
Preface

1. Building Plant Organs

1.1. Plant Organs: What Are They? Where Are They From? How Are They Connected?

Next to the clearly visible, above-ground parts—the leaves, flowers, fruits and stems—plants also comprise a less-visible half, hidden below ground: root systems. The green or colorful above-ground parts are essential for photosynthesis and reproduction (1, 2), while roots are important for nutrient and water uptake, anchoring, mechanical support, and storage (3–5). In contrast to mammals, plants generate new organs and tissues throughout their whole life. This often results in enormous organisms, such as giant sequoias or the Trembling Giant, a clonal colony of a single quaking aspen with a massive underground root system. Surprisingly, organs, such as leaves and lateral roots, are positioned at fairly regular spatial and temporal intervals and this requires tight coordination of the underlying molecular processes (3, 6). Especially since these organs develop from a subset of cells, often deeply embedded between various plant tissues. In addition, to control overall plant growth and reproduction, the various above- and below-ground organs need to communicate (7).

1.2. Model Systems

A good model is simple in structure, easy to study, to grow and to multiply, amenable to genetic analyses, and can increase our understanding of plant organogenesis fast. In the past decades, a lot of progress has been made by studying the model plant *Arabidopsis thaliana* or Thale Cress, and a recent special Plant Journal Issue was dedicated to this (8). However, for example, *Arabidopsis* has a small shoot apical meristem that is deeply buried between rosette leaves, is virtually impossible to access, and cannot be grown in culture. Thus, most studies on *Arabidopsis* organ initiation concern the induction of floral meristems from the inflorescence apex, which is more easily accessed (9–11). An alternative system is tomato because its vegetative shoot apical meristem is relatively large and therefore can be dissected without problems, grows vigorously under defined culture conditions, and is well suited for a wide variety of micromanipulations (6, 12, 13).

The first chapters of this book will give an up-to-date overview of the above- (Chapters 1 and 2) and below-ground parts (Chapters 3 and 4) in monocot and dicot plants. We especially highlight

aspects of why monocot and dicot roots are ideal model systems for organogenesis (Chapters 2 and 3). However, on the one hand we need to translate this information to economically interesting crops, or further investigate this directly in these crops (4, 14, 15). On the other hand, we need other simpler systems to understand the evolution of organs and to provide insight in the underlying molecular networks (e.g. Chapters 5 and 6). The chapters in this book provide exactly that, focusing on tools to study organogenesis in *Arabidopsis*, but also taking it further to cereal crops and highlighting emerging model systems.

While it is not always straightforward to translate particular techniques and approaches that work well in, for example, *Arabidopsis* to crop plants, several examples are discussed in this book on the level of shoot kinematics (Chapter 17), immunolocalization (Chapters 14 and 15), 3D root systems (Chapter 11) and a lateral root-inducible system (Chapter 9). In addition, to address specific questions, for example on the level of evolutionary biology, we need to start using other model systems. A few of these emerging model systems are introduced here, such as brown algae (Chapter 6), *Physcomitrella* (Chapter 2), and Podostemaceae (Chapter 5). More details on how to grow and study the brown alga *Ectocarpus* are provided in Chapter 22. There are obviously a number of other models for plant organogenesis that are not addressed here, but that have recently been reviewed, such as the *Arabidopsis* petal (16).

1.3. Plant Organogenesis

Organogenesis entails the regulation of cell division, cell expansion, cell- and tissue-type differentiation, and patterning of the organ as a whole. De novo organogenesis is especially important in plants, as most of plant development takes place post-embryonically. Therefore it is essential to gain insight into how organs are initiated and how they develop. However, this very often is subject to technical difficulties as these processes take place embedded deep in tissues or are difficult to access or visualize. Furthermore, plant cells are enclosed in a rigid wall making a tight control of the direction of polar cell growth and of the positioning of cell division planes very important for plant organogenesis. To study this, we need specialized techniques that are described in this book.

One of the very first steps in the development of a plant is the formation of ovules and embryos. The ovule and embryo of *Arabidopsis thaliana* have been established as an excellent model system with which to study organogenesis at the molecular and genetic level (17–19). How to study and image these structures is addressed in Chapters 9 and 18.

A new plant organ develops from a subset of cells that has been specified, primed, etc. and which will undergo a series of cell divisions to give rise to a new plant part, such as a leaf, a flower, and a lateral root. To visualize the contribution of each cell and cell

division to building the mature organ, it is necessary to establish cell lineages. An elegant tool to achieve this is described in Chapter 13.

The totipotency of several plant cells is reflected in their ability to regenerate tissues and organs. An approach to study this is described in Chapter 21.

2. Novel Techniques

Due to the difficulties associated with studying particular processes, the development of novel, more sensitive techniques is essential. For example, the use of fluorescence-activated cell sorting (FACS) brought about a revolution in cell-specific analyses of transcriptomes and hormone levels in *Arabidopsis* (20, 21). Here, the use of this approach in the shoot apical meristem is described (Chapter 16). However, it is also important to get closer to the proteins, and as cell-specific proteome analyses are still difficult, other techniques have been developed. For example, ribosome pull down provides insight into the translome (Chapter 19), and localizing RNAs and proteins in plants is useful (Chapters 20 and 21). In addition, classical genetics has its limitations, as exemplified through redundancy and embryo lethal mutations. To circumvent this, chemical genetics was put forward as an ideal tool, as described in Chapter 12.

3. Mathematical Modelling

Finally, as our knowledge increases, we need computer-based approaches to bring everything together. In several areas of plant organogenesis, this has been used successfully. Auxin has been a major focus of mathematical modelling, and this is reflected in a wide range of models describing the distribution and role of auxin (22–25). However, these *in silico* approaches are not always easy to use by wet-lab scientists. We therefore also need simpler, user-friendly systems, such as the one in Chapter 23.

References

1. Fletcher JC (2002) Shoot and floral meristem maintenance in *Arabidopsis*. *Annu Rev Plant Biol* 53:45–66
2. Niinemets U (2007) Photosynthesis and resource distribution through plant canopies. *Plant Cell Environ* 30:1052–1071
3. De Smet I (2012) Lateral root initiation: one step at a time. *New Phytol* 193:867–873
4. De Smet I, White PJ, Bengough AG, Dupuy L, Parizot B, Casimiro I, Heidstra R, Laskowski M, Lepetit M, Hochholdinger F, Draye X, Zhang H, Broadley MR, Peret B,

- Hammond JP, Fukaki H, Mooney S, Lynch JP, Nacry P, Schurr U, Laplace L, Benfey P, Beeckman T, Bennett M (2012) Analyzing lateral root development: how to move forward. *Plant Cell* 24:15–20
5. Smith S, De Smet I (2012) Root system architecture—insights from *Arabidopsis* and cereal crops. *Phil Trans R Soc B* 367:1441–1452
6. Reinhardt D, Mandel T, Kuhlemeier C (2000) Auxin regulates the initiation and radial position of plant lateral organs. *Plant Cell* 12:507–518
7. Suarez-Lopez P (2005) Long-range signaling in plant reproductive development. *Int J Dev Biol* 49:761–771
8. Issue S (2010) *Arabidopsis*: a rich harvest 10 years after completion of the genome sequence. *Plant J* 61
9. Hamant O, Heisler MG, Jonsson H, Krupinski P, Uyttewaal M, Bokov P, Corson F, Sahlin P, Boudaoud A, Meyerowitz EM, Couder Y, Traas J (2008) Developmental patterning by mechanical signals in *Arabidopsis*. *Science* 322:1650–1655
10. Heisler MG, Ohno C, Das P, Sieber P, Reddy GV, Long JA, Meyerowitz EM (2005) Patterns of auxin transport and gene expression during primordium development revealed by live imaging of the *Arabidopsis* inflorescence meristem. *Curr Biol* 15:1899–1911
11. Reddy GV, Heisler MG, Ehrhardt DW, Meyerowitz EM (2004) Real-time lineage analysis reveals oriented cell divisions associated with morphogenesis at the shoot apex of *Arabidopsis thaliana*. *Development* 131:4225–4237
12. Fleming AJ, Mandel T, Roth I, Kuhlemeier C (1993) The patterns of gene expression in the tomato shoot apical meristem. *Plant Cell* 5:297–309
13. Reinhardt D, Frenz M, Mandel T, Kuhlemeier C (2003) Microsurgical and laser ablation analysis of interactions between the zones and layers of the tomato shoot apical meristem. *Development* 130:4073–4083
14. Den Herder G, Van Isterdael G, Beeckman T, De Smet I (2010) The roots of a new green revolution. *Trends Plant Sci* 15:600
15. Lynch JP (2007) Roots of the Second Green Revolution. *Aust J Bot* 55:493–512
16. Irish VF (2008) The *Arabidopsis* petal: a model for plant organogenesis. *Trends Plant Sci* 13:430–436
17. Lau S, Slane D, Herud O, Kong J, Jurgens G (2012) Early embryogenesis in flowering plants: setting up the basic body pattern. *Annu Rev Plant Biol* 63:483–506
18. De Smet I, Lau S, Mayer U, Jurgens G (2010) Embryogenesis—the humble beginnings of plant life. *Plant J* 61:959–970
19. Schneitz K (1999) The molecular and genetic control of ovule development. *Curr Opin Plant Biol* 2:13–17
20. Petersson SV, Johansson AI, Kowalczyk M, Makoveychuk A, Wang JY, Moritz T, Grebe M, Benfey PN, Sandberg G, Ljung K (2009) An auxin gradient and maximum in the *Arabidopsis* root apex shown by high-resolution cell-specific analysis of IAA distribution and synthesis. *Plant Cell* 21:1659–1668
21. Birnbaum K, Shasha DE, Wang JY, Jung JW, Lambert GM, Galbraith DW, Benfey PN (2003) A gene expression map of the *Arabidopsis* root. *Science* 302:1956–1960
22. Grieneisen VA, Xu J, Maree AF, Hogeweg P, Scheres B (2007) Auxin transport is sufficient to generate a maximum and gradient guiding root growth. *Nature* 449:1008–1013
23. Merks RM, Van de Peer Y, Inze D, Beemster GT (2007) Canalization without flux sensors: a traveling-wave hypothesis. *Trends Plant Sci* 12:384–390
24. Bayer EM, Smith RS, Mandel T, Nakayama N, Sauer M, Prusinkiewicz P, Kuhlemeier C (2009) Integration of transport-based models for phyllotaxis and midvein formation. *Genes Dev* 23:373–384
25. Smith RS, Guyomarc’h S, Mandel T, Reinhardt D, Kuhlemeier C, Prusinkiewicz P (2006) A plausible model of phyllotaxis. *Proc Natl Acad Sci USA* 103:1301–1306



<http://www.springer.com/978-1-62703-220-9>

Plant Organogenesis
Methods and Protocols
De Smet, I. (Ed.)
2013, XVI, 356 p., Hardcover
ISBN: 978-1-62703-220-9
A product of Humana Press