and RGA deficient type: ga1-3gai-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

DELLLA 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, srl1 of rice, sln1c of barley and rht 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 noduleation 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) (Achard 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 DALLA 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.
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Conflict of Interests

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

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