



The makings of a gradient: spatiotemporal distribution of gibberellins in plant development

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The gibberellin phytohormones regulate growth and development throughout the plant lifecycle. Upstream regulation and downstream responses to gibberellins vary across cells and tissues, developmental stages, environmental conditions, and plant species. The spatiotemporal distribution of gibberellins is the result of an ensemble of biosynthetic, catabolic and transport activities, each of which can be targeted to influence gibberellin levels in space and time. Understanding gibberellin distributions has recently benefited from discovery of transport proteins capable of importing gibberellins as well as novel methods for detecting gibberellins with high spatiotemporal resolution. For example, a genetically-encoded fluorescent biosensor for gibberellins was deployed in *Arabidopsis* and revealed gibberellin gradients in rapidly elongating tissues. Although cellular accumulations of gibberellins are hypothesized to regulate cell growth in developing embryos, germinating seeds, elongating stems and roots, and developing floral organs, understanding the quantitative relationship between cellular gibberellin levels and cellular growth awaits further investigation. It is also unclear how spatiotemporal gibberellin distributions result from myriad endogenous and environmental factors directing an ensemble of known gibberellin enzymatic and transport steps.

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Introduction

Plants use phytohormones—a suite of mobile small molecules—as potent regulators that coordinate and adjust development to suit environmental conditions. The gibberellin phytohormones were discovered nearly a century ago when delivery of a gibberellin was revealed to be the mechanism by which a fungal plant pathogen, *Gibberella fujikuroi* (now reclassified as *Fusarium fujikuroi*),

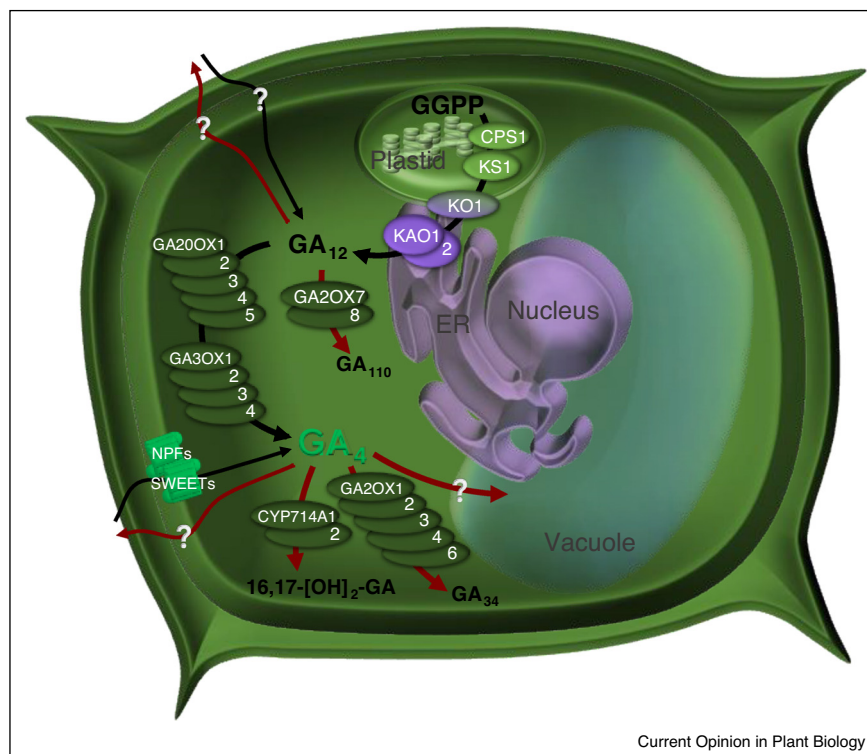
tailors the growth of infected rice plants [1]. Plant breeders have since tailored the growth of cereal crops for dramatic yield increases through genetic manipulation of gibberellins or DELLA proteins involved in gibberellin signalling [2]. Farmers have even used direct application of gibberellins or gibberellin inhibitors to tailor the growth of crops, for example to increase the size of table grapes [3]. The success of these human and microbial strategies for regulating plant growth depends on the ability of gibberellins to influence plant growth in a variety of developmental contexts, and thus answering the question of where and when endogenous gibberellins influence plant development has been of great interest for several decades. This review will focus on recent developments as the spatiotemporal distribution of gibberellins has of late received significant attention.

Timely accumulation of gibberellins in specific tissues is relevant for organ size and morphology as well as for key developmental transitions. Gibberellin levels are low in dry mature seeds, but after imbibition and exposure to light [4], *de novo* gibberellin biosynthesis promotes germination, in part through stimulating cell division and expansion in the radicle [5]. Accumulation of gibberellins in the shoot apical meristem of short-day grown *Arabidopsis* is required for the transition to flowering, but gibberellin catabolism is subsequently required for normal development of the inflorescence [6]. Gibberellins are also mobile across cells and organs, for example in *Pisum sativum*, where growth of gibberellin mutant pea plant scions was complemented after grafting to wild-type root-stocks [7]. The spatiotemporal distribution of gibberellins influencing these and other aspects of plant development is the result of an ensemble of distinct and independently regulated enzymatic and transport activities.

Gibberellin biosynthesis, catabolism and transport

Gibberellin biosynthesis in plants proceeds in stages defined by three cellular compartments: plastids, endoplasmic reticulum (ER) and cytoplasm [8] (Figure 1). The first steps occur in the plastids where *ent*-copalyl diphosphate synthase and *ent*-kaurene synthase promote the conversion of geranylgeranyl diphosphate to *ent*-kaurene. In the ER, two membrane-associated cytochrome P450 monooxygenases (CYP), *ent*-kaurene oxidase and *ent*-kaurenoic acid oxidase, convert *ent*-kaurene to gibberellin A₁₂ (GA₁₂) though *ent*-kaurene oxidase also associates with the outer envelope of plastids thereby bridging

Figure 1



Gibberellin biochemistry in Arabidopsis. Model of subcellular localization of gibberellin biosynthetic and catabolic pathways as well as putative intra/intercellular movements of gibberellins. Gibberellin accumulation and depletion steps are depicted with black and red arrows, respectively. Biosynthetic steps occur in the three cellular compartments (plastids, endoplasmic reticulum (ER) and cytoplasm); the corresponding enzymes are reported with the following nomenclature: *ent*-copalyl diphosphate synthase, CPS; *ent*-kaurene synthase, KS; *ent*-kaurene oxidase, KO; *ent*-kaurenoic acid oxidase, KAO; gibberellin 20-oxidase, GA20ox; gibberellin 3-oxidase, GA3ox. Gibberellin deactivation enzymes convert either precursors or bioactive gibberellins into inactive catabolites. Shown here are members of GA2ox and CYP714A families. Transporters belonging to NPF and SWEET families import extracellular GA₄. Potential mechanisms for GA₄ export and GA₁₂ transport remain poorly understood.

plastid and ER steps of the pathway [9]. The last steps occur in the cytoplasm where enzymes belonging to GIBBERELLIN 20 OXIDASE (GA20ox), and GIBBERELLIN 3 OXIDASE (GA3ox) families promote the final conversions into bioactive GA₁ and GA₄. For individual family members of the five GA20ox and four GA3ox enzymes in Arabidopsis, promoter-reporter fusions driving β -glucuronidase (GUS) revealed highly localized expression domains, while genetic studies revealed overlapping functions [10–13]. For example, *AtGA3ox1* is expressed in stamen filaments and *AtGA3ox2–4* are expressed in anthers, but mutation of *AtGA3ox1* results in silique fertility defects only in combination with mutation of *AtGA3ox3* [10,11].

Gibberellin can be inactivated through at least three distinct mechanisms as evidenced by biochemical and genetic studies in Arabidopsis and rice [14–17]. Precursors and bioactive gibberellins are substrates of GA METHYL TRANSFERASE (GAMT), GIBBERELLIN 2 OXIDASE (GA2ox) and CYP714A catabolic enzymes and higher order mutants in the GA2ox and

CYP714A classes display gibberellin overproduction phenotypes. As for Arabidopsis gibberellin biosynthetic genes, the eight *AtGA2ox*, two *AtGAMT* and two *AtCYP714A* genes exhibit localized expression patterns in various organs and developmental stages, potentially serving to modulate gibberellin spatiotemporal distributions initiated by patterns of gibberellin biosynthesis [14–16].

Gibberellin transport can also affect spatiotemporal distributions, because gibberellins are known to be mobile over short and long distances in plants. Gibberellin movements have been associated with inducing flowering in Arabidopsis [18] and sex determination in *Lygodium japonicum* ferns [19]. More recently, movements of gibberellins have been also discovered in cucumber, where GA₉ moves from ovaries to sepal and petal tissues where it is converted to the bioactive GA₄ [20]. In Arabidopsis, GA₁₂ is the GA₄ precursor associated with long-distance transport; it has been suggested that GA₁₂ moves from root to shoot via the xylem and from photosynthetic source to sink tissues via the phloem [21,22].

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