Book review

Vascular differentiation and plant hormones. R. Aloni, 339 pp., illus. 2021. Springer Nature Switzerland, Cham, ISBN 978-3-030-53201-7 (hardcover, €108.99) and 978-3-030-53202-4 (e-book, €85.59).

Vascular differentiation in plants is among the most fascinating fields in botany. In my student days in the 1960s, our Botany Department at Leiden University had just installed an experimental laboratory to study vascular differentiation and related processes in *in vitro* tissue cultures. We were taught to distinguish three distinct aspects: (1) determination (why are certain cells destined to turn into cambial initials or vascular elements?); (2) differentiation proper (the actual developmental process of divergence from the mother cells); and (3) lignification (a crucial component of xylem development within vascular systems). Plant hormones were very much at the centre of many pioneering studies, duly cited by Roni Aloni in his new book. So “*Vascular Differentiation and Plant Hormones*” gave me a welcome opportunity to learn how far we have advanced in the last 50 years.

The book is organised into 21 chapters, that are each concluded by concise summary statements and rich bibliographies for further reading. Following a general introduction, chapter 2 describes the structure, development, and patterns of primary, secondary, and regenerative vascular tissues. This chapter is well illustrated and provides the anatomical basis for later chapters. There are a few details that may confuse the uninitiated reader, for instance, the impression is given that torus-margo bordered pits are typical for all intertracheid contacts, instead of being restricted to a majority (but not all) of the conifers. I also do not think that due to intercellular spaces between compression wood tracheids, heavily lignified compression wood is favoured by the paper industry for easy fibre separation in pulping.

Chapter 3 introduces the main hormonal signals that regulate vascular differentiation: auxin (IAA), the young leaf signal; gibberellins, the mature leaf signals; cytokinins, the root cap signals; ethylene, the gaseous signal; abscissic acid (ABA) the regulator of stress responses (and not so much of leaf or branch abscission as the name would suggest); jasmonates, to activate defence responses; brassinosteroids (BRs), strigolactones (SLs) and florigen are also briefly discussed. Crucially, the chapter ends by emphasising “cross-talk” between these different signalling biomolecules in complex processes such as vascular differentiation, opening up possibilities for multiple morphogenetic scenarios.

Chapter 4 is devoted to the importance of phosphate and nitrate in soils, impacting respectively on strigolactone and cytokinin levels in the roots, and thereby affecting root development.

Chapter 5 takes a central position as it deals with phloem and xylem differentiation promoted by low versus high levels of auxin, which in turn induce complete (xylem) or partial (phloem) programmed cell death in the conducting elements. Genome analysis suggests that auxin signalling pathways had already evolved in early nonvascular plants. This chapter also contains much detail on gene expression, transcription factors, and master switches involved in the differentiation processes, and the — in my opinion questionable — use of cultured mesophyll cells of *Zinnia elegans* as proxies for tracheary elements.

Chapter 6, on apical dominance, describes the competition for hormonal signal in the shoot (auxin) and root (cytokinin) in interplay with gibberellins, sugars, and strigolactone, which explains this phenomenon. Chapters 7 and 8 deal with leaf and flower development and their intricate vascularisation under hormonal and genetic control. Chapter 9 discusses the origin of lateral roots and elegantly shows that they can be initiated by ethylene produced by young protoxylem vessels near the pericycle. Chapter 10, on vascular regeneration and grafting, describes very interesting natural and manipulated de- and re-differentiation phenomena in xylem and phloem, as orchestrated by plant hormones — crucial for establishing vascular continuity in growing trees and graft-scion contacts. Regulation of cambial activity (chapter 11) is a key subject for understanding tree growth forest dynamics. Here the roles in cambial activity of auxin, gibberellins, cytokinins, and ethylene are discussed separately, before dealing with the mechanisms underlying cambial dormancy, the role of the social status of the tree, and woodiness versus herbaceousness. Although rich in useful information, I missed an attempt to understand quantitative fluctuations in cambial activity (radial increment) in terms of hormonal mechanisms. Chapter 12, on the regulation of juvenile–adult transitions and rejuvenation, is somewhat disappointing — there is conflicting evidence on hormonal mechanisms for softwoods and hardwoods. The author takes issue with the concept of “*cambial age*” because hormonal rejuvenation has been demonstrated in experiments. I am not sure whether that completely disqualifies the concept — food for thought.

Chapter 13, on the control of tracheid size, vessel widening, and vessel density along the plant axis, is a very important one in my opinion: it reiterates and strengthens the well-known auxin gradient or six-point hypothesis first proposed by Aloni and Zimmermann in 1983 and gives a holistic explanation of general patterns of conduit widening and decreasing vessel density at increasing distances from the shoot apex. These patterns, going back to Sanio (1872), have received renewed interest in recent years in work by Olson, Anfodillo, and others as bare necessities for optimal hydraulic architecture and now have their causal morphogenetic/hormonal mechanism presented in this book. Of course, questions remain — e.g., how to bring the “linear” conduit widening hypothesis in line with the wave-like concentration patterns of auxin along the trunk’s axis revealed by Wodzicki *et al.* in 1987? Chapter 14, on circular vascular tissues, vessel endings, and tracheids in organ junctions, offers a coherent hypothesis on the functions of hydraulic segmentation at branch-trunk and leaf-stem junctions and hormonal flows resulting in high auxin levels as underlying causal mechanisms.

Ray differentiation and radial pathways are discussed in chapter 15. Radial ethylene flows in cross-talk with axial auxin and gibberellin flows are held responsible for common developmental patterns. The well-documented relationships between vessel diameter and density, and plant size in non-stressed and stressed woody plants are elegantly explained in chapter 16 by Aloni’s 3-point vascular adaptation hypothesis, in combination with the six-point auxin gradient hypothesis mentioned above for vessel widening as a function of distance to the shoot apex. This relationship interestingly also holds true for protoxylem vessels in monocots such as *Zea mays*. Chapter 17, on regular and traumatic resin ducts in conifers, reports on the roles of hormones like auxin, jasmonate, and ethylene in their development; the latter are especially operative in the initiation of traumatic ducts. Chapter 18, on reaction wood (compression wood and tension wood) formation, cites from the large body of partly conflicting literature and sensibly concludes that hormonal mechanisms need further elucidation.

Wood evolution, discussed in chapter 19, speculates that auxins have driven the origin of vessel perforations and that gibberellins were responsible for fibre specialisation. I find this unconvincing because the experimental evidence of pathological rather than normal perforations induced in a conifer, and the promotion of *phloem* fibre formation in the vessel-bearing gymnosperm *Ephedra* cannot be used as evidence on the course of wood evolution. The hormonal control of ring-porosity, an evolutionary specialisation of deciduous dicots is discussed more robustly.

Chapter 20, on host-parasite interactions and gall-induction by insects, reinterprets these phenomena as hormonal manipulation of vascular development in the hosts by the parasite or gall-inducing insect, fine-tuning hydraulic architecture to the parasite’s or insect larvae’s advantage. Although auxin and cytokinin synthesis by gall-inducing insects has been demonstrated, no success has been achieved in inducing highly structured galls by the application of these hormones in special concentrations and ratios. Stress hormones in the host, like jasmonic acid and salicylic acid, act in partial defence of the host to holoparasites. Chapter 21, the last chapter, deals with plant tumours, such as crown galls with their fairly highly organised vascular organisation, and finally compares plant tumours with animal (including human) tumours. Cross talk between these very different subjects has lead — *inter alia* — to promising applications of plant hormones like jasmonates in human cancer therapy.

So this book clearly shows the enormous advances in our understanding of hormonal control in vascular differentiation. If the reader is confused by the above summary statements on the roles of plant hormones, that confusion is caused by the multiple roles that these hormones play, sometimes synergistically, often antagonistically, in very complex processes. Causal explanations then need sophisticated experimental evidence, and in many cases that evidence is lucidly presented and nicely illustrated by the author. Where such evidence is not yet robust, Aloni has confidently offered various cause-and-effect hypotheses that need further testing. It is anticipated that this book will stimulate much new research on hormonal control of vascular differentiation — a field that is not only relevant in general plant biology, but that also has important applications in agriculture and forestry. For me, it provided much food for thought.

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