

Genomic Analysis of DELLA Protein Activity

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Changes in gene expression are the main outcome of hormone signaling cascades that widely control plant physiology. In the case of the hormones gibberellins, the transcriptional control is exerted through the activity of the DELLA proteins, which act as negative regulators in the signaling pathway. This review focuses on recent transcriptomic approaches in the context of gibberellin signaling, which have provided useful information on new processes regulated by these hormones such as the regulation of photosynthesis and gravitropism. Moreover, the enrichment of specific *cis*-elements among DELLA primary targets has also helped extend the view that DELLA proteins regulate gene expression through the interaction with multiple transcription factors from different families.

Keywords: Gibberellin • Hormonal regulation • Transcription.

Abbreviations: bHLH, basic helix–loop–helix; GR, glucocorticoid receptor; JAZ, jasmonate ZIM-domain; PIF, phytochrome-interacting factor.

Introduction

Gibberellins are a class of plant hormones that regulate multiple aspects of development, from seed germination to fruit growth, including the control of organ size, photomorphogenesis and floral induction (Yamaguchi 2008). Molecular and genetic studies in the past 20 years have helped decipher the cellular events responsible for gibberellin activity in several plant species, such as *Arabidopsis thaliana* and rice, and have unveiled a very high degree of conservation in the signaling mechanism. Although several physiological studies suggest a role for gibberellins in the control of cell processes other than gene expression (Bethke et al. 1997), strong evidence indicates that the endpoint of gibberellin signaling is the regulation of transcriptional activity. This conclusion is derived from two observations. First, genetic analysis has revealed that most of the control that gibberellins exert on plant development occurs through a small set of nuclear proteins, named DELLAs (Sun and Gubler 2004), which interact with and regulate the activity of several transcription factors (see below). Consequently, and secondly, several reports have documented rapid changes in gene expression

in response to gibberellin treatments, from very specific ones—such as the classical up-regulation of α -amylase gene expression in barley aleurone cells (Fincher 1989)—to transcriptomic changes observed more recently with the use of genomic approaches (Table 1).

DELLA proteins mediate the regulation of gene expression by gibberellins

DELLA proteins constitute a subgroup of the GRAS family of plant-specific, loosely defined transcription factors. The name was coined on the basis of a short stretch of amino acids (D-E-L-L-A) in their N-terminal region, which is tightly conserved among all plant species. They also present additional conserved motifs, such as the VHYNP domain; a poly(serine/threonine) stretch; two leucine heptads repeats which may mediate protein–protein interactions; a putative nuclear localization signal; and a putative SH2 phosphotyrosine-binding domain. Several plant species possess a single DELLA gene, such as *SLENDER RICE1* (*SLR1*) in rice (Ikeda et al. 2001) or *PROCERA* in tomato (Marti et al. 2007, Bassel et al. 2008, Jasinski et al. 2008), while the *DELLA* genes in other plants such as the Brassicaceae have undergone multiplication. For instance, DELLAs are encoded by five genes in Arabidopsis: *GAI*, *RGA*, *RGL1*, *RGL2* and *RGL3* (Peng et al. 1997, Silverstone et al. 1998, Lee et al. 2002, Wen and Chang 2002, Tyler et al. 2004). Careful phenotypic analysis of *dellaKO* mutants in Arabidopsis indicates that each of the five proteins displays a distinct preferential role in a particular process in the plant, although with a certain degree of redundancy in some cases. For example, while only the pentuple *dellaKO* mutant seems to rescue completely the defects caused by gibberellin deficiency, *GAI* and *RGA* are the major DELLAs controlling cell expansion in hypocotyl, shoot and root; and *RGL2* becomes the major DELLA protein regulating germination under certain conditions (Dill and Sun 2001, King et al. 2001, Fu and Harberd 2003, Cheng et al. 2004, Tyler et al. 2004, Cao et al. 2005). In agreement with this, it has been proposed, based on promoter-swapping studies, that the functional diversification of the different DELLA proteins in Arabidopsis is the result of subfunctionalization probably due to changes in their regulatory sequences (Gallego-Bartolomé et al. 2010).

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Table 1 Transcriptomic analyses for the study of DELLA protein function in Arabidopsis

DELLA protein	Description	Reference
All	Transcriptome of gibberellin-deficient mutant <i>ga1</i> during germination.	Ogawa et al. (2003)
GAI, RGA, RGL1, RGL2	Comparison of the transcriptomes of a quadruple <i>dellaKO</i> mutant in the <i>ga1</i> background in two developmental stages: germination and flower development.	Cao et al. (2006)
RGA	Search for DELLA targets misregulated upon RGA induction under the control of a glucocorticoid-inducible promoter. Confirmation by chromatin immunoprecipitation for some of them.	Zentella et al. (2007)
All	Comparison of the transcriptomes of <i>ga1</i> and the triple <i>gid1abc</i> receptor mutants in response to gibberellin application.	Willige et al. (2007)
GAI, RGA, RGL1, RGL2	Analysis of the transcriptome of a quadruple <i>dellaKO</i> mutant in the <i>ga1</i> background in response to NaCl.	Achard et al. (2008)
RGA	Changes in gene expression caused by induction of <i>35S::RGA:GR</i> during flower development in the <i>ga1 rga gai</i> mutant.	Hou et al. (2008)
All	Analysis of the transcriptome of dark-grown seedlings of the pentuple <i>dellaKO</i> mutant in the <i>ga1</i> background.	Cheminant et al. (2011)
GAI	Search for DELLA targets misregulated upon the induction of <i>HS::gai-1</i> in etiolated seedlings. Confirmation for some of them in <i>GAI::gai-1:GR</i> seedlings.	Gallego-Bartolomé et al. (2011a)
All	Analysis of the transcriptome of a pentuple <i>dellaKO</i> mutant in the phases of minimal and maximal daily growth under short days.	Arana et al. (2011)
RGL2	Analysis of the transcriptome of <i>ga1 rga rgl2</i> compared to <i>ga1 rga</i> in seeds after imbibition for 5 d in the cold.	Stamm et al. (2012)

As mentioned, complete loss of DELLA function mimics the phenotype of continuous gibberellin application (Dill and Sun 2001, Cheng et al. 2004, Tyler et al. 2004, Cao et al. 2005). Therefore, DELLAs can be considered as negative elements of gibberellin signaling. In support of this idea, DELLA proteins are degraded in response to gibberellin accumulation. Importantly, this destabilization requires the N-terminal region of the protein, containing the DELLA domain (Dill et al. 2001). Accordingly, DELLA protein variants lacking this motif are stable even in the presence of high gibberellin levels. For instance, the stable variants *gai-1* and *rga-Δ17* cause dwarfism in Arabidopsis equivalent to that caused by gibberellin deficiency (Peng et al. 1997, Dill et al. 2001). The mechanism by which gibberellins modulate DELLA accumulation is also conserved at least between monocots and dicots (Fig. 1). Gibberellin signaling initiates with the binding of the hormone to the GID1 receptor, which is encoded by a single gene in rice (Ueguchi-Tanaka et al. 2005), and by three paralogs (*GID1a*, *GID1b* and *GID1c*) in Arabidopsis (Griffiths et al. 2006, Nakajima et al. 2006, Willige et al. 2007). The gibberellin-loaded GID1 receptor interacts with and inactivates the DELLA proteins (Willige et al. 2007, Ariizumi et al. 2008, Murase et al. 2008, Shimada et al. 2008), and subsequently promotes their polyubiquitination by an E3 ubiquitin ligase, a process that is mediated by the F-box proteins SLEEPY1 and SNEEZY in Arabidopsis (McGinnis et al. 2003, Ariizumi et al. 2011). Interestingly, several dicotyledonous plants have evolved GID1 paralogs—*AtGID1b* in the case of Arabidopsis—with the ability to interact with DELLA proteins in a gibberellin-independent and gibberellin-hypersensitive

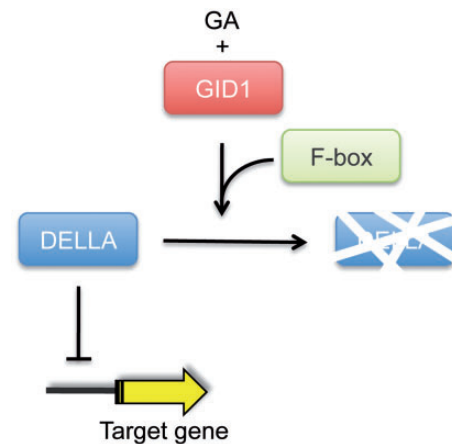


Fig. 1 Simplified scheme of gibberellin signaling. DELLA proteins regulate the expression of gibberellin target genes, and they undergo polyubiquitination and subsequent degradation by the proteasome in response to the interaction between the hormone and the GID1 receptor. Polyubiquitination is facilitated by the participation of an F-box protein encoded by SLEEPY1 and its paralog SNEEZY.

manner, probably to adapt to low gibberellin cellular environments (Yamamoto et al. 2010). Very probably, all gibberellin signaling operates exclusively through the GID1 receptors—at least at the seedling stage—based on the unequivocal coincidence between genes misregulated in the *ga1* mutant defective in gibberellin biosynthesis and the *gid1* receptor triple mutants, and on the inability of exogenous gibberellin to recover the

transcriptomic defects seen in the *gid1* triple mutants (Willige et al. 2007).

The localization of DELLA proteins in the nucleus is in agreement with a role in the regulation of gene expression (Silverstone et al. 1998, Dill et al. 2001). However, there is no evidence for direct binding of these proteins to DNA, which suggests that they probably interact with DNA-binding transcription factors. The aforementioned recent evidence suggests that this is the case, given that, for example, the regulation by DELLAs of the expression of several light-regulated genes is mediated by physical interaction with the transcription factor PHYTOCHROME-INTERACTING FACTOR3 (PIF3), and with other PIF paralogs (Davière et al. 2008).

Given these observations, a big challenge in the field is to explain how a single hormone can exert so many—and so diverse—functions during the plant's life cycle. Also, in particular, how DELLA proteins can accurately turn on and off the expression of specific sets of genes in a context-dependent manner. This mini review summarizes the genomic approaches that have been recently undertaken, and the way in which the information obtained improves our knowledge of gibberellin signaling.

Context-dependent transcriptional regulation by DELLA proteins

Consistent with the widespread role of gibberellins in controlling different aspects of a plant's life, several transcriptomic approaches show that there is only a marginal overlap between sets of genes mobilized by DELLAs in different organs and/or physiological contexts (Table 1). Interestingly, genes involved in gibberellin metabolism are among the genes regulated by DELLAs under all circumstances examined. In general, genes encoding GA 20-oxidases and GA 3-oxidases are under positive regulation by DELLAs, while GA 2-oxidase genes are repressed (Cao et al. 2006, Zentella et al. 2007, Hou et al. 2008, Arana et al. 2011, Cheminant et al. 2011, Gallego-Bartolomé et al. 2011a). This result confirms that the mechanism for feedback regulation of gibberellin metabolism operates through DELLA proteins, although their precise role has not been elucidated.

As expected, transcriptomic analyses of DELLA mutants have provided a good molecular description of already known processes regulated by gibberellins, and have identified the possible targets in the regulatory circuits that would be subject to modulation by these hormones. For example, it has long been known that gibberellins regulate cell expansion (Cowling and Harberd 1999). Microarray analyses indicate that DELLAs participate at different levels in the transcriptional cascade that promotes cell expansion. First, DELLAs act early in the cascade, regulating genes encoding other transcriptional regulators such as the growth-promoting factors *PRE1* and *PRE5* (Bai et al. 2012a, Ikeda et al. 2012), whose expression is repressed by DELLAs (Lee et al. 2006, Gallego-Bartolomé et al. 2011a). Secondly, DELLAs also control the expression of the downstream genes involved in the process of cell elongation itself,

including those that encode enzymes involved in the biogenesis and modification of the cell wall components, or enzymes responsible for the modification of cell wall structures in Arabidopsis (Cao et al. 2006, Zentella et al. 2007, Hou et al. 2008, Arana et al. 2011, Cheminant et al. 2011, Gallego-Bartolomé et al. 2011a), and in other species such as tomato or rice (Tsuji et al. 2006, Carrera et al. 2012). However, plant growth is subtended not only by cell expansion, but also by cell division, and DELLAs have been found to decrease the cell division rate in roots and aerial organs through the up-regulation of the expression of genes encoding cyclin-dependent kinase inhibitors, such as *KRP2* and *SIM* (Achard et al. 2009), or through the cross-talk with cytokinin signaling (Moubayidin et al. 2010), in agreement with a more general function of DELLAs in the regulation of plant size. Importantly, for this function to be exerted, DELLAs need only be expressed in the endodermis (Ubeda-Tomas et al. 2009), and gibberellin levels are higher in elongating endodermal cells (Shani et al. 2013), opening up the possibility that size control by gibberellins is directed by specific cell types.

Similarly, the involvement of gibberellins in reproductive development has been assigned to different phases, from floral induction (Langridge 1957, Blázquez et al. 1998) to the development of floral organs (Wilson et al. 1992, Goto and Pharis 1999). Accordingly, microarray analyses focused on these developmental processes have identified a subset of genes that could explain this regulation. DELLAs repress several MADS-box and other homeotic genes (Cao et al. 2006, Hou et al. 2008), which is in line with functional and genetic analyses that showed that the direct regulation of floral homeotic genes by the DELLA protein RGA is important for proper flower development (Yu et al. 2004). More recently, transcriptional regulation of these MADS-box genes and other flowering time integrators by DELLAs has been shown to operate through their known activators, the SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPLs) transcription factors, both in leaves and in the meristem (Galvao et al. 2012).

Finally, several transcriptomic analyses with Arabidopsis have yielded a set of genes regulated by gibberellin during seed germination. Although the first attempt to identify such targets was based on the application of GA₃ to gibberellin-deficient seeds, and not necessarily aimed at identifying DELLA targets (Ogawa et al. 2003), more recent analyses with DELLA mutants have confirmed the initial results (Cao et al. 2006). Interestingly, temporal examination of gene expression has revealed that the earlier changes after gibberellin application occur in the regulation of genes encoding transcription factors, such as *AtMYB34/ATR1*, several *DOF* genes and *ATHB-16*, followed by the up-regulation of genes encoding enzymes related to cell wall structure, seed coat rupture and radicle protrusion (Ogawa et al. 2003, Zentella et al. 2007). The combination of transcriptomic and functional analyses of misregulated genes revealed an even more important role for *GNC* and *GNL*, encoding two GATA-type transcription factors whose loss of function caused increased resistance to DELLA-dependent inhibition of seed germination (Richter et al. 2010).

Extensive phenotypic analysis of loss- and gain-of-function mutants in these two transcription factors also confirmed their participation as negative regulators of gibberellin signaling not only during germination, but also during vegetative growth and in reproductive development. Finally, alternative transcriptomic studies with rice embryoless half seeds also confirmed the role of *SLR1* (the only rice *DELLA* ortholog) upstream of *GAMYB* transcription factors during germination and also in other developmental processes (Tsuji et al. 2006).

New DELLA functions uncovered through transcriptomics

A more exciting outcome of DELLA-related transcriptomic studies is the identification of new, previously unsuspected functions for gibberellins. Such results have been possible through two strategies: (i) meta-analysis of the obtained gene data sets with sets of genes regulated by other pathways; and (ii) the identification of individual genes or groups of genes that link gibberellin signaling with a specific biological process.

As an example, gibberellin-deficient seedlings display a transcriptomic profile in darkness that resembles that of light-grown wild-type seedlings (Cheminant et al. 2011), which is very much in agreement with a role for gibberellins in the repression of photomorphogenesis in darkness (Achard et al. 2007, Alabadí et al. 2004, Alabadí et al. 2008). The overlapping set of genes was strikingly enriched in those coding for proteins that participate in photosynthesis (Achard et al. 2007). Interestingly, gibberellin-deficient plants accumulate large amounts of protochlorophyllide (a phototoxic precursor of Chl), but they are notably more resistant to photooxidative damage when transferred to the light (Cheminant et al. 2011). This is due to the DELLA-dependent up-regulation of *POR*, the gene encoding the enzyme protochlorophyllide oxidoreductase, suggesting a function for DELLA proteins in the protection of plants prior to light exposure. In fact, the key regulator of anthocyanin biosynthesis, *PAP1* (Borevitz et al. 2000), has also been found in transcriptomic analyses as a putative direct target up-regulated by DELLAs (Gallego-Bartolomé et al. 2011a), suggesting that the involvement of DELLAs in the promotion of photoprotection is achieved in different ways. This could be relevant for instance during de-etiolation, but also at the beginning of every diurnal cycle, as suggested in an alternative study in which the circadian regulation of DELLA stability showed an impact in the expression of these and other genes involved in stress resistance (Arana et al. 2011). Indeed, DELLAs probably have a more extensive role in stress resistance than previously suspected. Transcriptomic analysis of DELLA gain- and loss-of-function mutants in response to high NaCl concentrations and meta-analysis with published data revealed that a significant number of genes that respond to oxidative stress were also under the control of DELLA proteins (Achard et al. 2008). These analyses led the way to establishing that stress-induced DELLA accumulation would induce the

expression of genes encoding enzymes for the detoxification of reactive oxygen species, thereby delaying senescence and promoting stress tolerance.

An equivalent study looking for early DELLA target genes in very young dark-grown seedlings showed that DELLA repressed the expression of *MSG2/IAA19* (*MSG2/IAA19*) (Gallego-Bartolomé et al. 2011a, Gallego-Bartolomé et al. 2011c), a gene encoding an Aux/IAA protein that acts as a negative element in the auxin signaling pathway. One of the main functions of this protein is the regulation of auxin action during tropic responses such as gravitropism or phototropism (Tatematsu et al. 2004), and its repression by DELLAs suggested the possible involvement of gibberellins in the modulation of these sorts of responses. Indeed, the hypocotyls of gibberellin-deficient mutants specifically display an enhanced gravitropic reorientation capacity, without affecting phototropism (Gallego-Bartolomé et al. 2011c, Rodrigo et al. 2011). Interestingly, the attenuation of gravitropism by gibberellins through the regulation of *MSG2/IAA19* has been proposed to be particularly relevant to establish plant orientation under competing tropic stimuli, such as during shade avoidance or during seedling emergence from the soil (Gallego-Bartolomé et al. 2011c).

The regulation of *MSG2/IAA19* expression is not the only example of cross-talk between gibberellins and other hormones uncovered through transcriptomics. In the context of hypocotyl gravitropic reorientation and apical hook formation, transcriptional regulation by DELLAs of *PIN7*, encoding an auxin-efflux carrier, can also contribute to the interaction between gibberellins and auxin (Gallego-Bartolomé et al. 2011a, Gallego-Bartolomé et al. 2011b). Also relevant in this context seems to be the gibberellin-dependent up-regulation of *WAG2* on the concave side of the apical hook (Willige et al. 2012). This gene encodes a protein kinase that phosphorylates PIN auxin transporters, and the *wag2* mutant is defective in apical hook maintenance in darkness and in the formation of the auxin gradient across this structure (Willige et al. 2012). The importance of post-translational regulation of PINs by DELLAs has also been proposed in other spatial contexts such as root growth (Willige et al. 2011) and root gravitropism (Lofke et al. 2013).

In addition, *ACC SYNTHASE5* (*ACS5*) and *ACS8*, which encode the key enzyme in ethylene biosynthesis, have also been identified in this way. In particular, their expression is repressed by DELLA proteins, and *dellaKO* mutants have a significantly higher content of ethylene compared with the wild type (Gallego-Bartolomé et al. 2011b). Together with the effects on auxin transport, this molecular interaction very probably contributes to the enhanced curvature of the apical hook associated with high gibberellin activity (Vriezen et al. 2004, Gallego-Bartolomé et al. 2011b, An et al. 2012).

Primary target genes of DELLA proteins

Most of the transcriptomic studies carried out to date in connection with gibberellin signaling do not distinguish between

Table 2 Transcriptional regulators that interact with DELLA proteins

Transcription factor	Family	Physiological context	Reference
PIFs	bHLH	Hypocotyl elongation, apical hook development, Chl synthesis	De Lucas et al. 2008; Feng et al. (2008); Gallego-Bartolomé et al. (2010, 2011b); Cheminant et al. (2011)
SPT	bHLH	Seed germination	Gallego-Bartolomé et al. (2010); Josse et al. (2011)
ALC	bHLH	Fruit development	Arnaud et al. (2010)
MYC2	bHLH	Gibberellin–jasmonic acid cross-talk	Hong et al. (2012)
EIN3	EIL	Gibberellin–ethylene cross-talk, apical hook development	An et al. (2012)
SPLs	SBP-box	Floral induction	Yu et al. (2012)
BES1, BZR1	BES1/BZR1	Gibberellin–brassinosteroid cross-talk	Bai et al. (2012b); Gallego-Bartolomé et al. (2012); Li et al. (2012)
SCL3	GRAS	Seed germination, hypocotyl elongation, root growth	Zhang et al. (2011)
IDD1/ENY	C2H2 Zinc finger	Seed germination	Feurtado et al. (2011)
JAZs	JAZ	Gibberellin–jasmonic acid cross-talk, biotic stress, root growth	Hou et al. (2010); Wild et al. (2012); Yang et al. (2012)
BOIs	RING finger	Seed germination, floral induction	Park et al. (2013)

the primary set of genes directly regulated by DELLA proteins, and those secondary targets that are affected as a consequence of primary alterations.

The first committed approach to the identification of DELLA primary targets was based on the use of transgenic plants expressing the *RGA* gene under the control of a glucocorticoid-inducible promoter (Zentella et al. 2007). In these plants, the application of dexamethasone induced a fast up-regulation of *RGA*, which in turn provoked subsequent transcriptional changes. Among the genes whose expression was quickly altered upon *RGA* induction were those related to gibberellin metabolism, again suggesting that DELLA proteins are intimately linked to the feedback regulatory mechanism that controls gibberellin homeostasis. However, even more importantly, eight of the early target genes were confirmed as direct targets of *RGA* by chromatin immunoprecipitation of their promoter regions, suggesting that DELLAs may act in the vicinity of the target promoters, even if they do not directly bind DNA. Interestingly, among the genes directly up-regulated by *RGA* was *XERICO* (*XER*), which encodes a RING-H2 E3 ubiquitin ligase that promotes ABA synthesis in response to dehydration (Ko et al. 2006), and this up-regulation was in agreement with the repression caused by gibberellin treatments. The induction of *XER* expression by DELLAs could thus represent one of the mechanisms to explain the known antagonistic roles of gibberellins and ABA in different situations, such as germination and floral initiation (Razem et al. 2006). This has been further supported more recently in seeds, where *rgl2* mutants display lower levels of *XER* expression (Piskurewicz et al. 2008), but the relative importance of this particular regulation in the control of ABA synthesis still has to be tested.

A second approach analyzed the transcriptomic response following the conditional induction of the stable *gai-1* allele

under the control of a heat shock-inducible promoter in etiolated seedlings (Gallego-Bartolomé et al. 2011a). With this strategy, around 150 genes were identified based on their rapid up- or down-regulation in response to *gai-1* induction. Subsequent experiments with wild-type and mutant versions of *GAI* and other DELLA proteins indicated that the regulation of these target genes is a general ability of DELLA proteins, and not of *gai-1* in particular. Remarkably, the use of a transgenic line expressing *gai-1* fused to the glucocorticoid receptor (*gai-1:GR*) in combination with cycloheximide showed that DELLAs could regulate the expression of these target genes even in the absence of additional protein synthesis, indicating that this transcriptional control is direct and these genes are primary targets. This mechanism was confirmed for one of them, *ACS8*, for which we showed by chromatin immunoprecipitation that binding of PIF5 to its promoter region was reverted upon DELLA accumulation (Gallego-Bartolomé et al. 2011b).

A general mechanism of transcriptional regulation by DELLA proteins

The mechanism for the regulation of *ACS8* expression based on the sequestration of PIF5 by DELLAs is just another example of the relevance that the DELLA–PIF interaction has for transcriptional regulation in response to gibberellins (de Lucas et al. 2008, Feng et al. 2008). Importantly, the stability of these growth-promoting transcription factors is decreased by light, which means that this interaction represents a cross-talk node between gibberellin and light signaling (Davière et al. 2008). In agreement with this model, there is a significant overlap between DELLA- and PIF-dependent transcriptomes, and an

enrichment of G- and E-boxes (the *cis*-regulatory elements recognized by PIFs) in the promoters of DELLA targets (Gallego-Bartolomé et al. 2011a). In fact, the physiological relevance of this mechanism is strengthened by the observation that DELLA accumulation oscillates in a circadian fashion, and the lowest DELLA levels coincide with PIF peaks at the end of the night, resulting for instance in maximal cell expansion rates (Arana et al. 2011). Apart from PIFs, other basic helix–loop–helix (bHLH) transcription factors have also been identified as DELLA interactors, such as ALCATRAZ (ALC) (Arnaud et al. 2010) and SPATULA (SPT) (Gallego-Bartolomé et al. 2010, Josse et al. 2011) (Table 2).

However, the comparison between the temporal transcriptomic patterns in a *dellaKO* mutant and in the wild type indicates that DELLA proteins also regulate gene expression in daily phases in which PIFs are not present (Arana et al. 2011). This observation agrees with the enrichment of *cis*-elements other than G- or E-boxes in the promoters of DELLA targets during seedling growth (Gallego-Bartolomé et al. 2011a) and also during seed imbibition (Stamm et al. 2012). Therefore, DELLA proteins could act through alternative transcription factors to control the same and other physiological processes. Indeed, DELLAs interact with transcription factors other than bHLHs (Table 2); for instance, with the C2H2 zinc finger protein IDD1/ENY (Feurtado et al. 2011), BES1 and BZR1 (Bai et al. 2012b, Gallego-Bartolomé et al. 2012, Li et al. 2012), EIN3 and its paralog (An et al. 2012), MYC2 (Hou et al. 2010, Hong et al. 2012) and the SPLs (Yu et al. 2012), as well as with the transcriptional regulators that do not bind DNA directly, including SCL3 (Zhang et al. 2011), several members of the JAZ (jasmonate ZIM-domain) family (Hou et al. 2010, Wild et al. 2012, Yang et al. 2012) and the four members of the BOI family (Park et al. 2013). Some of the interactions with these non-DNA-binding transcriptional activators have been confirmed as biologically relevant. For example, gibberellins modulate jasmonic acid signaling and the response to pathogens (Navarro et al. 2008) through the DELLA–JAZ interaction (Hou et al. 2010, Wild et al. 2012).

Moreover, the activation by RGL2 of reporter constructs under the control of *cis*-elements recognized by DOFs in Arabidopsis protoplasts (Stamm et al. 2012) suggests that the activity of these transcription factors might also be subjected to regulation by DELLAs. Thus, the modification of the activity of transcription factors, either by sequestration or by interaction at the target promoters (Fig. 2), could constitute a widespread strategy for transcriptional regulation by gibberellins involving DELLAs. In addition, it has been observed that gibberellins affect histone methylation at the *GA 20ox1* gene in tobacco (Fukazawa et al. 2010), possibly to regulate the binding of the RSG transcription factor to this promoter, which suggests that gibberellins might also regulate transcription through the interference with chromatin remodeling. This exciting possibility is further supported by the extensive overlap between genes regulated by gibberellins and by BRAHMA, a member of the SWI/SNF complex involved in

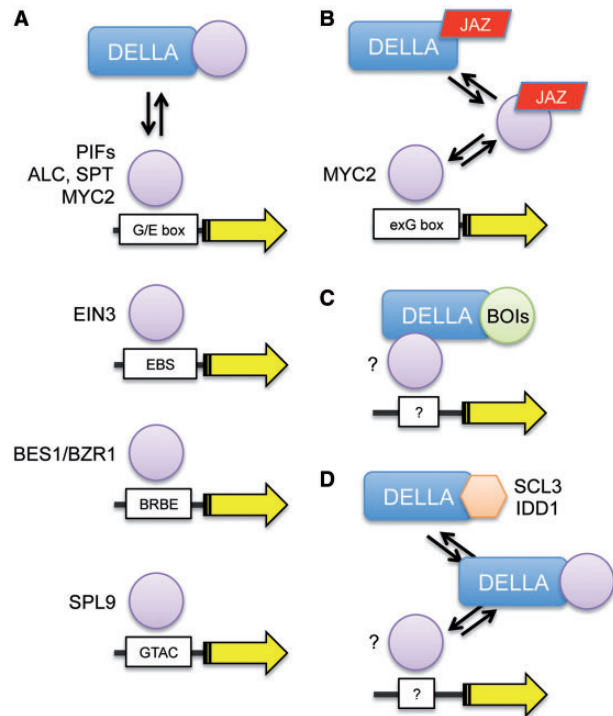


Fig. 2 Mechanism of DELLA-mediated transcriptional control. Based on current experimental evidence gathered through the combination of genomic and molecular genetic studies, DELLAs regulate gene expression through at least three mechanisms. (A) Sequestration of DNA-binding transcription factors that induce or repress the target genes. This has been demonstrated for the bHLH transcription factors of the PIF family, for the brassinosteroid-dependent BES1 and BZR1 transcription factors, for EIN3 (which binds to the ‘EBS’ element [ATTTCAAA] and regulates the expression of *HOOKLESS1*), and has been proposed for the interaction with SPL9 and other SPLs (which bind *cis*-elements with the core GTAC sequence), for ALCATRAZ (ALC) (an additional bHLH transcription factor that regulates the expression of genes involved in ovary/fruit morphology) and for SPATULA (whose genetic interaction with DELLAs predicts mutual functional interference). (B) Interaction with the JAZ negative regulators of jasmonate signaling, thereby relieving the repression of MYC2 transcriptional activity. This mechanism is further supported by the enrichment of MYC2-binding sites (extended G-boxes) in the promoters of DELLA primary targets identified with genomic tools. (C) The presence of DELLA in transcriptional complexes, as indicated by chromatin immunoprecipitation studies on DELLA primary targets. The modifications caused by DELLA in this case, and the corresponding interacting partners are unknown, although the BOI RING finger proteins might act through this mechanism. (D) Other known interactors of DELLA proteins, such as SCL3 and IDD1, might reflect an additional layer of regulation through which these partners would modulate the ability of DELLAs to interact with DNA-binding transcription factors (PIFs and others). Genetic interactions agree with the model presented here, but molecular proof is not available yet.

chromatin remodeling, in Arabidopsis (Archacki et al. 2013). Nonetheless, it is not clear at this point to what extent BRAHMA regulates the common genes in a DELLA-dependent or -independent manner.

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