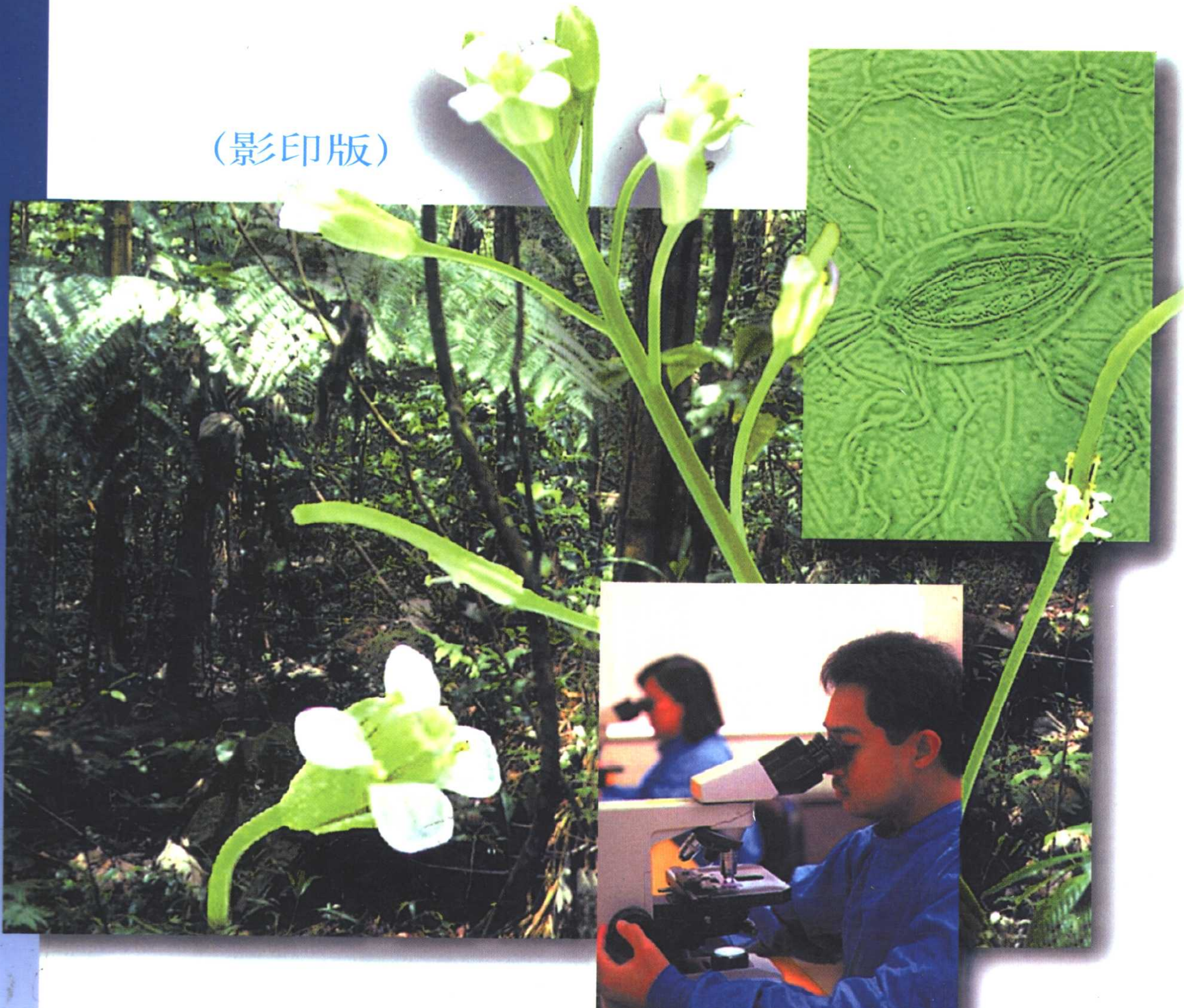
现代生物学精要速览

Instant Notes in

PLANT BIOLOGY

植物生物学

（影印版）



A.J. Lack and D. E. Evans

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A. J. Lack & D. E. Evans

School of Biological & Molecular Sciences,
Oxford Brookes University, Oxford, UK

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内 容 简 介

本套丛书是国外优秀教材畅销榜的上榜教材，面向大学本科生，由英国著名大学具有丰富教学经验的一流教授编写。它以一种风格独特的描述方式，全面、系统地概括了学科的核心内容和前沿动态，并以一种便于学习、利于复习的形式，使学生能快速、准确地掌握知识，很好地指导学习和考试。书中英文使用最为自然、易懂的语句，是提高专业外语的最佳用书。本书是该系列中的植物生物学分册，共约17个章节。

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ABBREVIATIONS

2,4-D	2,4-dichlorophenoxyacetic acid
2,4,5-T	2,4,5-trichlorophenoxyacetic acid
ABA	abscisic acid
ABP	auxin-binding protein
ACC	1-aminocyclopropane-1-carboxylic acid
ACS	ACC synthase
ADP	adenosine diphosphate
AMP	adenosine monophosphate
AS	asparagine synthase
ATP	adenosine triphosphate
bp	base pair
CAM	crassulacean acid metabolism
CaMPK	calmodulin-dependent protein kinases
CFP	cyan fluorescent protein
CoA	coenzyme A
DAG	diacylglycerol
DDT	1,1-bis(p-chlorophenyl)-2,2,2-trichloroethane
DNA	deoxyribonucleic acid
ems	ethylmethanesulfonate
ER	endoplasmic reticulum
FADH	flavin adenine dinucleotide (reduced)
Fd	ferredoxin-dependent
GA	gibberellic acid
GA	Golgi apparatus
GARE	gibberellic acid response element
GDH	glutamate dehydrogenase
GFP	green fluorescent protein
GM	genetically modified
GOGAT	glutamate synthase
GS	glutamine synthase
GSH	glutathione
GST	glutathione-S-transferase
GUS	β-glucuronidase
IAA	indole-3-acetic acid
IP_3	inositol triphosphate
LDP	long day plant
LSD	lysergic acid diethylamine
mRNA	messenger ribonucleic acid
NAA	naphthalene acetic acid
NADP	nicotinamide adenine dinucleotide phosphate
NADPH	nicotinamide adenine dinucleotide phosphate (reduced)
NE	nuclear envelope
NPA	1-N-naphthylphthalamic acid
NR	nitrate reductase
Pa	Pascals
PCR	polymerase chain reaction
PEP	phosphoenolpyruvate
PG	polygalacturonase
PGS	plant growth substances
P_i	inorganic phosphate
ppm	parts per million
PIP_2	phosphatidyl inositol bisphosphate
RAPD	random amplified polymorphic DNA
RET	resonance energy transfer
RFLP	restriction fragment length polymorphism
RNA	ribonucleic acid
RNase	ribonuclease
SAM	s-adenosyl methionine
SAUR	soybean auxin upregulated gene
SDP	short day plant
SI	self-incompatibility
T-DNA	transferred DNA
TGN	*trans* Golgi network
UTP	uridine diphosphoglucose
UV	ultraviolet
VIR	virulence region for infection
YFP	yellow fluorescent protein

PREFACE

Plant science has always been a fundamental area of biology, but the emphasis in the subject has changed radically in the last two decades with a plethora of new information, much of it deriving from techniques in molecular biology. This has deepened our understanding of plant processes and has illuminated almost all aspects of plant biology. The ability to analyze genomes and to transfer genes has opened possibilities for plant biotechnology and genetic manipulation undreamed-of in earlier decades. There have been advances in ecological knowledge that, with increased awareness of the richness of biodiversity, have shed new light on the relationships between plants, other organisms and their interdependence. Plant breeders, ecologists and many people outside plant biology have become acutely conscious of the aesthetic and economic value of the resources, so often dwindling, of the plant kingdom.

In this book we have covered all these aspects of modern plant biology. We have written it keeping in mind an undergraduate faced with a range of advanced courses, needing an affordable text that gives insight into the whole range of plant science. Its scope and depth are suitable for a first and second year undergraduate student of plant biology; specialism will need an advanced text. We have also aimed it at molecular biologists and biotechnologists needing an accessible route to understanding the basis of the systems on which they work. It is intended to provide the fundamental background required for true understanding. It should aid undergraduates in their learning and give insight for specialists into areas of plant science not their own. As in all Instant Notes books we have provided 'Key Notes' at the start of each section. These are intended solely as revision notes, e.g. before an exam, to prompt a reader's memory after reading the section fully. We have kept technical and jargon terms to the minimum needed for understanding; any such term is defined at first mention. We have assumed minimal previous knowledge of biology and hope that the book will prove useful to journalists, environmentalists and those with a genuine interest in the key issues of plant biology as they seek to be informed about the issues that they deal with.

The book is divided into four major sections; structure (Sections B–D); physiology and regulation (Sections E–J); ecology, genetics and wider significance (Sections K–O); and plant diversity (Sections P–R). Throughout we have included insights from modern and advanced techniques and, where possible, explain how understanding is gained. Much of the recent genetic and molecular research has been done on a few key plant species, of which *Arabidopsis thaliana* (arabidopsis) is pre-eminent. This small short-lived weed of arable land has become the single best-known plant species and is used as a model for other plants, the '*Drosophila*' of the plant kingdom. The sequencing of its entire genome was finished as we were writing the final sections of this book. We have used it as an example wherever possible. Many sections are illustrated with diagrams designed to aid understanding and to be reproducible. Throughout, we have had in mind the needs of undergraduates under pressure to make rapid progress and have sought to supply the essentials upon which good understanding can be quickly built.

A.J. Lack and D. E. Evans

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We would like to thank our families for their support throughout the writing, Margaret Evans for assistance with diagrams and Profs. John Bryant, Jeremy Roberts and Chris Hawes who have given advice, read sections, made comments, and supported us generally in the task of authorship. We also wish to thank the team at BIOS for their patience and encouragement and their referees and chief editor, Dr David Hames, for their valuable comments. Perhaps our main debt for the subject matter of this book is to those who introduced us, as students in Aberdeen and Aberystwyth, to the field of plant biology and to the students we have taught over many years at Oxford Brookes. Without their input, we would not have been able to come even close to communicating the fundamentals of plant science simply and understandably.

CONTENTS

A1 INTRODUCTION

Key Notes

What is a plant?

Flowering plants are by far the most important plants and this book is primarily a study of them. The most fundamental dividing line between living organisms is that between prokaryote and eukaryote cells. Within the eukaryotes there are three main multicellular kingdoms, plants, animals and fungi, and a heterogeneous, mainly unicellular, kingdom Protista. We include here only plants and some plant-like Protista.

Unifying features of plants

Plants are photosynthetic and autotrophic (with very few exceptions), have chlorophyll *a* and *b* except for some algae, have a cellulose cell wall and a cell vacuole, and have an alternation of diploid and haploid generations. Vegetative structure is similar across most vascular plants; reproductive structures differ.

What is a plant?

The science of plant biology is primarily the study of **flowering plants** or **angiosperms**. Flowering plants are by far the most important group of plants in the world, providing the overwhelming majority of plant species (over 250 000 in all) and most of the biomass on land, and they are the basis for nearly all our food. This book is mainly about flowering plants.

Historically, the science of **plant biology**, or **botany**, has included all living organisms except animals, but it is clear that there is a major division of life between cells with a simple level of organization, the **prokaryotes**, and those with much more complex cells, the **eukaryotes**. The prokaryotes include bacteria and bacteria-like organisms and will not be considered further in this book except in relation to plants, although some retain plant-like names, such as referring to the gut 'flora' for the bacteria in mammalian guts, and 'blue-green algae' for the **cyanobacteria**. Among eukaryotes three main multicellular kingdoms are recognized: **animals**, **plants** and **fungi**. There is a fourth heterogeneous group of eukaryotes that are mainly unicellular but with a few multicellular groups such as **slime molds** and large **algae**. Some of these have affinity with animals, some with plants, some with fungi and some have no obvious affinity. They are grouped together, for convenience, as a kingdom, the **protists**, **Protista** (or Protoctista).

There is no clear boundary between protists and plants, and authors differ in which organisms they consider in which kingdom. Multicellular **green algae** and, to a lesser extent **brown** and **red algae**, have many features in common with land plants and are the dominant photosynthetic organisms in shallow seas. Unicellular planktonic groups form the basis of the food chain in the deep sea. All these algae are photosynthetic, like plants, and share some characters. They are considered in this book for comparison with other plants in Section P. Other protists, animals and fungi will not be considered further except in relation to plants. Plant groups other than flowering plants, such as mosses, ferns and conifers, differ in various ways and these are considered in Sections P, Q and R.

Unifying features of plants

To characterize the features that define plants as different from other eukaryotes is almost impossible since every feature has exceptions, but usually these exceptions are among plants that have lost the feature or are among the algae on the boundary between protists and plants.

- They are **photosynthetic** and obtain all their nutrients from inorganic sources, i.e. they are **autotrophic** and the start of a food chain. Many protists, particularly among the plankton, are also photosynthetic. A few plants derive all or part of their nutrients from other organisms (Topics M6, M7) but these are closely related to other, photosynthetic, flowering plants.
- The photosynthetic pigment is **chlorophyll**, and in all plants except some algae, there are two forms, ***a*** and *b*, contained within chloroplasts.
- The cells have a **cell wall** made predominantly of the polysaccharide **cellulose**, and a **vacuole** in addition to the **cytoplasm**.
- There is an **alternation of** diploid and haploid **generations** (Topic P1). Often one of these is much reduced and may not live independently.

Vegetative structure and physiology is similar throughout the seed plants (flowering plants, conifers and some smaller groups) and there are many similarities with other vascular plants as well, but the reproductive structures differ markedly. Larger algae and bryophytes differ more fundamentally in vegetative and reproductive structure (Section P).

B1 THE PLANT CELL

Key Notes

Cell structure

The plant cell has a cell wall and plasma membrane enclosing the cytoplasm. Organelles, bounded by membranes, occur within the cytoplasm and are supported and moved by the cytoskeleton. The nucleus contains DNA and nucleoli. Many plant cells have a large vacuole.

Cell membranes

The endomembrane system of the cell is involved in synthesis and transport. The nucleus is surrounded by a nuclear envelope. The endoplasmic reticulum (ER) is divided into perinuclear ER and cortical ER, and may be smooth or rough (coated with ribosomes). Material from the ER is modified and sorted in the Golgi apparatus (GA) from which it travels in vesicles to the plasma membrane or the vacuole.

Organelles of metabolism

Mitochondria generate adenosine triphosphate (ATP) from stored food reserves. Chloroplasts carry out photosynthesis. Microbodies include peroxisomes containing catalase and glyoxysomes containing enzymes of lipid biosynthesis.

The cell wall

The cell wall is a dynamic, metabolic structure made up predominantly of carbohydrate. Adjoining cells are inter-connected by plasmodesmata, in which membranes bridge the wall. Everything within the plasma membrane is the symplast; outside it is the apoplast, which is a water-permeated space, in which hydrophilic molecules are dissolved.

Related topics

The cell wall (B2)
Plastids and mitochondria (B3)
Membranes (B4)
Cell division (B6)
Nucleus and genome (B5)

Cell structure

Plant cells show a wide range of shapes and internal structures, depending on their function. *Figure 1* illustrates the key features of a typical plant cell. Other cells, such as reproductive cells and conducting cells may be very different in appearance. It consists of a **cell wall** in close contact with a **plasma membrane** surrounding the **cytoplasm**, which is made up of aqueous fluid **cytosol** and many **organelles.** These organelles are supported and moved by a meshwork of fine protein filaments, the **cytoskeleton,** which includes **microtubules** made up of the protein **tubulin** and **microfibrils** made up of the protein **actin.** The nucleus contains genetic information in **chromosomes** and **nucleoli** that contain machinery for the production of **ribosomes.**

In most plant cells, there is a **vacuole** that may occupy up to 90% of the cell volume, surrounded by a membrane, the **tonoplast.** It contains solutes dissolved in water. It is important in storage and osmotic regulation (Topic B4).

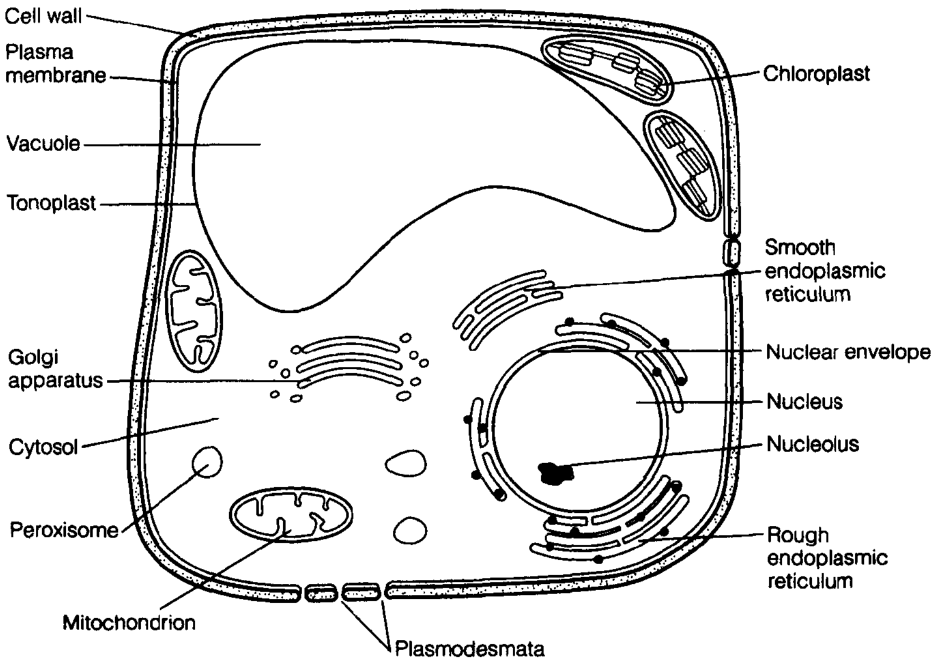

Fig. 1. Features of a typical plant cell.

Cell membranes

The cell contains a system of membranes termed the **endomembrane system** involved in the synthesis and transport of materials. The nucleus is bounded by two membranes, the **inner** and **outer nuclear envelope**, with **nuclear pores** to permit traffic of material. The outer nuclear envelope may be joined to a membrane system, the **endoplasmic reticulum (ER)** which may be **smooth** (site of lipid synthesis) or **rough** (coated with **ribosomes**; site of protein synthesis). In plant cells, the ER is often divided into **perinuclear ER** (ER around the nucleus) and **cortical ER** (ER at the cell periphery). Material from the ER is trafficked to the **Golgi apparatus (GA)**, a series of stacked membrane compartments **(cisternae)** in which modifications are carried out by enzymes. Material leaving the GA travels in **vesicles** to its destination, either the **plasma membrane** or the **tonoplast** (vacuolar membrane).

Organelles of metabolism

Plant cells have two major organelles of energy metabolism, one, the **chloroplast**, not being found in animal cells. **Mitochondria** (Topic B3) are bounded by a double membrane and generate adenosine triphosphate (ATP) from stored food reserves (carbohydrate, lipid; Topic J4). **Chloroplasts** (Topic B3) belong to a group of organelles known as **plastids**. Chloroplasts photosynthesize (Topics J1 and J2), using the energy of sunlight and carbon from carbon dioxide to produce carbohydrate. **Amyloplasts** are plastids modified to store starch. Plant cells also contain **microbodies** that are small membrane-bounded organelles. **Peroxisomes** contain catalase to remove toxic hydrogen peroxide produced in metabolism and **glyoxysomes** contain some enzymes of lipid biosynthesis.

The cell wall

Surrounding the cell is a **cell wall** that is a metabolically active and constantly modified structure made up predominantly of structurally strong complex polysaccharides (Topic B2). Adjoining cells may be inter-connected by **plasmodesmata**, pores through the wall where plasma membrane and ER connect. Everything within the plasma membrane is termed the **symplast**; everything outside it is the **apoplast**, which is a water-permeated space, in which hydrophilic molecules are present in solution. Cell walls function to adhere adjacent cells together in the formation of tissues and organs.

B2 THE CELL WALL

Key Notes

Cell wall structure

Primary cell walls are made up of cellulose microfibrils surrounded by a matrix of polysaccharides including hemicelluloses and pectins. Secondary cell walls contain cellulose microfibrils surrounded by polysaccharides and lignin.

Cell wall synthesis

Cellulose microfibrils are synthesized from uridine diphosphoglucose (UDP glucose) by cellulose synthase, an enzyme complex forming rosettes in the plasma membrane. Matrix materials are synthesized in the Golgi apparatus and deposited into the wall by secretory vesicles that fuse with the plasma membrane.

Cell wall function

Cell walls are essential for adhesion and the growth and formation of the plant body. Primary cell walls have high tensile strength and oppose turgor. Lignified secondary walls give greater strength. Cell walls act as a barrier to pathogens and deter herbivory. Primary cell walls are generally permeable to water and small molecules. The dynamic nature of primary cell walls permits cell expansion and plant growth.

Plasmodesmata

Plasmodesmata are structures in which membranes from adjacent cells connect through a pore in the cell wall. They link adjacent plasma membranes and cytoplasm. The desmotubule is a tube of endoplasmic reticulum in the center of the pore surrounded by globular proteins. The structure permits regulated transport between the cells.

Related topics

The plant cell (B1)
Roots (C2)
Herbaceous stems and primary growth (C3)
Woody stems and secondary growth (C4)

Cell wall structure

Almost all plant cells have a **primary cell wall.** It is made of a long-chain polysaccharide, **cellulose**, aggregated into bundles to form fibers, **microfibrils** 10–25 nm in diameter. The orientation of the microfibrils is governed by the **cytoskeleton** (see cell wall synthesis, below) and the fibers are laid down in a coordinated fashion so that the plasma membrane is covered in layers (*Fig. 1*). The orientation of the fibers changes as the cell develops. Microfibrils have a great tensile strength; their strength is further enhanced by interlinking between the fibrils by a **matrix** composed of **hemicelluloses** and **pectins.** Between cells, there is a **middle lamella,** an adhesive region rich in **pectic polysaccharides** where adjacent cell walls adhere to one another.

Some cells of strengthening and vascular tissues develop a **secondary cell wall,** between the primary wall and the plasma membrane. Secondary cell walls also contain cellulose **microfibrils,** infilled with polymerized phenolic

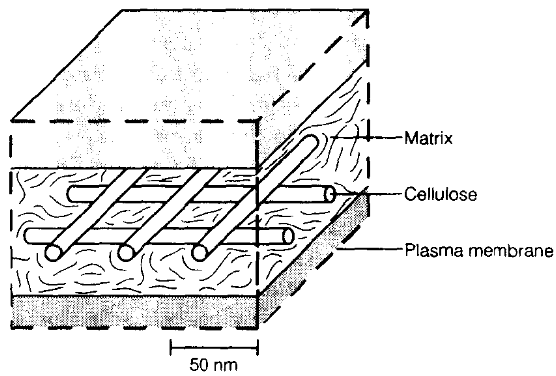

Fig. 1. The primary cell wall consists of cellulose microfibrils deposited in layers surrounded by a matrix of hemicelluloses and pectins.

compounds, **lignins**, that strengthen the wall. This is evident in **wood** (Topic C4). Lignin protects against digestion of the wall by fungal enzymes and against mechanical penetration by fungal hyphae and other pathogens (Topic M4). Secondary walls are produced in layers, with the cellulose fibrils orientated in different directions; this 'lamination' gives considerable strength to the structure.

Cell wall synthesis

The **primary cell wall** is deposited while the cell is increasing in size. Cellulose is deposited by an enzyme complex, **cellulose synthase** that appears as a rosette in the membrane (*Fig. 2*). Cellulose is synthesized from **uridine diphospho-glucose** (UDP glucose) which is added simultaneously to the end of several strands, forming a **cellulose fiber** (or **microfibril**) at the cytoplasmic face of the membrane. As the strand elongates, the rosette moves in the membrane, extruding the strand to lie along the outer face of the membrane. The rosettes move parallel to fibers within the cell, the **cortical microtubules**. **Matrix materials** (hemicelluloses, lignin, pectic substances) are synthesized in the **Golgi apparatus** and transported to the plasma membrane in **secretory vesicles** that discharge their contents into the wall. New wall material is deposited at its inner face – that is the face adjacent to the plasma membrane.

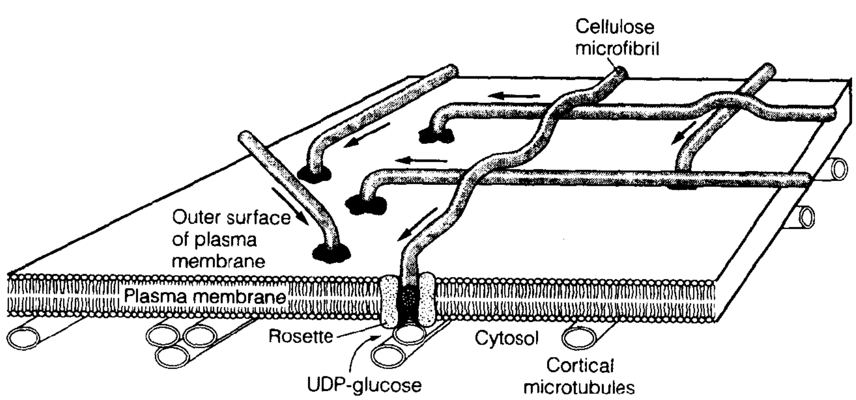

Fig. 2. The deposition of cellulose microfibrils by rosettes of cellulose synthase follows the underlying pattern of cortical microtubules, part of the cytoskeleton. (Redrawn from Raven, P.H. et al. (1992) Biology of Plants, *6th Edn, W.H. Freeman.)*