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**Article:**

Bennett, T [orcid.org/0000-0003-1612-4019](https://orcid.org/0000-0003-1612-4019) (2020) The evolution of hormonal signalling in plant development. *Seminars in Cell & Developmental Biology*. ISSN 1084-9521

<https://doi.org/10.1016/j.semcdb.2020.09.002>

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# The evolution of hormonal signalling in plant development

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Key words: Phytohormones; long-distance signalling; strigolactone; cytokinin; gibberellin; auxin; plant development; plant evolution

Plant hormones have long been recognised as key regulators of plant growth and development. As demonstrated by a very significant body of research, almost every developmental process in seed plants is subject to regulation by hormonal signals. And, where examined, it is clear that hormonal signals are very important in the growth and development of the bryophytes (mosses, liverworts, hornworts) and non-seed vascular plants (lycophytes and monilophytes). However, it is also clear that there are fewer hormonal signals in bryophytes than in seed plants; there has thus been considerable innovation in hormonal signalling during the evolution of land plants. In putting together this special issue of *Seminars in Cell & Developmental Biology*, my aim has been to provide a series of insights into the evolution of hormonal signalling in land plants, highlighting some of the excellent ongoing research in this field. From an editorial perspective, there were three key questions that underpinned development of the special issue. Firstly, what is a plant hormone, and therefore what are the hormones in plants? Secondly, when and how did these hormonal signalling evolve (and continue to evolve) in land plants? And thirdly, why did hormonal signalling evolve to be such a key developmental mechanism in land plants, and particularly in seed plants?

The answer to the first question is essentially matter of opinion. Plant hormones were named by analogy to animal hormones, but clearly do not fit the same definition; they are not synthesised in specific tissues, and they do not have specific effects in specific tissues either. Strictly speaking, none of them are hormones at all, but that is clearly not a helpful approach! We might therefore define plant hormones as “mobile signalling molecules that act primarily in communication between tissues”. This is rather vague and unsatisfying, but it is exactly the nature of the ‘core’ hormonal signals in plants that they defy precise functional or structural classification. The proposed definition certainly includes the nine ‘canonical phytohormones’; auxin, cytokinins, gibberellic acid (GA), strigolactones, brassinosteroids, which are primarily developmental hormones; and abscisic acid (ABA), ethylene, jasmonic acid (JA) and salicylic acid (SA), which are primarily stress hormones. And it excludes molecules that are mobile but primarily involved in metabolism. But in between, the definition would seem to include a large number of additional molecules that act in a comparable way to these canonical phytohormones. For instance, a significant number of additional low molecular weight signals likely act as hormones, and in this issue, Wang et al [1] review progress in identifying new carotenoid-derived signalling molecules, and their evolution. Furthermore, members of several protein families, including small peptides of the CLE, CEP and phytosulfokine classes, and the rather larger PEPB proteins, have also been shown to act in a hormonal manner in flowering plants. In this issue, Whitewoods [2] and Jin et al [3] explore the evolution of CLE and PEPB hormonal signalling in land plants, respectively.

Thanks to a recent series of studies exploiting newly available genomic information across land plants, it is possible to give somewhat clearer answers to the second question, though the picture is still complex. Overall, hormonal signalling pathways seem to have evolved gradually by the

recruitment of signalling pathways – either *de novo* or by reconfiguration of existing pathways – for pre-existing molecules. In most cases, the nine canonical phytohormones are ancient molecules, but not necessarily ancient hormones. As discussed by Rashotte in this issue [4], cytokinin signalling predates land plants, and evolved through the assembly of previously unconnected factors in charophyte algae. The story is similar for ethylene signalling, which also predates land plants [5], while ABA and auxin signalling both evolved at the base of land plants. Sussmilch & McAdam describe the evolution of ABA signalling in this issue [6], and discuss its changing functions through land plant evolution. The auxin signalling pathway also evolved by *de novo* assemblage of a signalling pathway from previously unconnected proteins [7]. The specific transport of auxin, which plays key roles in development across land plants, may have evolved even earlier [8]. Both JA and SA *might* be ancestral hormones in the land plant lineage. The JA signalling pathway is present in bryophytes, but JA is not – and a different ligand (dn-ODPA) uses the signalling pathway instead [9]. It is currently unclear which of JA and ODPA is the ancestral ligand. For SA, most components of the signalling pathway are present in bryophytes, but it has not been shown that SA acts through it, although there is certainly some evidence for effects of SA in liverworts [10]. Conversely, as discussed in this issue by Hernández-García et al [11], GA is not an ancient molecule or hormone in land plants, but both the molecule and its signalling pathway specifically evolved in vascular plants. Brassinosteroids are ancient molecules [12], but only seem to act as hormonal signals in vascular plants [13], though evolution of their signalling pathway is not well understood. Strigolactones are also ancient molecules in land plants, but seem to be the ‘youngest’ of the phytohormones, with the evolution of the canonical strigolactone signalling pathway only occurring in seed plants by duplication of a pre-existing signalling pathway – although there may have been convergent evolution of strigolactone perception in mosses [14].

And so to the final question; why is hormonal signalling so important in land plants? Land plants are exposed to highly heterogeneous and stressful environmental conditions (especially compared to marine algae), and have an extensive requirement to coordinate growth and physiology across different functional tissues in response to these conditions. However, the required responses are usually slow and simple, and need to filter out short-term environmental fluctuation. Unlike animals, plants do not require a complex nervous system to coordinate fast and complex movements in response to the environment. Simple hormonal signalling systems fulfil the same general purpose, but better adapted to the lifestyle of plants - and much cheaper to operate. Nevertheless, as Wheeldon and Bennett argue in this issue [15], where the complexity of plants, the specialization of their tissue systems and the distances over which communication is required have increased, so has the complexity of the signalling systems. The simplicity and ubiquity of plant hormone signalling systems therefore reflects not the simplicity of plants, but the most simple and elegant solution to the problem of coordinating responses to the environment.

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