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A DELLAcate balance: the role of gibberellin in plant morphogenesis

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The importance of gibberellin (GA) in vegetative and reproductive development has been known for some time. Recent studies have uncovered new roles of GA in leaf differentiation, photomorphogenesis and pollen-tube growth. Significant contributions to our understanding of GA-regulated morphogenesis include the identification of upstream regulators of GA biosynthesis, the elucidation of the function of GA signaling components, and the isolation of downstream targets. In addition, the mechanisms of interactions between GA and other hormone pathways are beginning to be revealed at the molecular level.

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Abbreviations

ABA	abscisic acid
AGL15	AGAMOUS-LIKE15
AP	APETALA
BEL	BELL
DDF1	DWARF AND DELAYED FLOWERING1
FUS3	*FUSCA3*
GA	gibberellin
GA20ox	GA 20-oxidase
GAI	GA-INSENSITIVE
GFP	green fluorescent protein
GID2	GA-INSENSITIVE DWARF2
KNOX	KNOTTED1-like homeobox
LEC	LEAFY COTYLEDON
LFY	LEAFY
LUE1	*LUCIFERASE SUPER-EXPRESSOR1*
PKL	PICKLE
POTH1	*POTATO HOMEOBOX1*
RGA	*Repressor of ga1-3*
RGL1	*RGA-like1*
RSG	REPRESSION OF SHOOT GROWTH
SLN1	*SLENDER1*
SLR1	*SLENDER RICE1*
SLY1	SLEEPY1
SNE	SNEEZY
SOC1	SUPPRESSOR OF CONSTANS1
SPY	SPINDLY

Introduction

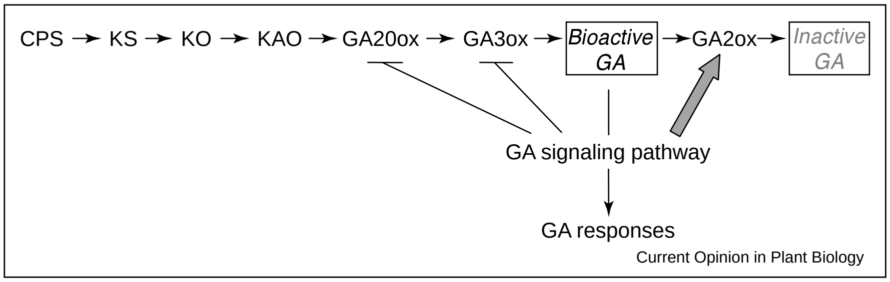
The plant hormone gibberellin (GA) has long been known to modulate development throughout the plant life cycle. Mutants that are impaired in GA biosynthesis or response tend to have small and dark green leaves and reduced stem length. Some of them are also defective in seed germination and floral development, and are delayed in flowering time (see [1•,2,3] for reviews). Conversely, plants with increased GA levels or GA signaling have a tall and spindly phenotype (reviewed in [4]).

Insight into mechanisms of GA-regulated plant growth and development has been gained from research into both GA biosynthesis and signaling pathways. The genes encoding GA biosynthetic enzymes (Figure 1) have been identified in numerous species. Among these enzymes, GA 20-oxidase (GA20ox) and GA 3-oxidase (GA3ox), corresponding to the last portion of GA biosynthesis, are particularly important for control of bioactive GA levels. In addition to biosynthesis, GA levels are also modulated by catabolism via GA2ox enzymes (Figure 1) and by feedback regulation through activity in the GA-response pathway. Transcript levels of some of the *GA20ox* and *GA3ox* genes are downregulated, whereas *GA2ox* genes are upregulated by elevated GA signaling or GA treatment (reviewed in [3,5,6]).

GA biosynthetic genes are expressed in specific cell- and tissue-types during development, and their transcript levels are often elevated in rapidly growing regions, such as the rib meristem of shoot apex, elongating internodes, developing anthers and embryo axes [3]. In rice, *GA20ox* and *GA3ox* are expressed in a pattern similar to that of GA signaling genes [7•], further suggesting that GA may be synthesized at the site of perception. Recent studies also suggest, however, that GA made in anthers and developing embryos is probably transported to regulate the growth of other floral organs and fruits. Similarly, GA that is synthesized in the embryo during seed germination needs to be transmitted to aleurone cells to induce the expression of hydrolytic enzymes [7•,8••].

GA signaling operates as a de-repressible system that is moderated by DELLA-domain proteins, which are transcriptional regulators that repress GA responses (Figure 2). DELLA proteins are highly conserved among

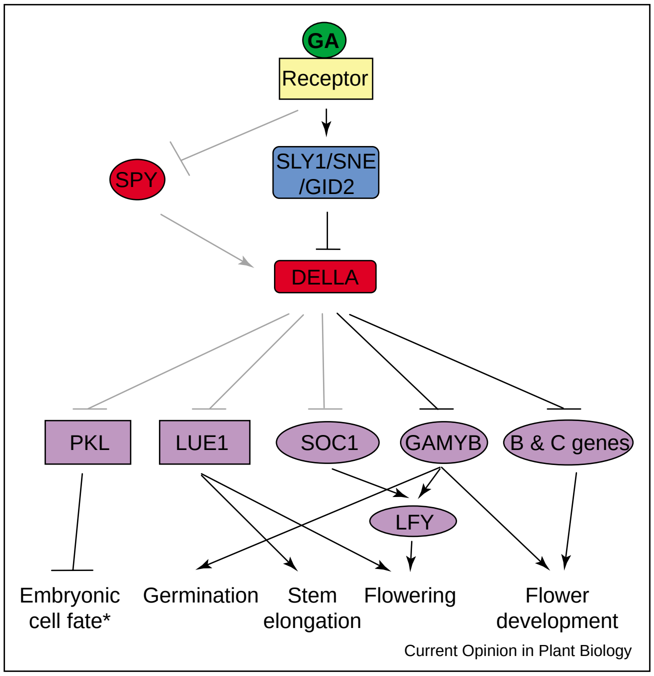
Figure 1



GA biosynthetic and catabolic enzymes, and feedback regulation of GA biosynthesis by the GA-response pathway. Bioactive GAs are synthesized from geranyl geranyl diphosphate via multiple enzymes that catalyze sequential steps in the pathway. Boxed italic text indicates metabolites. T-bars indicate the inhibition of gene expression, the block arrow indicates the promotion of gene expression. GA homeostasis is achieved by a feedback mechanism. An elevated activity in the GA-response pathway downregulates transcript levels of some of the *GA20ox* and *GA3ox* genes, but upregulates transcript levels of *GA2ox* genes. CPS, copalyl diphosphate synthase; GA2ox, GA 2-oxidase (encoded by multiple genes); GA3ox, GA 3-oxidase (encoded by multiple genes); GA20ox, GA 20-oxidase (encoded by multiple genes); KAO, *ent*-kaurenoic acid oxidase; KO, *ent*-kaurene oxidase; KS, *ent*-kaurene synthase.

different species, including *Arabidopsis*, barley, *Brassica*, grape, maize, rice, and wheat (reviewed in [1•]). A single DELLA protein gene is present in rice and barley (*SLENDER RICE1* [*SLR1*] and *SLENDER1* [*SLN1*], respectively) and functions to repress all aspects of GA responses in these species. Surprisingly, five DELLA protein genes (*GA-Insensitive* [*GAI*], *Repressor of ga1-3* [*RGA*], *RGA-like1* [*RGL1*], *RGL2* and *RGL3*) have been identified in *Arabidopsis*, with RGA and GAI being the major GA repressors during vegetative growth and floral induction [3,4]. During seed germination, RGL2 plays a major role, whereas RGA, RGL1 and RGL2 together modulate flower development [9,10•,11•].

Figure 2



Model of the GA signaling pathway. Ovals represent transcription factors, gray lines indicate hypothesized interactions. Arrows and T-bars indicate direct or indirect activation and inhibition, respectively. B genes encode PI and AP3; the C gene in this pathway encodes AGAMOUS; DELLA includes RGA, GAI, RGLs, SLR1, SLN1, and other orthologs. *PKL inhibits embryonic cell fate during post-embryonic development.

In response to GA, DELLA proteins are rapidly degraded by the ubiquitin-proteasome pathway [12•]. F-box proteins that mediate this degradation (as part of the E3 ubiquitin ligase SCF [Skp1-Cullin-F-box] complex) have been identified in *Arabidopsis* (SLEEPY1 [SLY1]) and rice (GA-INSENSITIVE DWARF2 [GID2]) [13••,14••]. Other components of GA responses include the positive regulator PHOTOPERIOD-RESPONSIVE1 (PHOR1) of potato, which shows similarity to the U-box ubiquitin E3 ligase and might also be involved in the degradation of DELLA proteins [15], and the negative regulator, SPINDLY (SPY), an *O*-linked *N*-acetylglucosamine transferase that has been identified in *Arabidopsis*, barley and petunia, and is hypothesized to modify and activate DELLA proteins (Figure 2; [1•,3,4]). In addition, the chromatin-remodeling factor PICKLE (PKL) is thought to function as a positive regulator of GA response [1•,4].

An important downstream component of GA response is the GA-inducible transcription factor GAMYB. This transcription factor was first identified for its role in promoting α-amylase expression in germinating barley seeds (reviewed in [16]), but GAMYB homologs have now been identified in other species. In addition to GAMYB, GA is known to induce the expression of GLABROUS1, a transcription factor that is required for trichome production, consistent with the role of GA in regulating trichome initiation and branching [17].