

# *Plant Development*



*Edited by*

Marja Timmerman





VOLUME NINETY ONE

CURRENT TOPICS IN  
DEVELOPMENTAL BIOLOGY

Plant Development

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*Edited by*

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## PREFACE

This book captures many of the major advances made in the field of plant developmental biology. Over the past 20 years, genetic screens in *Arabidopsis* and other species have yielded a wide array of developmental mutants whose analyses have greatly enhanced our understanding of plant morphogenesis. Perhaps because of an initial focus on mutants with clearly defined, non-pleiotropic phenotypes, transcription factors were prominently represented among the first genes isolated from these screens. The field has matured to a point, however, that complex networks comprising signal transduction pathways, transcription factors, and downstream target genes are becoming clear for an ever-increasing number of developmental processes. Significant progress has been made on analysis of the mobile positional signals critical to plant development, which has long remained a main challenge in contemporary plant development. Moreover, by utilizing real-time analyses and computer modeling developmental principles are being elucidated in the context of the whole organ or organism.

Given the wealth of tools and resources available in *Arabidopsis*, the analysis of development has progressed most substantially in this model species. Comparative studies at the molecular and genetic level are beginning to illuminate the history of morphogenesis in plants, revealing evolutionary changes in key molecular players that form the basis for the enormous morphological diversity present within the plant kingdom. Moreover, with the tremendous advances in genomics, more complex systems are becoming accessible. This will allow new insights to be tested in the context of incisive classical experiments that have been the cornerstone of developmental biology, and can provide new interpretations of such formative experiments at the molecular and cellular level. Several of the reviews provide an insight into this new trend.

The chapters presented in this book describe our current knowledge, prospective insights, and key outstanding questions of multiple fundamental facets of plant development. Chapter 1 outlines the formative events that sculpt the organization of the plant body during embryogenesis and discusses the molecular mechanisms that regulate these patterning processes. It emerges that auxin has a profound coordinating role in embryogenesis. One example of this is in the formation of the embryonic root (Chapter 3), where an auxin reflux loop specifies the stem cell niche. This chapter also presents the progress in our understanding of root meristem function, outlining the distinctive properties of stem cells within the root meristem



and the network that controls root growth through the coordinate regulation of cell division and elongation. Germination as well as numerous other developmental transitions and adaptive growth responses are regulated through the perception of light. How plants sense light and coordinate the molecular events underlying photomorphogenesis is presented in Chapter 2. The signaling networks that maintain the position and activity of stem cells within the shoot apical meristem and that organize the initiation of lateral organs on the meristem periphery are discussed in Chapter 4. The complexity of these networks is remarkable, but with the development of live imaging approaches and computational tools, our understanding of the central principles of shoot apical meristem function has rapidly advanced.

The next three chapters focus on patterning, growth, and the morphological diversification of lateral organs in plants. Chapter 5 describes the evolutionary distinct contributions of three highly conserved interlocking pathways to leaf polarity and outlines the unique contributions of mobile small RNAs as positional signals that refine the boundary between the upper and lower sides of the leaf. Chapter 6 compares the mechanisms that regulate leaf shape in simple and compound leafed model species. Auxin is recognized as a key player also in this aspect of development. The emergent picture is one in which developmental pathways that modulate determinacy within the leaf can vary auxin-signaling outputs to generate diverse compound and simple leaf forms. Recent insights into how plant organs reach their characteristic final shape and size are presented in Chapter 7. In addition to the genetic networks that affect organ size at the cellular level by regulating cell proliferation and expansion, insights into the systems that coordinate such cellular processes across the entire organ or modulate them in response to environmental stimuli are discussed.

New insights into the patterning processes that give rise to the precise arrangements of vasculature, stomatal complexes, and trichomes are outlined in Chapters 8 through 10. Interestingly, these tissue or cell patterns are generated through entirely distinct mechanisms. Chapter 8 describes the role of polarized auxin transport in generating the distinctive arrangements of vascular strands within leaves, stems, and roots. In contrast, stereotyped asymmetric cell divisions are at the center of stomatal patterning and, as outlined in Chapter 9, the spacing of such instructive divisions is regulated by signaling pathways involving secreted peptide ligands and receptor-like kinases. Finally, Chapter 10 discusses current models for trichome patterning, presenting evidence for the involvement of two parallel spacing mechanisms; a lateral inhibition mechanism that relies in part on plasmodesmatal movement of trichome inhibitor proteins and an activator-depletion mechanism in which inducers of trichome differentiation are depleted around incipient trichome cells.

Chapter 11 reviews our understanding of the networks that regulate the switch from vegetative growth to flowering in response to intrinsic signals and environmental stimuli in *Arabidopsis thaliana*, and then broadens the discussion to the control of flowering in perennial species. The contribution of miRNAs in regulating the transition to flowering is described in Chapter 12. This chapter also outlines the varied contributions of small regulatory RNAs to the specification of floral organ identity and the control of floral organ shape and size. The final chapter of the book focuses on the progress in understanding the development of the male and the female gametophytes, and their interactions during the process of double fertilization. Signaling molecules and downstream genetic pathways that direct the differentiation of distinct cell types within the developing gametophytes, pollen tube attraction, or fertilization are beginning to emerge. An exciting example is the recent finding that auxin acts as a morphogenic determinant in the patterning of the female gametophyte.

Besides providing timely reviews of new advances in many fundamental aspects of plant development, the chapters presented in this book illustrate clearly the diversity of patterning mechanisms that drive plant morphogenesis. Mobile transcription factors, secreted peptides, hormones, and small regulatory RNAs function as instructive signals feeding into a wide array of signaling pathways and gene regulatory networks. This wealth of new data also allows us to draw parallels with animal development. It is now probably safe to state, rather than speculate, that many of the individual molecular components are either different or wired differently, but that the logic of developmental circuitry is conceptually quite similar between plants and animals. This book is testimony to the progress in our understanding of plant development that has been made in a surprisingly short time.

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# GREEN BEGINNINGS – PATTERN FORMATION IN THE EARLY PLANT EMBRYO

Cristina I. Llavata Peris,\* Eike H. Rademacher,\* and Dolf Weijers

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## Abstract

Embryogenesis in plants transforms the zygote into a relatively simple structure, the seedling, which contains all tissues and organs that later form the mature plant body. Despite a profound diversity in cell division patterns among plant species, embryogenesis yields remarkably homologous seedling architectures. In this review, we describe the formative events during plant embryogenesis and discuss the molecular mechanisms that regulate these processes, focusing on *Arabidopsis*. Even though only a relatively small number of factors are known that regulate each patterning step, a picture emerges where locally acting transcription factors and intercellular signaling contribute to the specification and spatio-temporal coordination of the various cell types in the embryo.

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