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MOLECULAR BASIS OF THE DWARFISM CHARACTER IN CULTIVATED PLANTS. II. DELLA-PROTEINS: STRUCTURE AND FUNCTIONS

(review)

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Abstract

The wheat gene *Rht* (*Reduced height*) which predetermined the success of «Green revolution» and has been employed in creation of plant varieties with reduced stem elongation and resistant to stem lodging, encodes a protein containing highly conserved DELLA domain (J. Peng et al., 1999). Many other high-yield dwarf varieties also possess mutations in the genes coding DELLA proteins. Since the mutations did not affect viability and reproducibility of the plants the usage of the mutations for advanced plant breeding might be very promising (M. Ueguchi-Tanaka et al., 2007). Along with dwarfism, some mutations in the genes can lead to an opposite phenotype: to tall plants with spindly stems, the so called slender forms. What phenotype (dwarf or slender plant) would be developed depends on functionality of a protein region affected by the mutation. The paper considers in depth structure, posttranslational modifications, cellular localization and functions of DELLA proteins. The proteins being participants of complex protein-protein interactions play a role of repressors in gibberellin (GA) signal transduction. In the absence/or small concentration of GA DELLA proteins interact with specific transcriptional factor (TF) targets blocking their DNA binding activity and as a result restrain plant growth. In the presence of GA stem elongation is activated because this hormone promotes destabilization of DELLA proteins, releasing TF from their repression. Thus, restrained growth of the *rht* mutant as well as other naturally occurring dwarf plants is associated with accumulation of DELLA proteins in a result of their high stability. In turn, enhanced stability of the proteins can be caused by mutations in functionally important domains of either DELLA proteins or other players of GA signaling such as receptor GID1 and F-box proteins (GID2 in rice; SLY1 in *Arabidopsis*) of E3 ubiquitin protein ligase. They all participate in complex protein-protein interaction which is necessary for DELLA protein degradation via 26S-proteasome pathway (B.C. Willige et al., 2007; K. Hirano et al., 2010). The paper reviews a role of different functional motifs of DELLA protein in transduction of GA signal: DELLA, TVHYNP, polySTV on N-terminal part of a molecule and C-terminal GRAS-domain, containing the motifs LR, VHID, PFYRE and SAW. DELLA-proteins possess no DNA-binding site. Most probably their repressive function is associated with GRAS-domain via protein-protein interaction of LR region with target TFs (R. Zentella et al., 2007; K. Hirano et al., 2010). The polySTV domain plays a regulator role. Post-transcriptional modifications in the region are potentially able to change partners in protein-protein interaction and/or cellular localization of the DELLA proteins (M. Ueguchi-Tanaka et al., 2005; K. Hirano et al., 2010). A function of DELLA protein as an integrator of hormone signal ways and external factors is also discussed. In the context the DELLA proteins are considered as «correctors» of plant growth reaction depending on growth conditions (X.-H. Gao et al., 2011). Thus, the activity of DELLA proteins might underlie the plant phenotypic flexibility and promotes restrained plant growth under unfavorable environmental conditions.

Keywords: dwarfism, retard growth, gibberellin signal transduction, DELLA protein, repression function, proteolysis

Most dwarf plants possess mutations in DELLA proteins which repress gibberellic signal. These mutations, not affecting plant viability and reproducibility, are helpful in crop breeding [1]. The “Green revolution” which ensured an

impressive rise in wheat yields in 1940-1970 was predetermined by the use of genes *Rht* (*Reduced height*) responsible for a decreased plant height and a thickened stem [2, 3]. However, some mutations in the genes encoding DELLA proteins can lead to strong elongation of the stem (slender forms) and a constitutive response of the plants even in the absence of gibberellin (GA). Eventually, the effect of mutation (dwarf or slender plant phenotype) depends on the region of DELLA protein molecule which is damaged or modified. Since DELLA proteins are essential for GA signal transduction cascade and involved in crosstalk between signaling pathways for some hormones and external cues [4], an integrative role of these proteins as central regulators in GA signaling is obviously due to their predisposition to protein-protein interactions. To date, many functionally active motifs of DELLA proteins and their interacting partners which can enhance or block DELLA-mediated repression are reported [5, 6].

This review is focused on the molecular mechanisms underlying growth changes in plants with mutant DELLA proteins and/or their interacting partners involved in the regulation of DELLA protein activity.

DELLA is known to inhibit plant growth while GA activates growth due to DELLA degradation that results in derepression of the genes involved in plant growth control [7, 8]. If a mutation leads to higher DELLA stability, the plants are dwarf regardless of the GA presence or absence. An increased stability of DELLA protein may be caused by modifications in the domains necessary for binding to GA receptor *GID1* (Gibberellin Insensitive Dwarf 1) and/or E3 ubiquitin-protein ligase which are involved in GA signaling. These induce 26S proteasome-dependent degradation of DELLA proteins. Changes in DELLA structure which resulted in dwarfism were reported in *D8* (*Dwarf plant 8*) and *D9* maize mutants [2, 9, 10], *Rht* (*Reduced height*) wheat mutant [2, 11], *DWF2* (*Dwarf 2*) turnip mutant [12] and *VvGAI* (*Vitis vinifera GAI*) grape mutant [13] (Table).

Mutants which growth is not suppressed by DELLA proteins are phenotypically slender. Such a phenotype could result from fully repressed DELLA gene expression (seeing GA-independent growth occurs in the absence of a repressor) or from changes in the domains involved in interaction with transcription factors. Such mutations are found in genes encoding proteins *SLR1* (Slender rice 1) in rice [14] and *SLN1* (Slender 1) in barley [15], *La* and *CRY* in pea [16], *StRGA* (*Solanum tuberosum* repressor of *ga1-3*) in potatoes [17], *PRO* (Procera) in tomato [18] (see Table). Currently, genetic engineering makes it possible to modify the nucleotide sequences of DELLA genes in view to produce dwarf, semi-dwarf or slender plants.

GAI (*Gibberellic Acid Insensitive*), *RGA* (*Repressor of ga1-3*), *RGL1* (*RGA-like 1*), *RGL2* (*RGA-like 2*) and *RGL3* (*RGA-like 3*) genes are involved in DELLA control in *Arabidopsis* [14-16]. Only *GAI* and *RGA* seem to participate in growth inhibition. *GAI* and *RGA* proteins exhibit high homology (82 %). The roles of other genes in the repression of GA response differ but overlap (Fig. 1, A). All DELLA proteins (*RGA* mainly) are negative regulators of seed germination. *RGA*, *RGL2* and *RGL1* are also involved in flowering [1, 7, 22]. The role of *RGL3* in plant development still remains unclear.

Dwarf *ga1-3* mutants with low GA level are often used to investigate the GA signaling in *Arabidopsis*. These mutants are a suitable model for studying plant growth with no effect of GA (see Fig. 1, B). The plant height of *ga1-3* dwarf mutants was not influenced by *gai* mutation but slightly changed by *rga* mutation. Double mutations *GAI* and *RGA* restored the height of *ga1-3* plants to the wild-type level. Mutations in 3-5 genes of DELLA proteins converted short *ga1-3* plants into giants [7, 20, 22, 24].

Fig. 1. DELLA proteins involved in GA-mediated regulation of plant development in *Arabidopsis*: A — partial overlapping functions of DELLA and GAI (Gibberellic Acid Insensitive), RGA (Repressor of *gal-3*), RGL1 (RGA-like 1), RGL2, RGL3 (23), B — induction of GA-independent growth in dwarf *gal-3* mutant with loss of repressing function of DELLA proteins [7, 22, 24]; WT — wild type; *gai-16*, *rga-t2*, *rgl1-1*, *rgl2-1*, *rgl3-3* — mutations in DELLA proteins.

Special sites are responsible for the binding of DELLA proteins to specific interacting partners in GA signal transduction. The lesions in these sites can differently influence plant height. Highly conserved domains containing these sites are located at the N-end (DELLA, TVHYNP and polySTV) and the C-end (LR, VHIID, PFYRE and SAW) of DELLA molecule (рис. 2, A).

Fig. 2. Conservative regions of DELLA-family proteins (A, cited by [29] with additions) and a model GID1 (Gibberellin Insensitive Dwarf 1)-SLR1 (Slender rice 1)-GID2 (Gibberellin Insensitive Dwarf 2) complex (B, according to [5]).

A: DELLA (a), TVHYNP (b), VHI-ID (c), PFYRE (g) and SAW (h) named after characteristic amino acid sequences — DELLA for Asp-Glu-Leu-Leu-Ala (D-E-L-L-A), poly-STV for polySer-Thr-Val (c). LRI (d) and LRII (f) are leucine rich repeats; GRAS domain (Gibberellic Acid Insensitive, GAI; Repressor of *gal-3*, RGA; ScareCrow, SCR) is characteristic of GRAS family proteins and comprises several functional regions.

B: The regions of DELLA protein of rice (SLR1) which are involved in protein-protein interactions with GA receptor (GID1).

GID2 protein (an F-box subunit of the E3 ubiquitin ligase complex) and a transcription factor (TF). Six sites containing 1 to 3 amino acids (the positions in the primary structure of the protein indicated) are pointed by dots downward clockwise (HFY315, PYL321, HFT3327, LQ361, G576, DRF490). A replacement of amino acids in these sites results in the loss of function of the domain. GGF and LSL are the GID2 domains necessary to interact with SLR1.

DELLA family proteins are nuclear-localized [10, 25, 26] and containing nuclear localization signal [10, 20]. DELLA means a characteristic conserved sequence of Asp-Glu-Leu-Leu-Ala ((D-E-L-L-A) at the N-end of the polypeptide. The main functions of DELLA and TVHYNP domains are to recognize the GA signal by binding GA to the receptor GID1 protein and its lid domain, and to stabilize GA-GID1 complex [27, 28] (see Fig. 2, B). The size but not primary structure of the region between these domains is functionally essential [29, 30]. DELLAs with deletions or mutations in DELLA and TVHYNP domains be-

come unable to form DELLA-GID1 complex. That is why they are not recognized by 26S proteasome and remain active negative regulator of the GA signal [31]. Mutations and deletions in DELLA and VHYNP motifs result in a dominant GA-insensitive dwarfing phenotype in which the plant height is not restored by exogenous GA [15, 30, 32]. For example, the dwarfing *gai* mutants in *Arabidopsis* and *slr1-d1*, *slr1-d2*, *slr1-d3* in rice with a lesion in DELLA/TVHYNP domain are unable to binding to GID1 [19, 20]. Interestingly, two *SLRL* genes (*SLR1-like1*, *SLR1-like2*) encoding proteins lacking DELLA domain are found in rice. These SLRLs are GA-insensitive and repress GA signal in the presence of GA [33] (see Table). The SLRL is believed to mediate growth inhibition in rice shoots at flooding [34].

Mutations involved in the GA signal regulation

Mutant name	Protein	Loss/lesion of the protein function	Phenotype	Plant	References
DELLAs-mediated repression					
<i>gai-1</i>	GAI (Gibberellic Acid Insensitive)	GA-insensitive; failure to form GA-GID1-GAI complex; GAI stability (a 17-amino acid deletion in the conserved DELLA domain)	GA-insensitive dwarf plants	<i>Arabidopsis</i>	[19, 22]
<i>gai-t6</i>	GAI	GA-insensitive; failure to form GA-GID1-RGA complex; RGA stability; loss of repressor function (a 17-amino acid deletion in the conserved DELLA domain and a transposable element insertion in the C-end region of GRAS domain)	Normal height, a decreased GA-sensitivity	<i>Arabidopsis</i>	[35]
<i>rga-Δ17</i>	RGA (Repressor of <i>ga1-3</i>)	GA-insensitive; failure to form GA-GID1-RGA complex; RGA stability (lesion of DELLA domain due to deletion)	GA-insensitive dwarf plants	<i>Arabidopsis</i>	[22]
<i>rga-1</i>	RGA	GA-insensitive; loss of repressor function (67 amino acids deleted from the C-terminus)	Slight growth response to GA in dwarf mutants <i>ga1-3</i>	<i>Arabidopsis</i>	[35]
<i>rga-2</i>	RGA	Loss of repressor function (lesion of PFYRE domain due to Asp ₄₇₈ → Asn ₄₇₈ substitution)	Slight growth response to GA in dwarf mutants <i>ga1-3</i>	<i>Arabidopsis</i>	[20]
<i>rga-28</i> (<i>rga-t2</i>)	RGA	Loss of repressor function (lesion of LRI domain due to T-DNA insertion into coding region of <i>RGA</i>)	Slight growth response to GA in dwarf mutants <i>ga1-3</i>	<i>Arabidopsis</i>	[22]
<i>Brrga1-d</i>	BrRGA (<i>Brassica napus</i> repressor of <i>ga1-3</i>)	Failure of F-box of ubiquitin ligase complex to recognize DELLA proteins (lesion of VHIID region in the GRAS domain)	GA-insensitive dwarf plants	Rape	[12]
<i>d8-1</i>	D8 (Dwarf plant 8)	GA-insensitive; failure to form GA-GID1-D8 complex; D8 stability (a 4 amino acid deletion in the DELLA domain and single amino acid replacements in the DELLA and GRAS domains due to a deletion)	GA-insensitive dwarf plants	Maize	[2, 9, 10]
<i>d8(+)</i>	D8	Increased D8 stability in the presence of GA (Val ₁₀₃ insertion into the TVHYNP domain)	Deceased growth response to GA	Maize	[32]
<i>d9</i>	D9 (Dwarf plant 9)	GA-insensitive; failure to form GA-GID1-D9 complex, D9 stability (lesions in the DELLA and GRAS motifs due to single amino acid replacements)	GA-insensitive dwarf plants	Maize	[9, 10]
<i>rht-1</i>	Rht (Reduced height)	GA-insensitive; failure to form GA-GID1-Rht complex, Rht stability (DELLA lesion caused by a deletion)	GA-insensitive dwarf plants	Wheat	[2, 11]
<i>rht</i>	DELLA-subfamily protein	Decreased GA-sensitivity of DELLA protein (Leu → Pro substitution in the conserved DELLA domain)	Decreased growth response to GA	Sunflower	[36]
<i>cry-c</i>	CRY (Cryptodwarf)	Loss of the repressor function (Gly ₁₆₃ → Gln ₁₆₃ substitution)	GA-insensitive growth (slender plants)	Pea	[16]
<i>cry-s</i>	CRY	Loss of the repressor function (a frameshift deletion of the conserved amino acid located at position 152)	GA-insensitive growth (slender plants)	Pea	[16]
<i>la</i>	LA	Loss of the repressor function of DELLA protein (a conserved Gln ₈₅ excision due to an insertion)	GA-insensitive growth (slender plants)	Pea	[16]

						Table continued
<i>pro</i>	PRO (Procera)	Loss of the repressor function of DELLA protein (the VHIID lesion resulting in failure of F-box of ubiquitin ligase complex to recognize DELLA proteins)	GA-insensitive growth (slender plants)	Tomato		[18]
<i>dwf2</i>	DWF2 (Dwarf 2)	GA-insensitive; failure to form GA-GID1-DWF2 complex, DWF2 stability (lesion of structure of the conserved DELLA domain)	GA-insensitive growth	Turnip		[12]
<i>Strga</i>	St RGA (<i>Solanum tuberosum</i> repressor of <i>gal-3</i>)	Loss of the repressor function of DELLA protein (lesion in the structure of the LRI domain)	GA-insensitive growth (slender plants)	Potato		[17]
<i>slr1-1</i>	SLR1 (Slender rice 1)	DELLA protein is not synthesized (a non-sense mutation)	GA-insensitive growth (slender plants)	Rice		[14]
<i>slr1-d1</i> , <i>slr1-d2</i> , <i>slr1-d3</i>	SLR1	GA-insensitive; failure to interact with GID1, SLR stability (Val ₄₉ →Met ₄₉ substitution in the conserved DELLA domain in <i>slr1-d2</i> mutant or Leu ₉₉ →Phe ₉₉ and Met ₁₀₆ →Lys ₁₀₆ substitutions in the TVHYNP motif in <i>slr1-d3</i> mutant)	GA-insensitive dwarf plants	Rice		[37]
<i>slr1-d4</i>	SLR1	GA-insensitive; failure to form a stable complex with GID1 and GID2, SLR stability (lesion in the SAW domain structure)	GA-insensitive dwarf plants	Rice		[5]
<i>sln1(b, c)</i>	SLN (Slender 1)	Loss of the repressor function of DELLA protein (the C-terminal end truncated)	GA-insensitive growth (slender plants)	Barley		[15]
<i>sln1d</i>	SLN	GA-insensitive; failure to form GA-GID1-SLN complex, SLN stability (Gly ₄₆ →Glu ₄₆ substitution in the conserved DELLA domain)	GA-insensitive dwarf plants	Barley		[15]
<i>spy</i>	SPY (Spindly) (N-acetylglucosamine transferase)	DELLA activator-mediated repression Not capable of DELLAs glycosylation	GA-insensitive growth (slender plants)	Rice, <i>Ara-bidopsis</i>		[38, 39]
Positive regulators (proteins of F-box containing E3 ubiquitin ligase complex)						
<i>sly</i>	SLY (Sleepy)	Loss of DELLA protein recognition (the C-terminal end truncated)	GA-insensitive dwarf plants	<i>Arabidopsis</i>		[35]
<i>sly1-d</i>	SLY	Gain of DELLA recognition regardless its interaction with GA-GID1 (E→K substitution in the C-end LSL)	GA-insensitive growth in dwarf mutant <i>gai</i>	<i>Arabidopsis</i>		[35]
<i>gid2</i>	GID2 (Gibberellin Insensitive Dwarf 2)	Loss of DELLA protein recognition (replacements of amino acids in the F-box domain)	GA-insensitive dwarf plants	Rice		[40]
DELLA-dependent negative regulator — a GATA transcription factor						
<i>gnl</i>	GNL/CGA1 (GNC-like/Cytokinin-Responsive GATA factor 1)	Loss of the negative regulator function	Slender plants	<i>Arabidopsis</i>		[41]
<i>gnc</i>	GNC	Loss of the negative regulator function	Slender plants	<i>Arabidopsis</i>		[41]
Positive regulator (repression of DELLAs activity) — a GRAS transcription factor						
<i>scl3</i>	SCL3 (ScareCRow-like 3)	Loss of the negative regulator function	Enhanced sensitivity to GA biosynthesis inhibitor	<i>Arabidopsis</i>		[42]

The domain polySTV (polySer-Thr-Val) is a regulator. Transgenic rice plants with DELLAs deficient in polySTV were dwarfing [30]. Ser and Thr residues are found in polySTV which can be post-translationally modified (phosphorylated or N-acetylglucosaminated) [5, 29]. These modifications of DELLAs are believed to change their protein-protein interaction and (or) location. Phosphorylated DELLAs have been found in *Arabidopsis* and rice [43–45]. A role of DELLAs phosphorylation in GA signaling is discussed. SLR1 phosphorylation was shown to increase the protein stability in rice [45] though there was no reliable evidence for the effect of DELLA phosphorylation on the recognition of GA signal or degradation of the protein [7, 29, 43]. When seeking for negative regulators of GA signaling, the SPY (Spindly) protein was found in *Arabidopsis* and rice [38, 46]. The SPY is N-acetylglucosamine transferase which modifies proteins by Ser

and Thr glycosylation. The *spy* mutants of rice and *Arabidopsis* were phenotypically slender and characteristic of a decreased SPY expression [39]. It is believed that SPY-mediated DELLAs glycosylation blocks DELLAs phosphorylation. Nevertheless, it still remains unclear how does N-acetylglucosamination enhance the activity of DELLA-family proteins [7].

VHIID, LR (leucine repeats), PFYRE and SAW are the C-end located domains of the DELLAs (see Fig. 2, A), common to all members of a highly conserved GRAS family. The family comprises many transcription factors (TF). GRAS family is named after the first three members — GAI, RGA and SCR (ScareCRow) [47, 48]. The GRAS-containing TFs have been identified in *Arabidopsis* (33 TFs) and rice (60 TFs). These proteins are involved in plant growth and development and differ significantly by the presence of other functional domains [49].

Binding N-end DELLA and TVHYNP domains to the receptor protein GID1 is shown to be necessary but not sufficient to form a complex with E3 ubiquitin protein ligase and initiate proteolysis of DELLA proteins. The affinity to ubiquitin protein ligase increases only after an interaction between the GRAS domain of the DELLAs and GID1. A site-directed mutagenesis revealed the C-end region of VHIID together with PFYRE and SAW domains to be involved in association (see Fig. 2, B) [5]. In the VHIID mutants of rape (*Brrga1-d*) and SAW mutants of rice (*slr1-d4*) the DELLA proteins become more stable leading to dwarfism [5, 12] (see Table). The N-end-located VHIID and LR11 of the DELLAs putatively bind to GID2 in rice and SLY1 (SLEEPY1) in *Arabidopsis* which are the F-box proteins of the ubiquitin-protein ligase complex degrading DELLAs (see Fig. 2, B). When GID2 (or SLY1) lesions, the DELLA-ubiquitin-protein ligase complex failed to form, and DELLAs stability increased leading to the GA-unresponsive dwarf plants [5].

Deletions in the GRAS domain often led to loss of the repressor function in DELLA proteins that was expressed in the GA-independent growth response and the appearance of slender phenotype [5, 20]. Thus, a regulatory role of DELLAs in transcription is GRAS-associated [34]. Using biochips, the DELLA-regulated GA-dependent genes (GA-activated but DELLA-repressed) have been found [7, 50]. Among these genes there were *GA20ox2* and *GA3ox1* involved in GA biosynthesis, and *GID1a* and *GID1b* responsible for GA reception. On the contrary, an expression of the genes encoding GA reactivation was DELLAs-inhibited and GA-stimulated [16, 42, 50]. *XERICO* is one more positive target for DELLAs. Еще одна позитивная мишень DELLA — ген *XERICO*. Overexpression of *XERICO* led to accumulation of abscisic acids, the phytohormone responsible for activating drought resistance. Thus, DELLAs contribute to GA biosynthesis and reception and, at the same time, induce biosynthesis of abscisic acids, an antagonist to gibberellin. The proteins encoded by the other target genes of DELLAs are transcription factors of bHLH (basic helix-loop-helix), MYB and GATA types.

Chromatin immunoprecipitation revealed DELLAs association with promoter regions of the regulated genes. However, a DNA-binding domain of DELLAs is not found [7, 42, 50]. A transcriptional repression in these associations seems to be due to DELLAs-dependent inactivation of TFs which contain a DNA-binding site [51] (see Fig. 2, B). It is believed that the sites responsible for repressive functions are distributed along the GRAS domain of DELLAs, making it difficult to identify. In addition, investigation of DELLA repressive role is complicated by indirect regulation when different mutations in a gene alter protein conformation that can inhibit the TFs inactivation. In this, DELLAs usually reserve the ability to bind GID1. In vitro interaction of the N-end located DELLA and TVHYNP domains with the GID1 receptor changed DELLA

plex is unstable but its stability increases due to a two-step association with DELLAs: the N-terminal DELLA domain of DELLA protein binds to the GID1 N-terminal lid domain (position 5), and the C-terminal GRAS (Gibberellic Acid Insensitive, GAI; Repressor of *gal-3*, RGA; ScareCrow, SCR) domain of DELLA protein interacts with the C-terminal region of GID1 (position 6).

B. At DELLAs proteolysis-dependent inactivation a GA-GID1-DELLA complex has a high affinity to ubiquitin-proteasome multiprotein complex E3 SCF. E3 SCF comprises SKP-CUL-F-box (S phase Kinase-associated Protein 1 and Cullin) and RBX1 protein with Ring finger domain. F-box proteins recognize and bind the GRAS domain of DELLA protein (position 7). E3-associated ubiquitin-conjugated enzyme E2 tags ubiquitination of a target DELLA protein. The tagged DELLA protein undergoes proteolytic degradation by the 26S proteasome (position 8). Transcription factors, after a release from DELLA repression due to the degradation, activate the GA-dependent genes to launch growth and morphogenesis programs.

Г. In case of DELLAs proteolysis-independent inactivation which occurs under *GID1* overexpression the repressor function of DELLA protein is lost at a GA-GID1-DELLA complex formation (position 6).

It is believed that the DELLA-proteins as key components of GA signal transduction can integrate the signaling pathways of hormones and external stimuli [53]. The DELLAs activity may underlie the phenotypic plasticity and determine a low plant growth observed at strong light, drought, salinity, low temperature, an impoverishment of soil mineral composition and disease. An increased stability of DELLAs under the influence of stress factors (low temperature, salinity) evidences in support of the idea. DELLA proteins increased plant resistance to stress due to reducing growth rate and activating cellular antioxidant system [4, 7, 54]. In addition, the dwarf plants able to accumulate DELLA proteins possess an increased resistance to various stressors.

DELLA proteins are proved to be involved in light-dependent regulation (light signaling) of plant growth and de-etiolation of seedlings. They block PIFs (Phytochrome-Interacting bHLH Transcription Factors, the repressors of a phytochrome-dependent response). Additionally, DELLAs contribute to accumulation of the bZIP (basic region/leucine zipper) containing TF long-hypocotyl 5 (HY5), the main activator that promotes photomorphogenesis [17, 55, 56]. The mechanism of DELLAs-mediated PIFs repression is most well-studied. PIF3, PIF4 and PIF5 proteins are found in *Arabidopsis* and potato. When physically binding to promoters, they transcriptionally regulate expression of the genes encoding growth of etiolated seedlings [17]. DELLAs can form a complex with PIF by bHLH domain binding at low GA level in the light. When complexed with DELLAs, PIFs are unable to interact with promoters of the target genes. At dark and at high GA level the rate of DELLAs degradation rises interrupting repression of PIFs by the DELLAs. When released from DELLAs, PIFs bind to their target promoters to regulate transcription. Particularly, *GNC* (*GATA*, *Nitrate-Inducible*, *Carbon-Metabolism Involved*) and *GNL/CGA1* (*GNC-like/Cytokinin-Responsive GATA factor1*) are the genes transcriptionally controlled by the DELLAs and PIFs regulators. The encoded proteins (GATA TFs to bind GATA-containing DNA regions) play a repressor role in the GA signaling at seed germination, stem elongation and flowering. Their overexpressing mutants are dwarfs, whereas a loss-of-function *GNC* or *GNL/CGA1* mutants result in slender plants [41]. It is shown that DELLA can also directly interact with another protein of the bHLH family — ALC (Alcatraz), responsible for the formation of separation layer and the dehiscence in *Arabidopsis*. In this, as in interaction with PIF, DELLAs prevent the ALC association with its target promoters thus blocking transcription [57]. It yet remains discussable whether the repression mechanism of DELLA-PIF/ALC models is applicable to other bHLH TFs. These studies will help to identify the DELLAs involvement in ontogenetic processes [7].

Like the bHLH regulators, DELLAs are able to directly interact with the TFs of GRAS and JAZ families [34]. A transcriptional regulator SCL3 (Sca-

reCRow-like3), like DELLAs, belongs to the GRAS-family proteins but lacks of DELLA domain. The effect of the interaction between SCL3 and DELLAs is antagonistic. SCL3 represses the DELLAs function, being, therefore, a positive regulator [42]. Mutation in *slc3* results in a wild-type growth rate under normal conditions which reduced in the plants treated with paclobutrazol, a GA-biosynthesis inhibitor. Interestingly, DELLAs activate *SCL3* expression. SCL3 protein, like DELLAs, has specific target genes, and does not contain DNA-binding domain that is why it regulates transcription due to the associations with other TFs. Interaction between SCL3 and DELLA oppositely influenced transcription of SCL3- and DELLA-dependent genes involved in GA response and GA metabolic gene expression [34]. A recent research reported on the role of SCL3 and DELLA in the root development. In this, other GRAS-family TFs, the SHR (Short-Root) and the SCR responsible for the endodermal cell specialization, were controlled by SCL3 and DELLA regulators [58]. It has been shown that DELLA proteins activated a jasmonic signal transduction. For that, DELLAs directly interact with a soluble protein JAZ1, the key repressor of jasmonic signaling, and block its ability to inhibit MYC2 protein, the bHLH/LZ (basic helix-loop-helix/leucine zipper) TF which is bound to its specific promoter. This TF family is named after gene *v-MYC* (V-mycavian mielocytomatosis viral oncogene) which is the main transcriptional activator of jasmonat-induced genes expression [59, 60].

Due to interaction with the members of various signaling pathways, DELLA proteins, additionally to the involvement in DELLA-hinged GA signaling, are a central integrator of signal transduction pathways for many hormones and external stimuli. In the opinion of X.-H. Gao et al. [53], DELLA proteins can regulate plant growth and tolerance depending on environmental variables.

So, hereditary changes which determine the plant height are of interest for breeding. These can result from mutations in genes involved in regulation of cell metabolism at molecular, hormonal, epigenetic and transcriptional levels. Among the causes of shortened stems, breeders especially allocate changes in the regulation of GA activity common to various plant species. In breeding, the genotypes with mutations in DELLA proteins, the repressor of GA signal, seems to be the most viable, adaptive and expedient. These mutations often lead to a desired dwarf phenotype, but also slender forms can appear. Plant growth inversely correlates with DELLA resistance to degradation in the presence of GA. DELLA proteins are localized in the cell nucleus. Their molecules contain many high conserved regions involved in protein-protein interaction. DELLA proteins have no DNA-binding domains and indirectly regulate transcription of GA-dependent genes by blocking TFs that leads to growth retardation. GA, by inducing DELLAs proteolytic degradation via the ubiquitin-proteasome pathway, relieves DELLA-dependent repression of the TFs and restores growth. Mutants defective on ubiquitin-proteasome complex exhibit an increased stability of DELLA proteins leading to dwarfism. These mutations can affect either DELLA proteins, or their interacting partners in the signal transduction, i.e., proteins of soluble GA receptor (GID1) and F-box of ubiquitin ligase. Mutations leading to loss of DELLA repressor function seem to affect the GRAS domain. Whether a stability of DELLA proteins and their interactions with other proteins are influenced by posttranslational modifications (e.g., phosphorylation, glycosylation) remains an open question. The modifications affect the polySTV domain. Getting involved in diverse protein-protein interactions and being one of the key component in internal (hormones) and external (biotic/abiotic factors) signaling during plant growth, development and adaptation, DELLA-family proteins are not only a player of the GA signaling pathway, but act as a signaling integrator. Exactly activity of DELLA proteins is likely to underlie phenotypic plasticity and

enable a plant to restrain growth under adverse conditions.

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