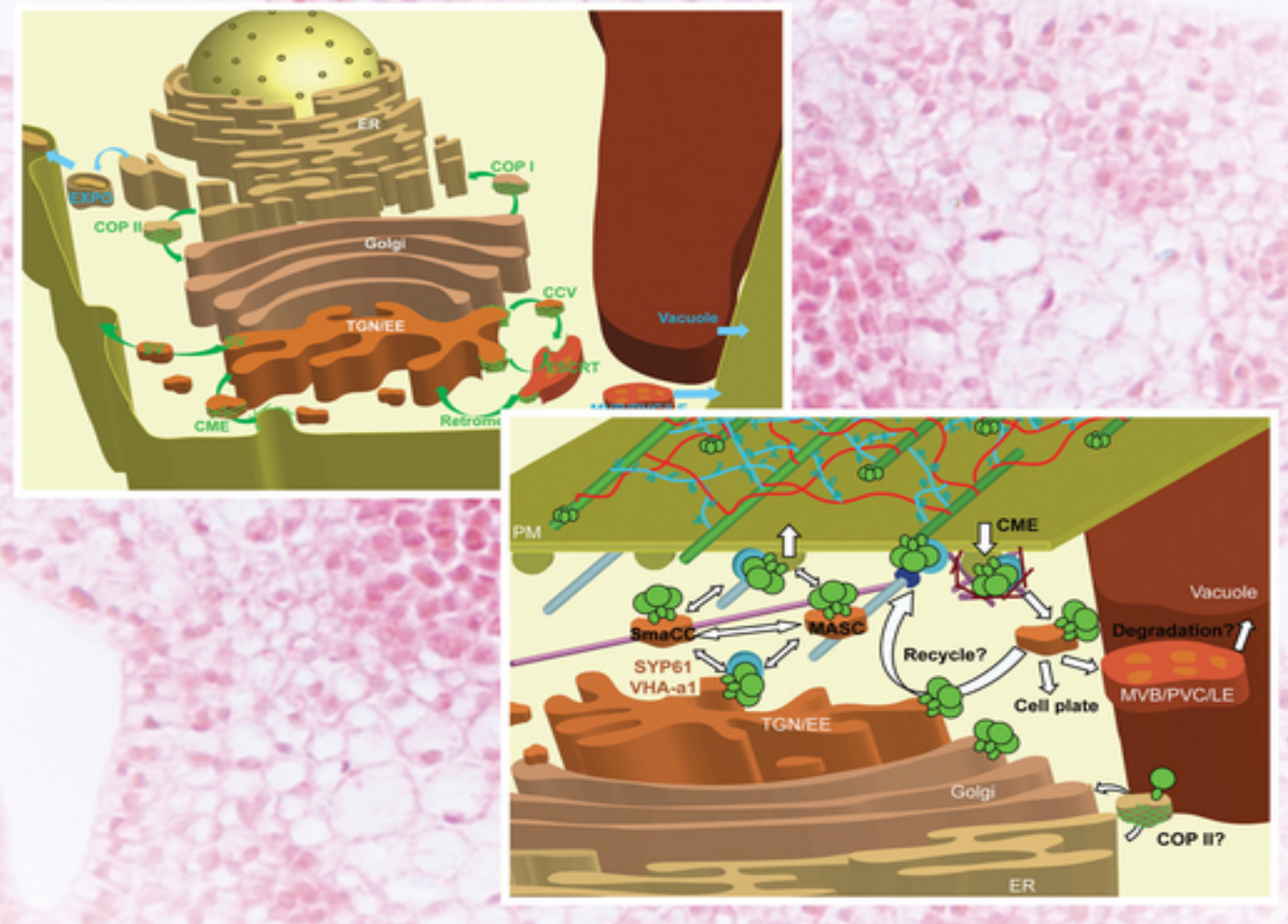
PLANT CELL WALL PATTERNING AND CELL SHAPE

Edited by **Hiroo Fukuda**



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WILEY Blackwell

Published by John Wiley & Sons, Inc., Hoboken, New Jersey

Published simultaneously in Canada

Library of Congress Cataloging-in-Publication Data

Plant cell wall patterning and cell shape / edited by Hiroo Fukuda.

pages cm

Includes bibliographical references and index.

ISBN 978-1-118-64737-0 (cloth)

1. Plant cell walls. I. Fukuda, H (Hiroo)

QK725.P4723 2014

572′.472–dc23

2014024315

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Preface

Hundreds of thousands of species of plants have evolved to thrive on Earth. One of the reasons for their prosperity must be the acquisition and clever use of cell walls. Plant cell walls dictate the plant life form by preventing cell migration, resulting in immobility of plants. On the other hand, cell walls produce the strength that allows plants to grow as huge trees and enable a unique strategy for the plant body plan by using cells hardened with cell walls as building blocks. Moreover, cell walls define cell shape, cell function, and sometimes cell fate through mechanisms such as asymmetric cell division and intercellular communication. An understanding of plant cell walls is therefore essential for an understanding of plant life.

A number of books about plant cell walls have already been published. Most books focus on the structure and biosynthesis of plant cell walls, providing invaluable knowledge of the biochemical and structural nature of plant cell walls. However, there are few books that provide detailed information about cell wall functions and their underlying mechanisms, despite recent conspicuous progress in these areas. I therefore planned a book entitled *Plant Cell Wall Patterning and Cell Shape*, describing current knowledge of the spatiotemporal regulation of plant cell organization in view of cell walls.

This book is grouped into three sections: (1) *Factors Controlling Plant Cell Wall Patterning*; (2) *Cellular Mechanisms Underlying Various Cell Shapes*; and (3) *Developmental Regulations of Cell Shape*.

Spatiotemporal regulation of cell wall formation appears as cell wall patterns. Section 1 therefore deals with crucial

components for cell wall patterning. In Chapters 1 and 2, current knowledge of the biosynthesis of cell wall components, including cellulose microfibrils, is described as a basis for cell wall patterning. Membrane traffic, which is another key component for cell wall patterning, is described in Chapter 3. Mechanisms underlying cell wall patterning involve microtubule and actin filament dynamics beneath the plasma membrane. Chapters 4 and 5 therefore highlight regulation of microtubule and actin filament arrangement, respectively, in cell wall pattern formation.

A conspicuous function of cell walls is the formation of diverse cell shapes. Section 2 therefore describes new insights into cellular mechanisms leading to distinctive cell shapes. In plants, polarization of the plasma membrane leads to the formation of a locally specialized architecture of cell walls, resulting in various shapes of plant cells with specific functions. Recent progress in this field has revealed that Rho-like GTPases from plants (ROPs) play a crucial role in polarization of the plasma membrane to form distinct plant cell shapes. Chapters 6–8 therefore deal with the role of ROPs in the shape of three different cells such as pavement cells, xylem vessel cells, and pollen tubes. Chapters 9–11 describe current knowledge of the cell shape formation in root hair, trichome, and transfer cells, in which different cellular mechanisms such as lipid signaling and cytoskeleton are discussed.

Section 3 deals with the developmental regulation of specific types of plant cells such as guard cells, xylem cells, and phloem cells. Cell wall pattern and cell shape are both under developmental control. Cell-non-autonomous extracellular signals derived from neighboring cells or environmental cues regulate cell fate. Within the cell, transcriptional cascades finally determine a cell fate and then execute distinct cell-specific wall formation to lead to distinct cell shape. Signaling and transcriptional cascades

leading to cell differentiation are discussed in Chapters 12 and 13, respectively. Finally, Chapter 14 describes our current knowledge of inter- and intra-cellular signaling that determines phloem cell differentiation.

I would like to thank the authors who provided authoritative reviews as experts of their areas. I also thank Justin Jeffryes, Stephanie Dollan, and their colleagues at Wiley-Blackwell publishing who provided me with this opportunity as well as encouragement during completion of this task.

Hiroo Fukuda

Section 1
Factors Controlling Plant Cell Wall Patterning

Chapter 1
The Biosynthesis and Function of Polysaccharide Components of the Plant Cell Wall

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Introduction

The cell wall of land plants consists of three layers, namely the middle lamella, the primary cell wall, and the secondary cell wall. The middle lamella is directly derived from the cell plate generated during cytokinesis and the primary cell wall is deposited onto the middle lamella during the cell expansion process. The two cell wall layers are generally found in all cell types, whereas the secondary wall is deposited onto the primary cell wall in certain specific cell types after cell expansion has ceased (Albersheim *et al.*, 2011; Fig. 1.1).

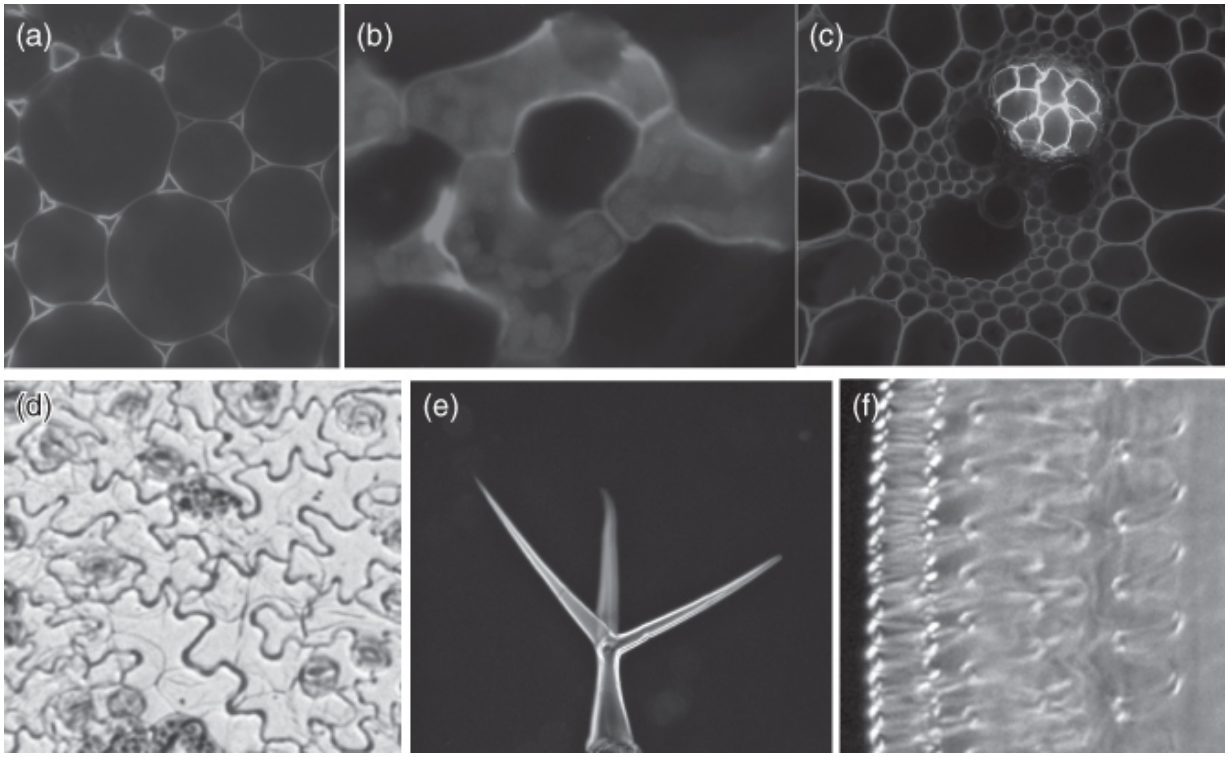

Figure 1.1 Various types of plant cells defined by the cell wall: (a–c) immunofluorescence labeling with monoclonal antibodies against cell wall polysaccharide epitopes; (a) JIM5, specific to homogalacturonan with a low degree of methylesterification; (b, c) CCRC-M1, specific to fucosylated xyloglucan; (d, e) bright field images of unstained specimens; (f) histochemical staining of lignin with phloroglucinol-HCl. A, parenchyma of *Oryza sativa*; B, spongy mesophyll of *Fagus crenata*; C, vascular of *O. sativa*; D, E and F, epidermis, trichome and xylem of *A. thaliana,* respectively.

The three layers differ from each other in terms of their chemical nature and physical properties, and they serve different biological functions. Although both the primary and secondary cell walls directly function as a mechanical housing capable of resisting both turgor pressure from the inside out and compression force from the outside in, only the primary cell wall can extend or deform in response to the force applied and thereby determine the direction and

rate of cell expansion (Burgert and Frantzl, 2007; Wasterneys and Collings, 2007; Fig. 1.1). In addition to these mechanical roles, the primary cell wall functions as an information processing system. Typical functions include non-cell-autonomous regulation of cell differentiation via apoplastic signaling (Irving and Gehring, 2012; Wolf *et al.*, 2012a), particularly in meristems, defensive responses to pathogens and parasites (Bradley *et al.*, 1992; Vorwerk *et al.*, 2004), and interactions with symbionts. The dynamics of the primary cell wall therefore play a pivotal role in determining cell shape and function during development and in response to environmental stimuli. Accordingly, in this chapter we will focus on the primary cell wall and the dynamic aspects of its major components, namely cellulose and matrix polysaccharides, in relation to its function.

Overview of the Plant Cell Wall

Plants devote a considerable amount of energy to constructing and maintaining the architecture of the plant cell wall, which is a biphasic composite consisting of crystalline microfibrils and an amorphous gel-like matrix; the former is embedded in the latter, which is intelligent enough to be able to self-organize and regulate cell shape and function during growth and, hence, the morphology of land plants.

For its assembly, remodeling, and disassembly, various types of structural and functional components must be secreted into the cell wall space. These include polysaccharides, structural proteins, enzymes, and small signaling molecules. Examination of the increasing number of currently available genome sequences of land plants tells us that each plant genome contains several thousand cell-wall-related genes which are implicated in biosynthesis, modification, and disassembly of the cell wall, and their

regulation with respect to transcription, membrane trafficking, and enzyme actions (Henrissat *et al.*, 2001; Coutinho *et al.*, 2003; Somerville *et al.*, 2004; Yokoyama and Nishitani, 2004; Brown *et al.*, 2005). The presence of such a large number of genes and proteins committed to cell wall dynamics apparently reflects the fact that cell wall type is dependent upon cell type, of which there are estimated to be more than 40 in a land plant. Transcriptomic analysis has demonstrated that different cell types have different expression patterns of cell-wall-related genes (Zhu and Wang, 2000; Demura *et al.*, 2002; Birnbaum *et al.*, 2003; Imoto *et al.*, 2005; Demura and Fukuda, 2007).

In addition to cell-type-specific variations, the chemical and physical nature of the cell wall is also hugely dependent upon the stages of growth and differentiation of the cell. This is rather self-evident as we have seen that the rate and direction of cell growth, and thus the final shape of the cell, is ultimately determined by the nature of the cell wall. Continued reduction in the tensile strength of the cell wall, which is termed ‘cell wall loosening’, is the direct cause of cell wall expansion followed by cell expansion, the ubiquitous process by which cell expansion is regulated. Accordingly, an anisotropic or localized modification of the primary cell wall within a cell will cause anisotropic cell growth, such as cell elongation in stem cortical cells and polarized cell expansion in leaf trichomes and pavement cells. The chemical and physical nature of the primary cell wall can therefore precisely determine the size and shape of individual cells and play a vital role in determining the morphology of the plant as a whole (Fig. 1.1; Somerville *et al.*, 2004; Cosgrove, 2005).

By contrast, the secondary cell wall has a static structure consisting mainly of crystalline cellulose microfibrils impregnated with lignin and suberin, and is responsible for

providing mechanical resistance as well as forming a diffusion barrier. In xylem and fiber cells, the secondary cell wall functions to resist compression force as well as tensile force, and it provides the cell with enough strength to support aerial parts of the plant body, or serves as a non-growing cellular pathway for the translocation of water and nutrients (Fig. 1.2; Demura and Fukuda, 2007). On the other hand, the diffusion resistance function of the secondary cell wall is most prominently found in the Casparian strip in the endodermis, in which lignin confers the hydrophobicity necessary for forming a diffusion barrier to the cell wall (Naseer *et al.*, 2012). These functions of the secondary wall are not directly related to the determination of cell shape and are therefore not discussed in this chapter.

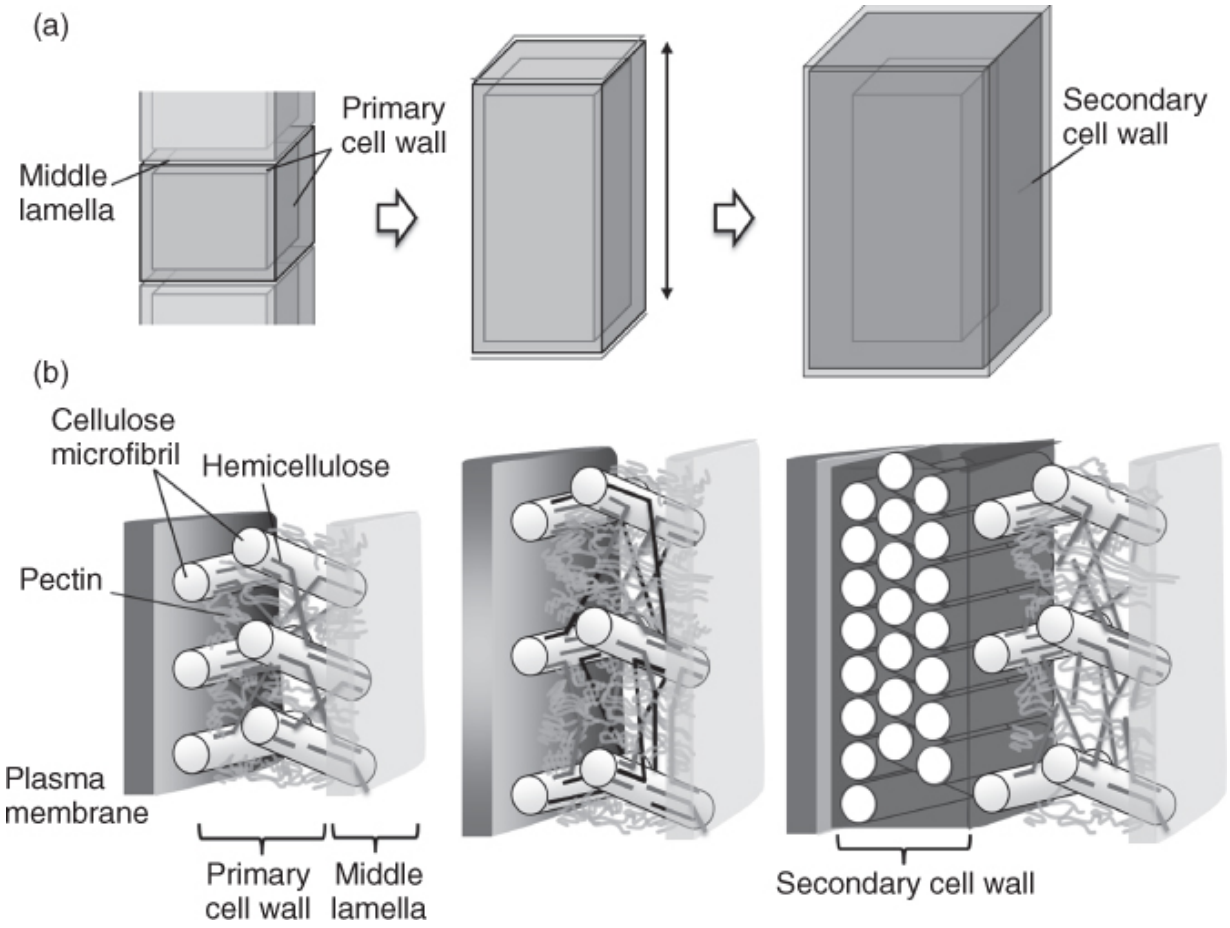

Figure 1.2 Cellulose/hemicellulose and pectin networks in the primary cell wall at successive stages of plant cell growth. (a) Processes of cell elongation and differentiation. (b) Major polymers and their likely arrangement in the cell wall. Newly secreted hemicelluloses (shown in black) and the other polymers (gray) are integrated into the cellulose/hemicellulose network.

Components of the Primary Cell Wall

The primary cell wall is composed of cellulose microfibrils, matrix polysaccharides, and structural proteins and can serve as an aqueous microenvironment harboring non-structural soluble components such as enzymes, signaling molecules, and ions (Carpita and Gibeaut, 1993; Cosgrove, 1997). In this section, we first describe the structural

features of the cellulose microfibrils and two major matrix polysaccharides – pectin and hemicellulose – before describing how they are organized to form the dynamic architecture of the primary cell wall.

Basic Structure and Cellulose Microfibrils

A single microfibril in land plants is circular or square when observed in cross-section. The dimension of the cellulose microfibril in land plants has been estimated by transmission electron microscopy, X-ray scattering (Jakob *et al.*, 1995), and solid-state ^{13}C nuclear magnetic resonance (NMR) (Newman, 1999; Kennedy *et al.*, 2007). The diameters suggested by these analyses range from 2.5 nm to 3.6 nm, which corresponds to 15–32 chains of β-1,4-glucan molecules (Somerville, 2006; Fernandes *et al.*, 2011) if it is assumed that each chain occupies 0.317 nm^2 (Nishiyama *et al.*, 2002).

In cellulose microfibrils, there are two types of domains conforming to a triclinic (termed cellulose I-α) form and a monoclinic (termed cellulose I-β) form. In land plants, the I-β form predominates. In the crystalline domain, β-1,4-glucan chains are arranged in parallel and undergo self-association via several interactions, which include the formation of intramolecular hydrogen bonds at O3…O5 and O2…O5, an intermolecular hydrogen bond at O3…O3, and hydrophobic intermolecular interactions. This structure renders the cellulose microfibrils insoluble in water, immune to enzymatic attack, and resistant to chemical agents.

Another important characteristic of cellulose is its high tensile strength and elastic modulus. The latter is estimated to be between 124 and 155 GPa for the cellulose I-β form, values that are comparable to that of gray cast iron (Nishino *et al.*, 1995). The crystallinity is frequently