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The gibberellin GID1-DELLA signalling module exists in evolutionarily ancient conifers

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Gibberellins (GAs) participate in controlling various aspects of basic plant growth responses. With the exception of bryophytes, GA signalling in land plants, such as lycophytes, ferns and angiosperms, is mediated via GIBBERELLIN-INSENSITIVE DWARF1 (GID1) and DELLA proteins. To explore whether this GID1-DELLA mechanism is present in pines, we cloned an orthologue (*PtGID1*) of *Arabidopsis AtGID1a* and two putative DELLA proteins (PtDPL; PtRGA) from *Pinus tabuliformis*, a widespread indigenous conifer species in China, and studied their recombinant proteins. PtGID1 shares with AtGID1a the conserved HSL motifs for GA binding and an N-terminal feature that are essential for interaction with DELLA proteins. Indeed, *A. thaliana 35S:PtGID1* overexpressors showed a strong GA-hypersensitive phenotype compared to the wild type. Interactions between PtGID1 and PtDELLAs, but also interactions between the conifer-angiosperm counterparts (i.e. between AtGID1 and PtDELLAs and between PtGID1 and AtDELLA), were detected *in vivo*. This demonstrates that pine has functional GID1-DELLA components. The Δ17-domains within PtDPL and PtRGA were identified as potential interaction sites within PtDELLAs. Our results show that PtGID1 has the ability to interact with DELLA and functions as a GA receptor. Thus, a GA-GID1-DELLA signalling module also operates in evolutionarily ancient conifers.

Gibberellins (GAs) are a class of phytohormones that function in a wide range of basic plant growth responses. These GA-mediated responses include seed germination, stem elongation, shade avoidance (in competitive interactions), leaf expansion, pollen maturation, and induction of flowering[1–4], but GAs can also induce temporary growth arrest under adverse environmental conditions[5]. Regarding our understanding of the GA signalling pathways *in planta*, progress has been made in the past few years primarily in rice[6] and *Arabidopsis thaliana*[7].

Angiosperms use the GA-GID1 (GIBBERELLIN-INSENSITIVE DWARF1)-DELLA pathway, which involves the nuclear GA receptor GID1[8], the repressor DELLA protein[9,10], and the F-box protein GID2/SLY1, which degrades the repressor DELLA protein to trigger GA-mediated downstream responses[5,11,12]. Although it has not yet been thoroughly studied, GA signalling in conifers should also follow the GID1-DELLA pathway; this molecule is present in early vascular plants such as the lycophyte *Selaginella moellendorffii*[13], but not in non-vascular bryophytes[14]. Hence, GID1-mediated GA signalling likely appeared after the divergence of vascular plants from mosses, which took place ~430 million years ago[15].

Arabidopsis thaliana possesses at least 10 similar DNA sequences for GID1, of which only three (*AtGID1a*, *AtGID1b*, and *AtGID1c*) encode proteins that function as GA receptors[16]; conversely, there is only one GID1 gene in rice (*OsGID1*). *At*GID1b is unique in that it can also interact with DELLAs in the absence of GA[17], indicating that there are GA-independent pathways for this interaction. However, *GID1* overexpression leads to a GA overdose phenotype, where plants are tall with long, light green leaves, fewer tillers, and dramatically reduced fertilities[8]. Leaf expansion, and stem and root elongation are reduced in *gid1*-knockout mutants, which is consistent with the GA-deficient phenotype[18].

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