Flowering Plants

STRUCTURE AND INDUSTRIAL PRODUCTS

AISHA SALEEM KHAN

WILEY

Flowering Plants

Flowering Plants

Structure and Industrial Products

Aisha Saleem Khan

Forman Christian College
Lahore
Pakistan

WILEY

This edition first published 2017

Registered Offices
John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, USA
John Wiley & Sons Ltd, The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial Office
The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

For details of our global editorial offices, customer services, and more information about Wiley products visit us at www.wiley.com.

Wiley also publishes its books in a variety of electronic formats and by print-on-demand. Some content that appears in standard print versions of this book may not be available in other formats.

Library of Congress Cataloging-in-Publication Data

Names: Khan, Aisha Saleem, author.
Title: Flowering plants : structure and industrial products / Dr. Aisha Saleem Khan.
Description: First edition. | Hoboken, NJ : John Wiley & Sons, Inc., 2017. |
Includes bibliographical references and index.
Identifiers: LCCN 2016051233 (print) | LCCN 2016052638 (ebook) |
ISBN 9781119262770 (cloth) | ISBN 9781119262800 (pdf) | ISBN 9781119262787 (epub)
Subjects: LCSH: Angiosperms. | Angiosperms–Utilization.
Classification: LCC QK495.A1 K43 2017 (print) | LCC QK495.A1 (ebook) |
DDC 582.13–dc23
LC record available at https://lccn.loc.gov/2016051233

Cover image: Courtesy of the author
Cover design: Wiley

Set in 10/12pt Warnock by SPi Global, Pondicherry, India

10 9 8 7 6 5 4 3 2 1

Dedicated to my dear and loving father without his support I would not have been able to write this book

Contents

Preface

My inspiration for writing a book on Applied Plant Biology came from many authors whose work has captivated my imagination, since I was an undergraduate student. I have been teaching Applied Plant Biology to undergraduate and postgraduate students for the last 12 years. It is not only my area of specialization but my passion as well.

Being a botanist, I always felt the urge for a book which relates plant structure with their important functional products and commercial applications. I believe that angiosperms structure and their important products need to be discussed together in order to have a clear understanding of how the plant architect influences the formation of important products.

The following book relates morphological aspects of flowering plants alongwith their products in different industries in a unique, informative, more conceptual and an interesting way with research-based and updated knowledge. There is a strong need to correlate flowers of angiosperms with their compounds of industrial importance as it is rare to find books which characterize and highlight important products of angiosperms from flowers, fruits and seeds alongwith their morphology. I am sure that with the necessary topics covered, the following book can be introduced as a textbook for all students of plant biology as it will capture their interest towards plants biology. Students all over the world find the study of plants more or less difficult or dry, which does not always aspire their general interest. One of the reason behind this is that the general consensus amongst the academic scientific community has negated the plant sciences its real position due to other emerging trends in biological sciences. Consequently, subjects characterized in the realm of fundamental sciences are loosing their inert value as one of the integral components in comprehending biology.

Although this book is primarily designed for the students of plant sciences, it is also be helpful for researchers who are associated with the different industries, as it covers plants products of commercial value that are being used by food, agriculture, pharmaceutical, beverages, textile, dye, floriculture, perfume, and cosmetic industries.

This book covers topics like making of bioengineered bacterial perfumes from roses, development of transgenic herbivores resistant plants, modern trends in developing ornamental medicinal plants, plant-derived nutraceuticals, plant pigments as dye-sensitized cells and also the role of plant hormones as antiaging molecules. Various distillation methods and techniques like supercritical CO_2 methods for extraction of essential oils, gas chromatographic and mass spectrometric techniques are also included. Life cycles of plants and evolutionary relationships in molecular phylogenetics are included with future perspectives to develop student's interests in plant biology.

It also explains diversity in floral cells which relate their metabolic activities, how cells of sepals differ from petals, ovary and stamens, and how they manage carbohydrates to fulfill their energy demands? In addition, it also covers the formation of important products within floral cells, intercellular and intracellular communications and different steps which are involved in making them commercial; molecular aspects of pollination, pigmentation and reproduction events in angiosperms are also discussed.

Acknowledgements

I am thankful to my dear students who motivated me and suggested me to write a book on the following subject. I am extremely thankful to Sara Dar, designer, for drawing computer illustrations of this book. I am also thankful to Dr. Samina Mehnaz, my chairperson for motivating me throughout writing of this book and also to my colleagues Dr. Aafia Aslam and Dr. Asma Maqbool. My sincere thanks are to my family members, my siblings and my dear friends.

I am also thankful to John Wiley & Sons for giving me this opportunity and for making my dream come true.

1

An Introduction to Flowering Plants: Monocots and Eudicots

There is no doubt about it that plants are main producers of ecosystem and important in every aspect of our daily lives. Many products which are used in food, nutraceutical, pharmaceutical, textile, cosmetics, perfumery, coffee, tea and beverage industries are in fact derived from plants. They are biosynthesized in different parts of plants and are known as *natural products* or *secondary metabolites*. Many of these compounds are defensive in nature which are produced during primary metabolic activities in plants. Many pigments in flowering plants are also secondary metabolites which are crucial for their pollination. Secondary metabolites include alkaloids, flavonoids, betalains, glycosides, tannins, terpenoids and saponins. They will be introduced in the next chapter.

This book deals with flowering plants, that is, *angiosperms* as they make one of the abundant group of plants of economic importance. However, before discussing major products of angiosperms, their biosynthesis and applications, it is important to discuss what are angiosperms? How did they evolve? What is their body organization and what kind of cells they have? So in the next section, a brief introduction of angiosperms and their classification is discussed.

1.1 An Introduction to Major Group of Angiosperms: Monocots, Eudicots and Basal Angiosperms

All plants are considered to be a group of related organisms which are capable to synthesize their own sugars during photosynthesis, possess the cell wall, and generally with the differentiation of their bodies in roots, stems, leaves, flowers or flower- like structures. But recent trends in molecular phylogenetics have shown that they are not as much closely related as thought before. In fact, plants can be best described as ‘a group of different organisms which evolved independently during course of evolution and share similar characteristics like ability to synthesize their own food within their chloroplasts, have chlorophyll *a* as a necessary photosynthetic pigment and possess the cell wall which largely comprises of cellulose’. Their body is differentiated in vegetative and reproductive organs (spore or seed-producing structures) and are therefore classified in one kingdom *plantae*. Division within kingdom plantae is based either on the presence or absence of vascular tissues (xylem and phloem) or spore-producing structures. *Bryophytes* like liverworts, hornworts and mosses are non-vascular spore producing plants while *pteridophytes* are vascular plants which produce spore, for

Flowering Plants: Structure and Industrial Products, First Edition. Aisha Saleem Khan.

example, ferns, horsetails and clubmossses. Other two major groups are seed-producing plants, that is, *gymnosperms* which produce seeds which are not enclosed within their ovaries, and *angiosperms* or flowering plants, in which seeds develop within carpels and are covered by ovary wall.

Angiosperms also known as *flowering plants* are the largest monophyletic group of seed producing plants which have evolved many efficient ways of survival over the period of time. They are unique from other group of plants due to the development of *endosperm* (nutritive tissue around embryo within seeds), flowers with carpels and stamens having two pairs of pollen sacs and phloem for transportation of sugars. Their fossils are over 135 million years old. Angiosperms are considered to be close relatives of living gymnosperms but some recent evidence suggested that seed ferns represent sister group to angiosperms. They are relatively evolved group of plants as compared with gymnosperms as they possess several mechanisms which ensure successful asexual and sexual reproduction, one of the main reason which makes them one of the abundant group of seed plants.

Although *monocots* (angiosperms with one cotyledons) and *dicots* (angiosperms with two cotyledons) are referred as two main groups of angiosperms but modern classification which is based on molecular evidences have characterized angiosperms as *core and basal* angiosperms according to their *monophyletic* origin (descendants of common ancestors) and facts provided by molecular data including studies from DNA sequences from chloroplasts gene *rbcL*. Therefore, modern system of plant taxonomy, that is, *Angiosperms Phylogeny Group* (APG) system is a molecular-based systematics which retains order and families of Linnean systems and includes groups which are monophyletic. APG I was published in 1998 which was followed by APG II in 2003 (Chase *et al*., 2003) and APG III in 2009 (Bremer *et al*., 2009) and then APG IV in 2016. However, further development in molecular techniques, advancement in techniques related to metabolomics and proteomics is exploring the molecular phylogenetics which will form foundation of evidence-based classification of flowering plants.

Evolutionary evidences suggest that *basal angiosperms* which are characterized by absence of xylem vessels are primitive, however, some recent phylogenetic analysis reported that *Amborella trichopoda* is sister to all extant angiosperms and is at the base of angiosperms phylogenetic tree. They are composed of only few species which include many aquatic plants like water lilies (Figure 1.1), *Amborella* and star anise. *Core* angiosperms are represented by monocots and *core eudicots*. They include three major groups including *monocots*, *eudicots* and *magnoliids*, and the latter group was once considered to be dicots but now it is placed in a separate group. Important magnoliids include plants like avocado, black pepper, magnolia, nut-meg, bay leaf, tuliptree or yellow poplar.

Eudicots also known as *true dicots*, composed of more than 75% of angiosperms and are characterized by their monophyletic origin and presence of *tricolpate* pollens (having three apertures). This group of angiosperms represents abundant clade of angiosperms. Figure 1.2 shows a cladogram of flowering plants based on information from APG I, II and III. A *cladogram* represents an evolutionary diagram which is used to explain evolutionary relationships within a group of related organisms which share common ancestors. Orders of basal angiosperms (Amborellales, Nymphaeales and Austrobaileyales) represent primitive groups whereas core eudicots are represented as advanced or modern group of flowering plants. Magnoliids like Laureales, Magnoliales, Canellales and Piperales are evolved with monocots. Eudicots represent abundant group of flowering plants, among which core eudicots include two highly evolved and

(a)

(b)

Figure 1.1 (a-b) Basal angiosperms, (a) *Nymphaea alba* from family Nymphaeaceae, (b) *Magnolia* sp. is another basal angiosperm which belongs to family Magnoliaceae.

diverse clades which evolved separately are *asterids* (lamiids and campanulids) and *rosids* (fabids and malvids) (based on APG III) which are classified on the basis of their tendency to produce fused or free petals (Figures 1.3 and 1.4). Evolutionary traits, apomorphies, which are important in classification are represented where the origin of a clade takes place. Eudicots represent group of many economically important plants like members of family Apiaceae, Asteraceae, Brassicaceae, Cucurbitaceae, Fabaceae, Malvaceae, Rosaceae and Solanaceae.

Other main group of flowering plants, that is, *monocots* represent one of the highly evolved clade with monophyletic origin (Figure 1.5). They are characterized by presence of only one cotyledon, non-woody stem, fibrous roots, long and slender leaves with parallel venation and scattered vascular bundles. They produce inconspicuous, mostly non-fragrant flowers with floral parts in multiple of three often which are arranged to form a *spikelet* in case of grasses. Table 1.1 shows comparison of monocots and eudicots. *Commelinid* clade represents most derived group of angiosperms which includes many plants from Arecales, Commelinales, Poales and Zingiberales. Monocots include palms, orchids and grasses which evolved about 60 millions years ago and are composed of almost 10,000 species. Fossils of palms and members from arum family are the oldest known monocots which are reported to found in rocks almost 100 millions years old. Monocots include many economically important plants which make our staple food like all cereals and grasses are monocots. They are important source of biofuel and bioenergy.

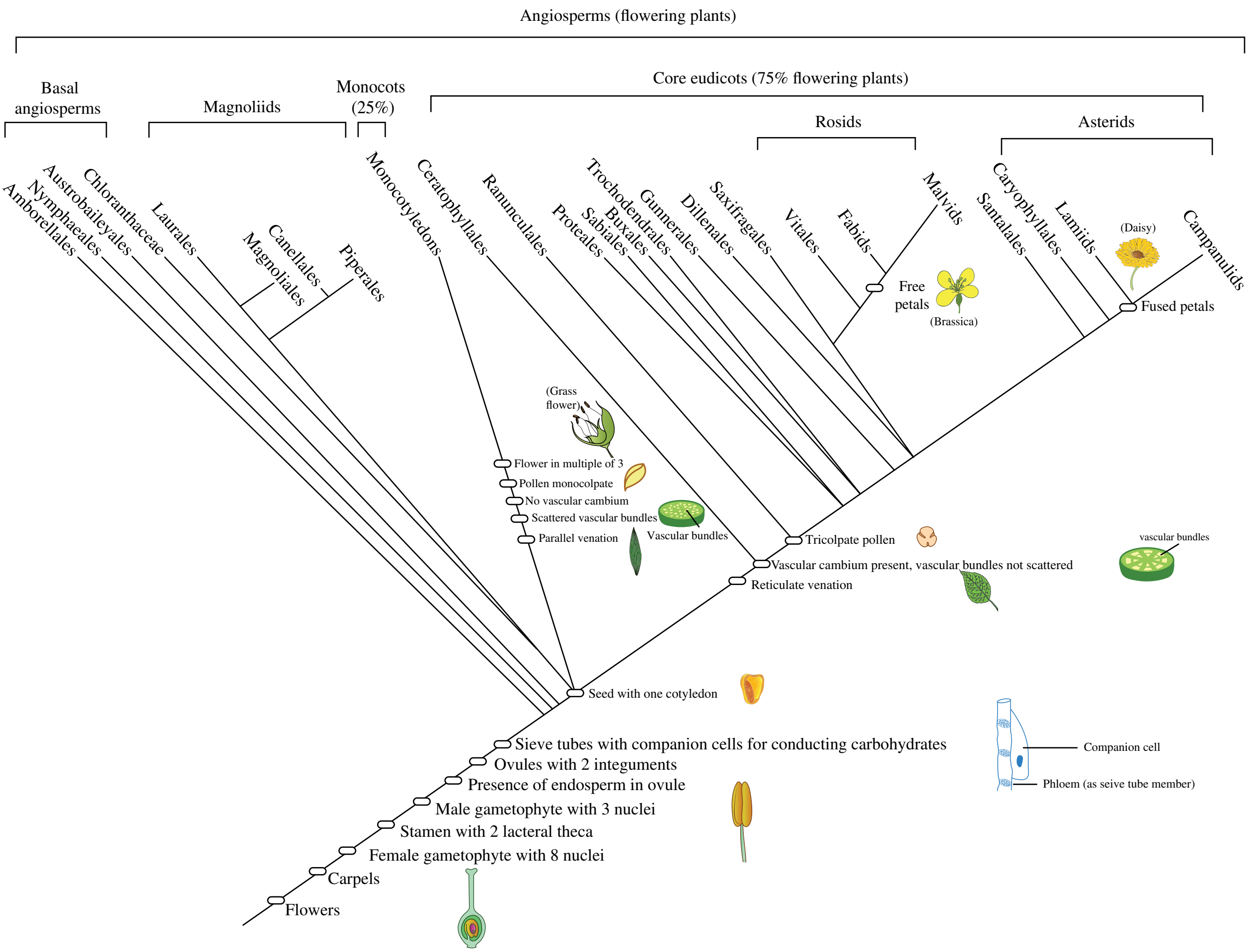


Figure 1.2 A cladogram of angiosperms based on information from the Angiosperms Phylogeny Group (APG III, 2009) (Bremer *et al*., 2009).

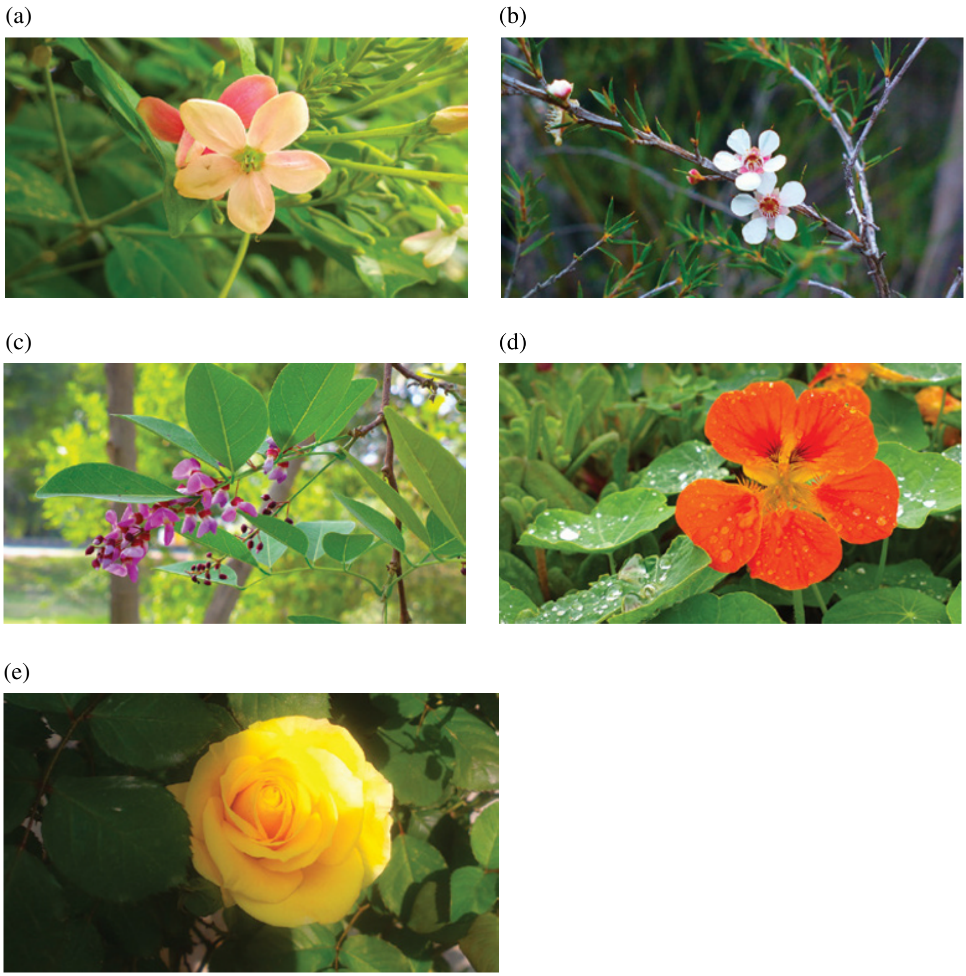


Figure 1.3 (a-e) Rosids (fabids and malvids) are characterized by the presence of free petals (a) *Quisqualis indica,* (b) *Chamelaucium uncinatum,* (c) *Millettia peguensis* is an economically important plant with insecticidal properties and antiviral activities, (d) *Tropaleum majus* is an ornamental member of family Tropaeolaceae, and (e) *Rosa* sp. which belongs to Rosaceae is one of the popular ornamental and medicinal shrub.

Before describing the functional products of angiosperms, their biosynthesis and industrial uses, it is important to revise and update knowledge about angiosperms cell. So the following section will be dealing with the structure of an angiosperm cell along with some updates.

1.2 Plant Cell: Revisions and Few Updates

All plant cells are surrounded by the *cell wall* which not only protects them but also gives them definite shape. A lipoprotein bilayer, that is, *plasma membrane* is present next to the cell wall and regulates the movement of molecules in and out of plant cells.

(a) (b) (c) (d)

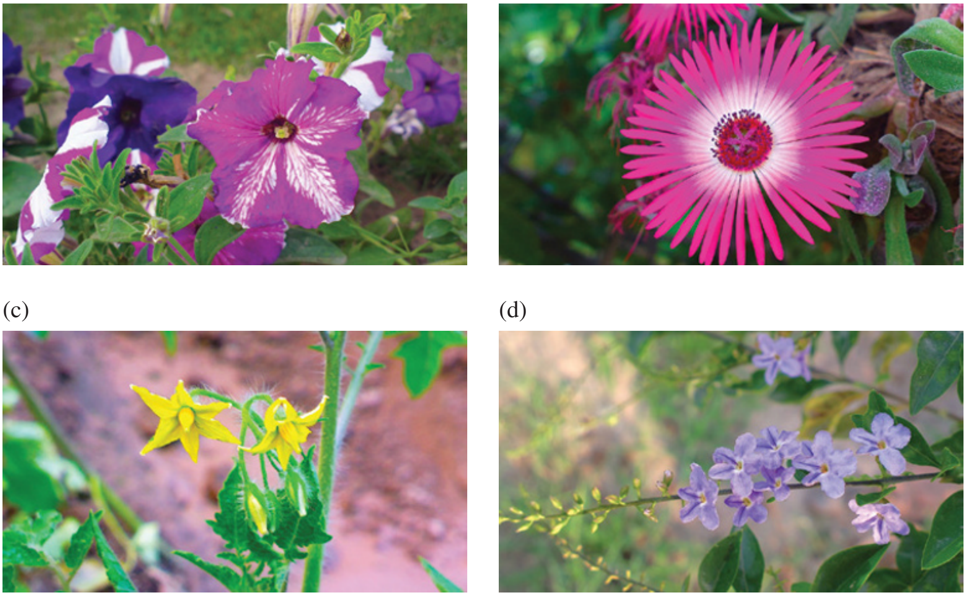


Figure 1.4 (a-d) Asterids (lamiids and campanulids) are core eudicots which are differentiated from other eudicots due to the presence of fused petals (a) *Petunia hybrid,* (b) Daisy, (c) *Lycopersicon esculentum*, (d) *Duranta erecta*.

(a)

Figure 1.5 (a-e) Monocots are composed of many economically important plants: (a) Wheat (*Triticum aestivum*) is a major cereal, bioenergy crop and a staple food worldwide.

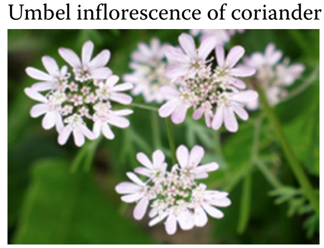
Figure 1.5 (Cont'd) (b) Arum lily (*Zentedeschia aethiopica*) showing spadix (in yellow) and spathe, (c) *Epipremnum aureum* is a popular house plant which removes many indoor pollutants, such as formaldehyde, xylene and benzene, (d) *Bambusa* sp., (e) *Canna indica* also known as canna lily is used in constructed wetland for the removal of organic pollutants and heavy metals.

Plasma membrane encloses many membrane-bound structures, that is, *organelles* which are present within a fluid *cytosol* which is the site for main metabolic activities of cell. Main organelles which are part of almost every plant cell include nucleus, mitochondria, plastids, vacuoles, endoplasmic reticulum, Golgi apparatus and ribosomes. However, in addition to this, plant cell may also contain microbodies, tannosomes, anthocyanoplasts and oil bodies depending upon their physiological role (Figure 1.6).

1.2.1 A Cellulosic Cell Wall is Crucial for all Plant Cells

Angiosperms show diversity in chemical composition of their cell wall which is the outermost covering of every plant cell whether it is a cell of root, leaf, stem, flower, fruit or seed. Each cell of these organs possess their own cell wall which gives them rigidity, support and a definite shape along with *cytoskeleton* which is composed of a network of microtubules and actin filaments. Cytoskeleton is involved in orientation of cellulose

Table 1.1 A comparison of two major group of core angiosperms.

Characteristics	Monocots	Eudicots
Root	Fibrous, vascular bundles are collateral	Taproot, xylem in centre
Stem	Soft, herbaceous with scattered vascular bundles **Wheat (*Triticum aestivum*)** 	Soft in non-woody herbs or woody but vascular bundles are compactly arranged **Coriander (*Coriandrum sativum*)** 
Leaf	Parallel venation 	Reticulate venation 
Flower	Ear of wheat 	Umbel inflorescence of coriander 
Fruit	Wheat hull or husk 	Coriander fruit 
Seed	Wheat grains (monocots) 	Seeds showing two cotyledons (eudicots) 
Pollination	Mostly wind pollinated	Pollination through insects and animals
Pollen grains	Monocolpate	Tricolpate

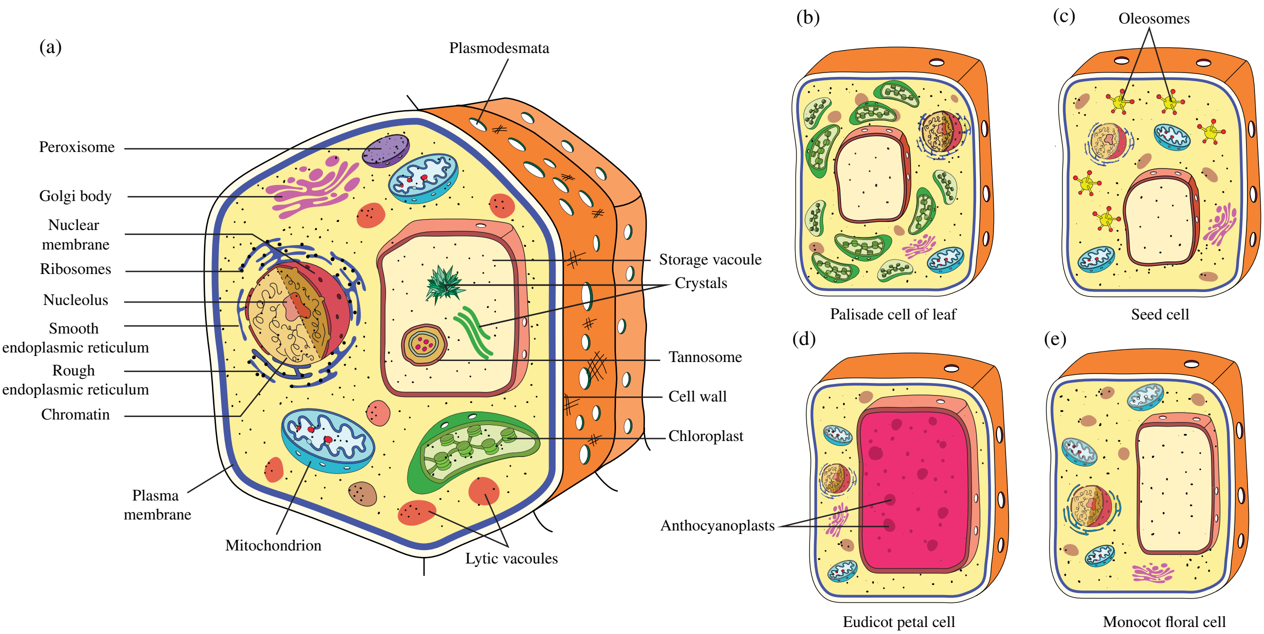


Figure 1.6 (a-e) Plant cells show differences depending upon their role: (a) A typical plant cell, (b) Cells of mesophyll of leaves contain abundant chloroplasts due to their role in photosynthesis, (c) Seed cells of many plants store lipid in form of oil bodies or oleosomes, (d) Cells of petals of many eudicots contain large vacuoles for storing water soluble pigments in order to attract their pollinators, (e) Vacuoles of sepals and petals (perianth) of most monocots are not as conspicuous as in eudicots, as many of them are pollinated by wind. (*See insert for color representation of the figure*.)

microfibrils and organizes the plane of cell division. Cellulose exists in the form of crystals in the cell wall and forms microfibrils which are embedded within the cell wall. The cell wall is also crucial for cell growth and development. Structural and chemical differences in the cell wall may exist within a tissue or and even within a cell. The cell wall of roots epidermal cells may be different from the cell wall of epidermal cell of stem, leaf or flower depending upon its physiological role.

Primary cell wall is characteristic of all plants cells and is composed largely of cellulose microfibrils which are embedded in a matrix of pectin and cross-linking glycans. The matrix of the cell wall is laid down in cell plate followed by synthesis of cellulose microfibrils after the plate has reached the side of cells. However, *secondary cell wall* is characteristic of xylem tracheary elements and fibers and involves deposition of *lignin*, a phenolic compound.

Primary cell wall is composed of almost 35% of cellulose, 35% pectin and 25% hemicelluloses compounds. Cellulose is the main carbohydrate of cell wall which exists as unbranched polymer of D-glucose molecules connected by ß-1,4 glycosidic linkage. Major hemicelluloses (branched polymer) of the cell wall are xylans, glucomannans, xyloglucans and ß-D-glucans. The protein part of the cell wall includes cyclins and expansins which are important for growth and development of the cell wall.

Pectin compounds are important constituents of the cell wall which are present in *middle lamella* which is the outer cementing layer of the cell wall. Galactouronic acids connected by α-1,4-D are basic units of pectins. Incorporation of methyl groups to carboxylic groups of these units make them esterified. Their linkage with Ca^{++} and Mg^{++} makes pectic compounds insoluble, thus, limiting cell wall application in food industry. Pectic compounds like galactouronic acids, rhamnogalactouronins (RGI and II) prevent the cell wall from dehydrating, give them shape and cause expansion. However, RGII in primary cell walls exists in form of dimer cross-linked with borate. This dimer provides enough support to the cell wall for its growth.

Secondary cell wall is different from primary cell wall in having more cellulose and due to the presence of lignin. Both are attached with each other by means of covalent bonding. In addition, secondary cell wall is composed of hemicellulose and lignin which is deposited between plasma membrane and primary wall and prevents enlargement of the cell. Precursors of secondary wall synthesis like monolignols are secreted into the cell wall space and become randomly cross-linked depending upon reactive oxygen species, generated by laccases and peroxidases which makes the cell wall resistant against pathogens and also gives structural support to the cell wall. Some alcohols like coniferyl, caumaryl and sinaply groups are also part of secondary cell wall along with deposition of lignin.

Monocots are different from eudicots in many ways. Some differences also exist in the cell wall, that is, presence of different polymers type and their abundance in the cell wall, presence of SiO_2 forming phytoliths, especially cell walls of commeliinids including grasses contain relatively small amount of pectin and structural proteins. The cell walls of monocots are composed of upto 30% cellulose, 25% hemicelluloses, 30% pectin and up to 10% glycoproteins with an increased amount of ferulate in plants like wheat, maize, rice and sugarcane which are linked with glucurunoarabinoxylans (GAX) (Molinari *et al.*, 2013). Furthermore, a unique feature of the cell walls of grasses includes accumulation of β-glucan in addition to GAX during their elongation.

Presence of gelatin-like properties of the cell wall which is due to *O*-acetylated of the cell wall polymers, increases its applications in food industry. However, their presence also limits their use in biofuel technology and modern research is focusing on reduction of *O*-acetylation of plants' cell wall (Gille & Pauley, 2012). In the cell walls of dicots, only side chains of galactosyl-residue in xyloglucans are *O*-acetylated, however, in monocots-like grasses glucosly-residues of xyloglucans are *O*-acetylated.

Recent emerging trends in cell wall technology include determination, modification and isolation of cell wall polymers for use in biomaterial, pharmaceutical and food industries through techniques like NMR and mass spectrometry. Orientation of cellulose fiber in the cell wall can be determined through Raman micro spectroscopic methods in herbaceous plants (Sun *et al.*, 2016). Recently, cotton fibre is considered to be a single-cell model for cell wall and cellulose research.

The cell wall not only provides protection to the cell but also provides passages for the entry and exit of molecules in the form of pores, known as *plasmodesmata* which are extensions of smooth endoplasmic reticulum and regulate transport of molecules within range of 900 daltons. A typical plant cell may have more than 10,000 plasmodesmata on all sides of the cell wall, the exception being the outer side of epidermal cells.

Plasmodesmata provide connections among cells for the transport of molecules, however, transport through plasmodesmata is not specific like cell membrane. There may be up to 1,000 to 10,000 or even more number of plasmodesmata present within a single plant cell. Plasmodesmata are of two kinds, primary and secondary. *Primary plasmodesmata* are formed during cell division. They are extensions of smooth endoplasmic reticulum in the form of tube, that is, desmotubules which are lined with plasma membrane through filamentous proteins (Figure 1.7). *Secondary plasmodesmata* are branched which develop during cell expansion. Plasmodesmata play important role during floral development and also involved in intercellular signaling especially in ovules.

1.2.2 Plant Plasma Membrane Allows Molecules to Enter Only Through Their Respective Channels

Plasma membrane is the lipid and protein part of a plant cell next to the cell wall which regulates the transport of molecules. The lipid part of membrane makes a bilayer of phospholipids which provides a barrier for transport of molecules due to its hydrophobicity. Significance of bilayer is to give support to many protein channels which are embedded within plasma membrane, and also for better trapping of molecules inside the cytosol. Non-lipid part of plasma membrane is composed of proteins which makes up to 75% of membrane and allows transport of molecules which cannot simply cross the membrane through diffusion. They include polar and large molecules like sugars or charged molecules like amino acids, nitrates, sodium, potassium, calcium, and so on. Concept of plasma membrane is just like a room, whereas proteins make the gates, where molecules will cross their respective *gates* or *channels* (Figure 1.8). Plasma membrane also regulates the movement of water molecules through aquaporins channels. Water molecules pass in a single row through this pore.

Although plasma membrane is the main membrane of cell, but organelles like mitochondria, chloroplasts, nucleus, vacuoles also have their own lipids bilayers which perform role of plasma membrane. Plant membranes also are composed of several

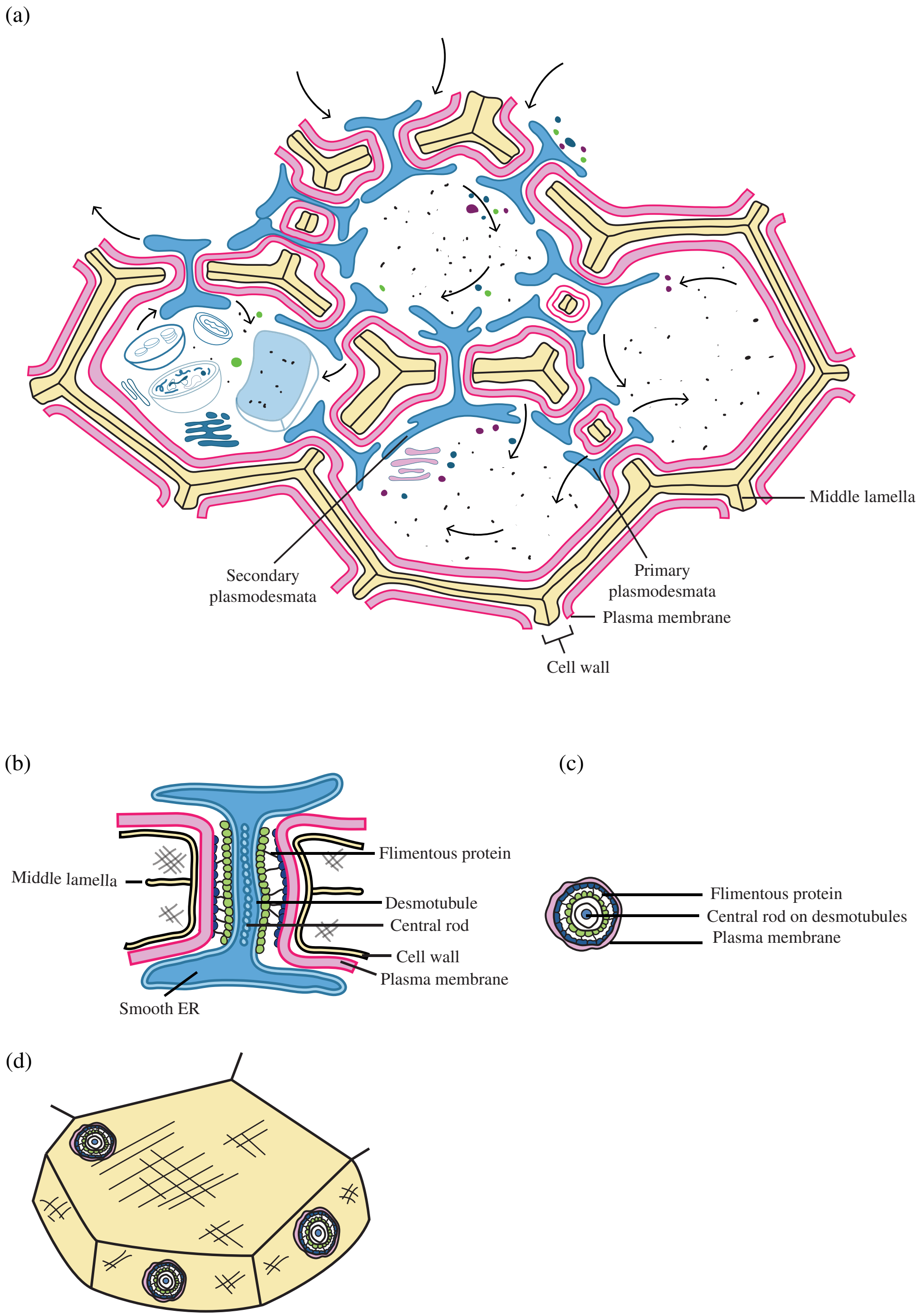


Figure 1.7 (a-d) (a) Plasmodesmata are extensions of smooth endoplasmic reticulum (SER) and main connections within the cell wall which allow transfer of water and other molecules from one cell to other, (b) Detailed structure of plasmodesmata showing desmotubule which extends from one cell to next through smooth ER, (c) Cross section of a desmotubule, (d) A view of plasmodesmata view within plant cell.

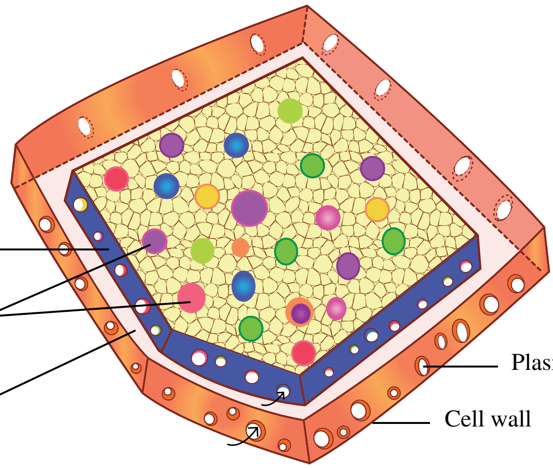


Figure 1.8 Plasma membrane of plant cells is enclosed in the cell wall which surrounds it from all sides (top view). Round circles on plasma membrane represent proteins which provide passage for regulation through plasma membrane. Gaps in the cell wall indicate plasmodesmata.

sterols, for example, sitosterols, stigmasterol being the most abundant one. However, membrane sterol composition is dependent upon ecophysiological conditions involved in growth and development.

1.2.3 Mitochondria Convert Energy of Glucose in ATP and in Reducing Powers

Mitochondria are the site of cellular respiration and synthesize energy in the form of ATP for various metabolic needs of cells. Mitochondria multiply by division and are maternally inherited.

Mitochondria have two membranes, outer and inner which are made up of phospholipid bilayers. However, outer membrane of mitochondria comprises mostly lipids, whereas the inner membrane contains almost equal amount of lipids as well as proteins. The inner membrane is folded to increase surface area for metabolic processes like the electron transport chain and these invaginations are known as *cristae.* Outer membrane of mitochondria have proteins, that is, porins through which they communicate with the cytosol of cell and allow transfer of molecule upto 10KD, such as glucose and many ions. However, inner membrane is more permeable to molecules like CO_2, H_2O having pores for transport of molecules like ATP, ADP and pyruvate. Many proteins which are required for metabolic activities of mitochondria are carried through binding with receptor in an energy-dependent transport.

Space between two membranes is *inter membrane space* and fluid part of mitochondrion within cristae is known as mitochondrial *matrix* which is site of many processes that are crucial for providing energy to the cell. Products from glucose breakdown are transported to mitochondria for further breakdown in order to release energy.

Mitochondria have their own DNA which is present in from of loops similar to bacterial DNA. It is present in multiple copies in matrix along with ribosomes. However, mitochondrial genome encodes only a few proteins, most of them are encoded in the nucleus. Mitochondrial genome of plants is larger in plants as compared with humans, and its size varies among different plants as in *Arabidopsis* it is 20 times larger, whereas in melon it is 140 times higher than in humans.

Mitochondria synthesize energy in the form of ATP (adenosine triphosphate), therefore, protein channels in membranes allow for transfer of ADP (adenosine diphosphate), Pi and ATP (also known as ATP and ADP *translocators*). ATP formation is immediately followed by its export through translocators to other organelles or cytosol of cell wherever energy is required within cell. ATP and ADP transport is important for cell as many processes, such as DNA replication, transcription, formation of larger molecules, translation, secondary metabolite formation and cell division are all dependent upon the availability of ATP. Therefore, mitochondria also accumulate near the site where energy demand is high in germinating pollen grain.

Mitochondria also play role in cell adaptation to abiotic stress and regulate metabolism of proteins which regulate homeostasis and are involved in programmed cell death. They are also source of providing energy to rapidly growing pollen tube cells.

1.2.4 Plant Vacuoles Store Water, Pigments and Compounds of Defensive Nature

Vacuole of plant cells serve as lytic and storage compartment, which maintains turgor and homeostasis under stress conditions. *Storage* vacuoles store water, pigments, nutrients, crystals, starch, protein bodies for the plant cell and also involved in growth of cell and also help in signaling. Molecules like calcium, sodium, potassium, magnesium, chloride, nitrate and water are stored in vacuoles and help increase in height and surface area. Calcium and potassium are required for many processes within plant cells, therefore, vacuoles serve to store them and facilitate their transport within the cell. Vacuoles have many enzymes which convert toxic products into non-toxic forms. Therefore, they also detoxify harmful products like xenobiotics, as revealed by experimental techniques involving isolation of vacuoles and through replacement of vacuolar content and mutants of vacuoles.

Just like membranes of many other organelles, vacuolar membrane or *tonoplast* is also a lipid bilayer with protein transporters. Vacuoles of floral cells occupy more parts of cell as they store pigments for pollination. They also modulate turgor during growth. Vacuoles also digest old organelles due to hydrolytic enzymes which are no longer required by cells and are therefore known as *lytic* vacuoles. Mitochondria are transferred to vacuoles by endocytosis.

Aquaporins were first discovered in the vacuolar membrane of seeds so named r-TIP (tonoplast intrinsic proteins). Vacuoles of many pollens are elongated and tubular in shape. In the petals of many flowers, sometimes vacuoles of neighbouring cells store different shades of pigments within the same petal, which differentiates it from the rest of petal, thus making contrasting patterns known as a *nectar guide* which serve as a guide for pollinators.

Vacuolar pH is important factor in determining the color of flowers as an increase in pH may give the blue shade in morning glory (Yagamuchi *et al.*, 2001). This increase in pH is due to an active transport of Na^+/K^+ from cytosol into the vacuole with the help of Na^+/K^+ pump. Vacuoles of epidermal cells store pigments like anthocyanin which protect them against UV radiations. Tonoplast of vacuoles storing anthocyanins pigments require transporters like *ATP binding cassettes* (ABC). Vacuoles, like protein-storing vacuoles, transfer nutrients to germinating seeds and main source of storing nutrients like Ca, Fe, Mg, P and Zn, thereby serving important role in nutrition. Vacuoles of all plants are composed of H + -ATPase, V-PPase and TIP, such as aquaporins which may differ in their role depending upon their location.

Plants vacuoles are also the site for storage of industrially important products like alkaloids and anthocyanins which are widely used in textile and food industries and are reported to have anti-cancerous properties. *Anthocyanins* are known to accumulate in pigmented structures within vacuoles known as *anthocyanoplasts* in plants like red cabbage, which may also contain enzymes for anthocyanins biosynthesis.

Channels like H^+-antiports, electrogenic uniport ion and ABC transporters facilitate transfer and accumulation of secondary metabolites in vacuoles. Two proton pumps on vacuolar membrane, that is, V-ATPases and V-PPases develop gradient across tonoplast membrane. Vacuoles are crucial for storage of plants' defensive compounds in order to prevent toxicity to the rest of the cell. They are also important for synthesis of saponarin which is inhibited without vacuoles (Marinova *et al.*, 2007). New technologists have developed to express economically important proteins in plants which accumulate in vacuoles and can further be used for cultivation of plants so large number of proteins can be produced at low costs.

1.2.5 Golgi Apparatus

It is involved in the modification of carbohydrates and proteins, and also transports them within the cell wherever they are needed in the form of vesicles. Golgi apparatus also modifies many proteins which are involved in pollination and fertilization processes within different floral cells. Within a plant cell, it constitutes a system of stacks of thin vesicles that are held together either in a flat or in a curved array. Individual stacks of cisternae that are filled with fluid with modification are present almost all over the cytosol within plant cell.

Golgi complex coordinates with endoplasmic reticulum, and form vesicles, that fuse and form a wider thin vesicle *cisternae*. Vesicles formed by smooth ER form cisterna on *cis* face of Golgi apparatus, however, at the *trans* face, vesicles are released or carried to their destination. These vesicles may move to plasma membrane and discharge their contents. Golgi bodies are also involved in forming cell wall machinery through the same process.

1.2.6 Nucleus Encodes Genes Required for Enzymes Forming Products of Commercial Applications

Nucleus is an important organelle due to the presence of nucleic acids DNA (deoxyribonucleic acid) and RNA (ribonucleic acid). DNA is main heredity material which is present on genes present on chromosomes which are thread-like structures. RNA synthesizes proteins for plants growth and metabolism through a process which we call *gene expression*.

All cells of plants possess their own nuclei. However, sieve cells of phloem loss their nuclei upon maturity and they are assisted by companion cells. Nucleus communicates with other organelles and cytosol by means of pores within nuclear membrane. Nuclear envelope is similar to plasma membrane and comprise of phospholipids as dominating lipids. Proteins which are part of nuclear membrane, facilitate transport of molecules and allow mRNA to leave the nucleus through nuclear pore. They also provide passage for transport of molecules like ATP from mitochondria within the nucleus to energize energy-dependent reactions like DNA and RNA synthesis. *Nucleotides* which are building blocks of DNA and made up of repeating units of sugar, phosphoric acid and nitrogenous bases that are synthesized within the cytosol of the cell. Four nitrogenous bases, adenine (A), guanine (G), cytosine (C) and thymine (T) exist in a pair attached by means of hydrogen bonds. Adenine and guanine form double hydrogen bonds within the centre of double helical structure. However, guanine and thymine are attached by means of three hydrogen bonds. In RNA, instead of thymine, uracil is present. Nucleus encodes genes for formation of enzymes which are involved in pathways which leads to the formation of products of industrial importance.

1.2.7 Plastids are Sites of Sugar and Fragrance Formation

Plastids are double membrane organelles derived from proplastids, which are undifferentiated plastids in meristematic cells of root and stem. Detailed sequence analysis of genes have revealed that all plastids are evolved from a single ancestral source and thought to be originated by the engulfing of a photosynthetic organism by a non-photosynthetic organism. Like mitochondria, they multiply by division and have maternal inheritance. Plastids possess their own circular genome known as ctDNA (circular DNA) or ptDNA (plastid DNA) which is 120-160kbp in size and makes up to 0.1% of the size of a nuclear genome. Many enzymes like DNA polymerase, helicase and primase have been purified from them. Angiosperms plastids possess both plastid-encoded and nuclear-encoded RNA polymerases (Sato *et al.*, 2003). During cell differentiation, they either differentiate into chloroplasts, chromoplasts or leucoplasts. *Leucoplasts* are colorless organelles which synthesize lipids and store starch in roots, tubers or seeds.

Chloroplasts arise from differentiation of proplastids. They possess their own circular chromosome and enzymes for gene duplication, gene expression and protein synthesis, however, majority of proteins are encoded in nucleus and later transported to chloroplasts. Chloroplasts are known to be evolved from cyanobacteria because their genome is similar to prokaryotic genome.

Chloroplasts are one of the most abundant plastids which are present in leaves of green plants. Their presence in any organ of plant is indicative of their role in formation of sugar through photosynthesis. They contain a lipid bilayer similar to other membranes, however, glycolipids are more common in a chloroplast membrane. Chloroplast lipids like monogalactosyl diacylgylcerols (MGDG) are in fact one of the most abundant lipids on our planet. The membrane of chloroplast is composed of pores which facilitate exchange of molecules and allow them to communicate with the cytosol of cell. Porins in outer membrane of chloroplasts are non-specific and allow transfer of molecule upto 3 nm in size. However, the inner membrane is composed of specific protein translocators which allow transfer of molecules between the cytosol and stroma.

Pigments which are involved in photosynthesis, that is, antenna pigments which are embedded in the lipid membranes of thylakoids which are disc shaped structures. A pile of thylakoids make *grana* which are interconnected through lamellae within chloroplasts. All angiosperms possess chlorophyll *a* as necessary pigments which are crucial for light reactions, however, other pigments, that is, chlorophyll 'b', carotenes and luteins, are also present on thylakoid membranes and transfer energy of sunlight to chlorophyll *a*. Fluid of chloroplast is known as *stroma* which contains starch grains, free ribosomes and enzymes for formation of carbohydrates during the Calvin cycle. Energy molecules like ATP and NADPH are synthesized through a series of photochemical reactions on thylakoids which diffuse in the stroma to provide energy for sugar synthesis. ATP and ADP translocators are present in the inner membrane of the chloroplast envelope. *Plastoglobuli* are oil containing bodies which are found within plastids of senescing leaves.

Chromoplasts are usually present in the petals of flowers giving red, organ and yellow shades. They have an undulated system of membranes without grana. They contain pigments either on the membrane or in the form of plastoglobuli as droplets. During fruit ripening, many chloroplasts are converted into chromoplasts due to the formation of lipid pigments which is evident through a change of color in many fruits like tomato, organ, mango, and so on. They are green when unripened, and turn into chromoplasts when mature. Plastids without pigments and lipids are leucoplasts, they are colorless plastids like amyloplasts. The white color of petals of many flowers is due to leucoplasts. *Carotenoids* are lipid-soluble pigments having 40 carbon atoms which accumulate in chromoplasts and give them that orange, yellow and red color to attract pollinators. However, the presence of carotenes in the chloroplast protects antenna pigments against high intensities of light and helps in the absorption of energy for photosynthesis.

1.2.8 Tannosomes are Chloroplast-Derived Organelles Which Contain Polymers of Tannins

Plants synthesize many molecules in response to the defense against pathogens and herbivores. Proanthocyanidins are type of flavonoids which are also known as *condensed tannins*. They play a defensive role against pathogens and UV radiation. Although tannins inclusions are previously reported to be synthesized by endoplasmic reticulum, recent ultrastructure studies revealed that they are derived from chloroplasts (Brillouet *et al*., 2013). Figure 1.9 shows developmental stages in the differentiation of chloroplast into *tannosomes* (tannin-containing organelles) which involves unstacking and inflation of thylakoids grana forming tannosomes, which are later encapsulated and transferred as shuttle from cytosol to vacuoles where they are stored in order to protect the rest of the cell from toxic effects of tannins.

1.2.9 Ribosomes

are the site for protein synthesis. They are membrane-bounded structures and consist of one large and one smaller subunit. However, the number of ribosomes depends upon the function of cell where they are present. Plant cells contain fewer ribosomes than animal cells. However, the cells of seeds in legumes contain large numbers of ribosomes.

1.2.10 Endoplasmic Reticulum

(ER) forms part of the endomembrane system and communicates with the nuclear envelope. It is a system of flattened membrane, sacks and tubules. ER without ribosomes is smooth endoplasmic reticulum (SER), whereas ER with ribosomes is rough