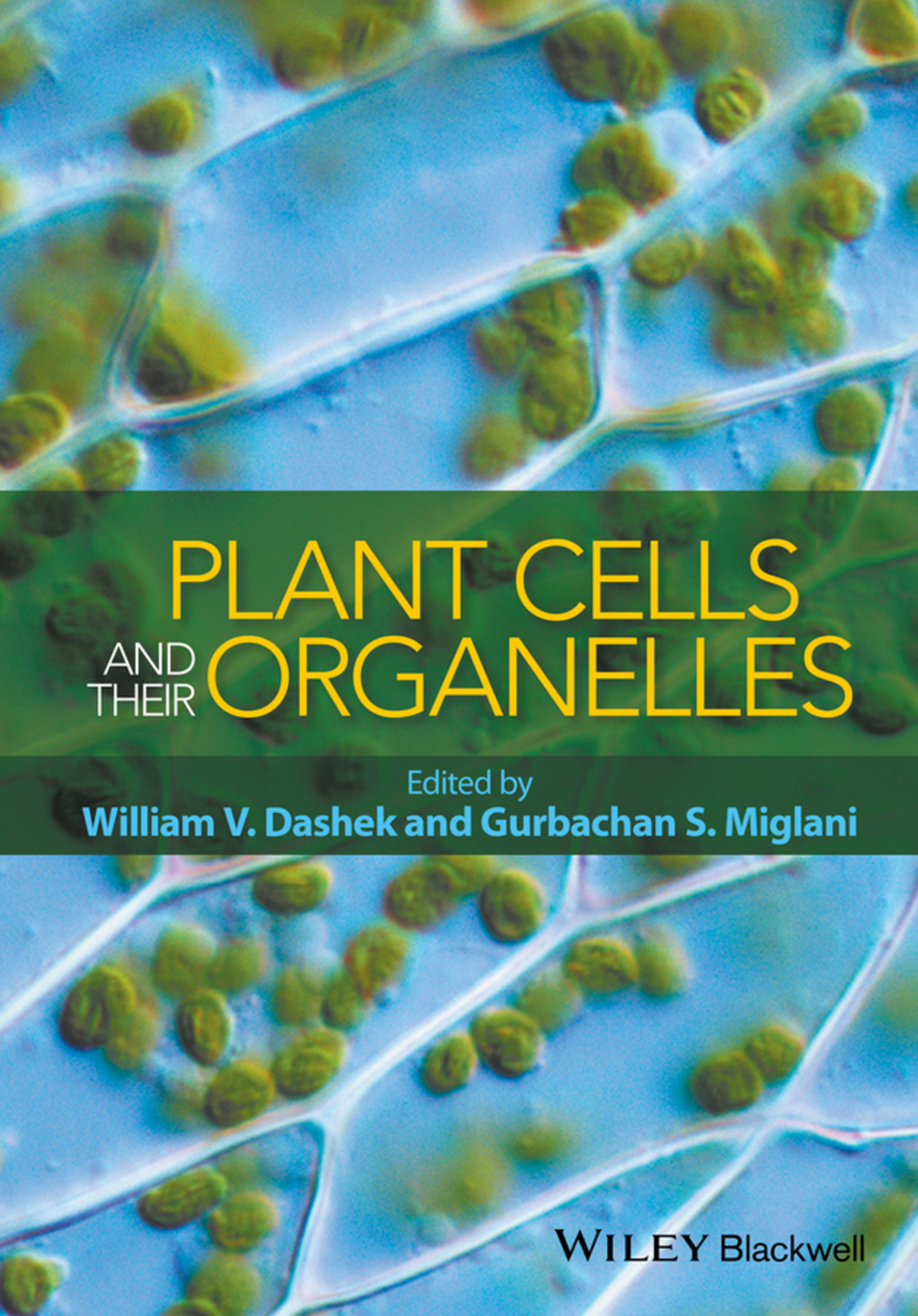

PLANT CELLS AND THEIR ORGANELLES

Edited by

William V. Dashek and Gurbachan S. Miglani

WILEY Blackwell

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Preface

Plant Cells and their Organelles is an advanced textbook to enhance the plant biology student's knowledge of the structure and function of plant cells and their organelles. The book assumes that the student has had introductory courses in plant science and chemistry. The book emphasizes the research literature in plant cell biology concerning cell and organellar structure. However, the literature from plant physiology, molecular genetics, and biochemistry has been utilized to augment the discussions of cell and organellar function.

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CHAPTER 1

An introduction to cells and their organelles

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Cells

Parenchyma, chlorenchyma, collenchyma, and sclerenchyma are the four main plant cell types (Figure 1.1, Evert, 2006). Meristematic cells, which occur in shoot and root meristems, are parenchyma cells. Chlorenchyma cells contain chloroplasts and lack the cell wall thickening layers of collenchyma and sclerenchyma. Certain epidermal cells can be specialized as stomata that are important in gas exchange (Bergmann and Sack, 2007). The diverse cell types (Zhang *et al.*, 2001; Yang and Liu, 2007) are shown in Table 1.1. Photomicrographs of certain of these cell types can be found in Evert (2006), Fahn (1990), Beck (2005), Rudall (2007), Gunning (2009), MacAdam (2009), Wayne (2009), Beck (2009), Assmann and Liu (2014) and Noguchi *et al.* (2014).

How do cells arise?

Cells arise by cell divisions (see Chapter 8 for mitosis and meiosis) in shoot and root (Figures 1.2 and 1.3) meristems (Table 1.2, Lyndon, 1998; McManus and Veit, 2001; Murray, 2012). The shoot apex is characterized by a tunica–corpus organization (Steeves and Sussex, 1989). The tunica gives rise to the protoderm and its derivative, the epidermis. In contrast, the corpus provides the procambium which yields the primary xylem and phloem. In addition, the ground tissue derives from the corpus originating the pith and cortex. Following divisions, cells can differentiate into tissues (Table 1.3) and organs of the mature plant body (Leyser and Day, 2003; Sachs, 2005; Dashek and Harrison, 2006). The leaf primodium arises on the apex (Micol and Hake, 2003). The mature angiosperm leaf consists of palisade cells and spongy mesophyll cells sandwiched between the upper and the lower epidermis (Figure 1.4). The epidermis possesses guard cells with associated stomata that function in gas exchange. *KNOX* genes affect meristem maintenance and suitable patterning of organ formation (Hake *et al.*, 2004). In dissected leaves, *KNOX* genes are expressed in leaf primordia (Hake *et al.*, 2004). Hake *et al.* (2004) suggest that

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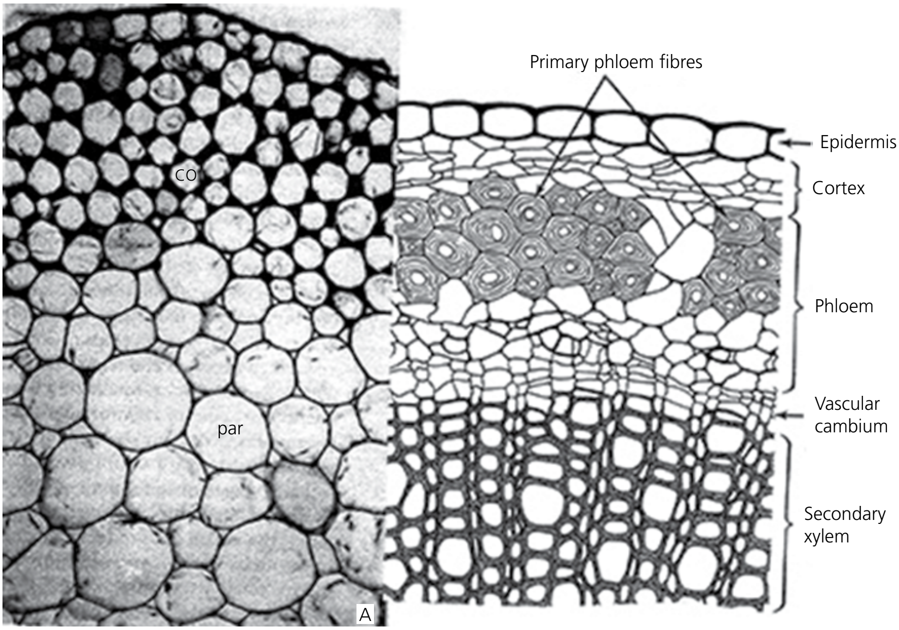


Figure 1.1 Plant cell types: Left: parenchyma (par) and collenchyma (co). Right: sclerenchyma. Source: Evert (2006). Reproduced with permission of John Wiley & Sons.

KNOX genes may be important in the diversity of leaf form. Extensive discussions of leaf development occur in Sinha (1999), Micol and Hake (2003) and Efroni *et al.* (2010). Under appropriate stimuli the vegetative apex can be converted to a floral apex (Figure 1.5). Photoperiod (Mazumdar, 2013), such as short days and long days and combinations of the two, is one such stimulus (Glover, 2007; Kinmonth-Schultz *et al.*, 2013). This induction results in the production of florigen (Turck *et al.*, 2008), the flowering hormone (Zeevaart, 2006). While early reports suggest that florigen is an mRNA species (Huang *et al.*, 2005), a more recent investigation indicates that florigen is a protein complex (Yang *et al.*, 2007; Taoka *et al.*, 2013). Taoka *et al.* state that florigen protein is encoded by the gene, Flowering Locus T, in *Arabidopsis* species (Shresth *et al.*, 2014). It is believed that florigen is induced in leaves and that it moves through the phloem to the shoot apex. Plant hormones (see Appendix A) can influence floral development (Howell, 1998). Gibberellins (Blázquez *et al.*, 1998), auxins, and jasmonic acid can affect petal development. In contrast, auxin can influence gynoecium development. The ABC model has been proposed for regulating the development of floral parts (Soltis *et al.*, 2006). The *A* gene expression is responsible for sepals, while the petals are the result of co-expression of *A* and *B* genes. The *B* and *C* genes are responsible for stamen development and carpels require *C* genes. In certain plants, vernalization (low temperature) can induce flowering in certain plants (Kemi *et al.*, 2013). A diagram of the mature angiosperm plant body is presented in Figure 1.6. Plant

Table 1.1 Plant cell types.

Cell types	Characteristics	References
Epidermal cells	Unspecialized cells; one layer of cells in thickness; outer covering of various plant parts; variable in shape but often tabular	Evert (2006)
Examples		
Guard cells	Specialized epidermal cells; crescent shaped; contain chloroplasts; form defines stomatal pore	Wille and Lucas (1984)
Subsidiary cells	Cells which subtend the stomatal guard cells	http://anubis.ru.ac.za/Main/ANATOMY/guardcells.html
Trichomes	An outgrowth of an epidermal cell; can be unicellular or multicellular	Callow (2000)
Parenchyma cells	Isodiametric, thin-walled primary cell wall; in some instances may have secondary walls; not highly differentiated; function in photosynthesis, secretion, organic nutrient and water storage; regeneration in wound healing	Evert (2006) and Sajeva and Mauseth (1991)
Examples		
Transfer cells	Specialized parenchyma cells; plasmalemma greatly expanded; irregular extensions of cell wall into protoplasm; transfer dissolved substances between adjacent cell; occur in pith and cortex of stems and roots; photosynthetic tissues of leaves; flesh of succulent fruits; endosperm of seeds	Dashek *et al*. (1971) and Offler *et al*. (2003)
Collenchyma cells	Lamellar or plate collenchyma, with thickenings on the tangential walls Angular collenchyma, with thickenings around the cell walls Present in aerial portions of the plant body	
Vascular cells		Evert (2006)
Phloem		
Sieve cells		
Sieve elements		
Companion cells	Specialized parenchyma cells; possess numerous plasmodesmatal connections	Oparka and Turgeon (1999)
Albuminous cells in gymnosperms	Absence of starch; cytoplasmic bridges with sieve cells; dense protoplasm, abundance of polysomes, highly condensed euchromatin and abundant mitochondria	Alosi and Alfieri (1972) and Sauter *et al*. (1976)
Xylem		
Tracheids	Long tapering cell with lignified secondary wall thickenings; can have pits in walls; devoid of protoplasm at maturity; not as specialized as vessels; widespread	Tyree and Zimmerman (2002)
Vessels		Fukuda (2004) and Evert (2006)

(*Continued*)

Table 1.1 (Continued)

Cell types	Characteristics	References
Specialized cells – Hydathodes (modified parts of leaves and leaf tips or margins)	Consist of terminal tracheids epithem, thin-walled chloroplast-deficient cells, a sheath with water pores; guttation discharge of liquid containing various dissolved solutes from a leaf's interior	Lersten and Curtis (1996), https://www.biosci.utexas.edu/ and Maeda and Maeda (1988)
Laticifer cells	Cells or a series of cells which produce latex	Fahn (1990), Pickard (2008) and Botweb.uwsp.Edu
Simple	Single-celled	
Compound and articulated	Union of cells compound in origin and consist of longitudinal chains of cells; wall separating cells remain intact, can become perforated or entirely removed	
Salt glands	Modified trichomes, two-celled and positioned flat on the surface in rows parallel to the leaf surface; occur in *Poaceae*;	Evert (2006), Tan *et al*. (2010), Oross *et al*. (1985) and Thomson *et al*. (1988)
	Cap cell – large nucleus and expanded cuticle	Naidoo and Naidoo (1998)
	Basal cell – numerous and large extensive partitioning invaginations of plasmalemma	
Nectaries	Found in nectarines; produce nectar, usually at the base of a flower	Fahn (1990), Nicolson and Nepi (2005) and Paiva (2009)
Idioblasts	Crystal-containing cells	Lersten and Horner (2005)
Example		
Raphides	Produce needle-shaped crystals	
Mucilage cell	Occur in a large number of dicots, common in certain cacti; slimy mucilage prevents evaporation of water by binding to water; a parenchyma cell whose dictyosomes produce mucilage as in seed coats; cell walls are cellulosic and unlignified	http://www.sbs.utexas.edu/masuetl/weblab/webchap9secretory/9.1-2.html, Western *et al*. (2000) and Arsovskia *et al*. (2010)
Oil cells	Specialized cells appear like large parenchyma cells; can occur in vascular and ground tissues of stem, and leaf cell wall has three distinct layers; cavity is formed after the inner wall layer has been deposited	Rodelas *et al*. (2008), http:brittanica.com and Lersten *et al*. (2006)
Druses	Spherical aggregates of prismatic crystals	Lersten and Horner (2005)
Cells in non-angiosperms		
Bryophytes		
Gemmae	One to many cells	http://buildingthepride.com/faculty/pgdavison/bryology_links.htm
Hydroids	Water-conducting cells	http://www.Biology-online.org
Leptoids – Pteridophytes	Organic compound-conducting cells; sporogenous cells present in sporangia of sori	

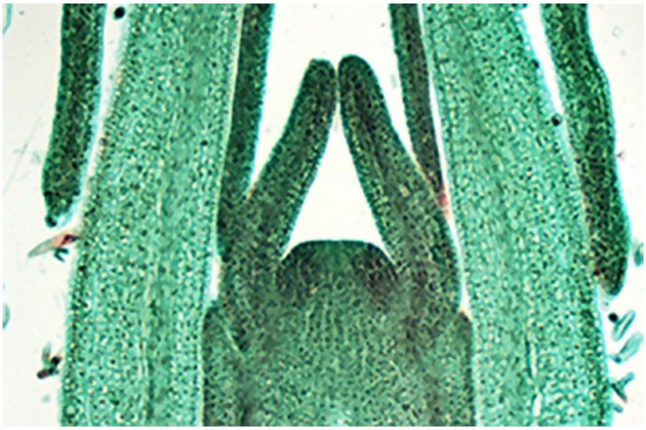


Figure 1.2 Angiosperm shoot meristem section. Source: Alison Roberts. Reproduced with permission of University of Rhode Island.

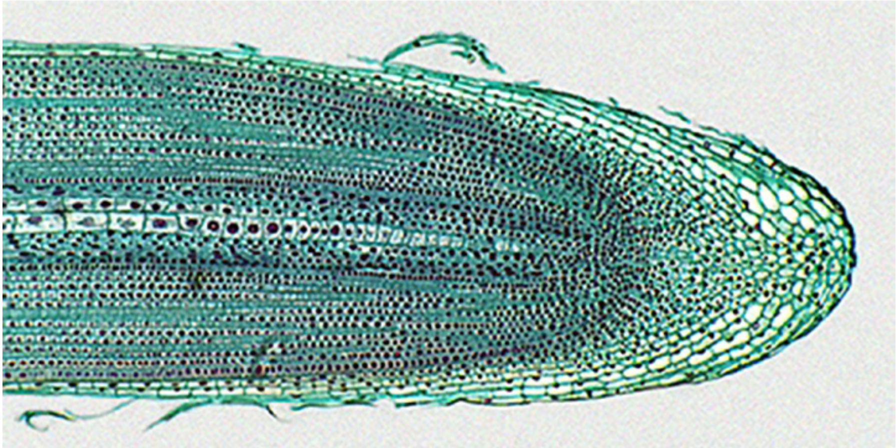


Figure 1.3 Angiosperm root meristem section. Source: Alison Roberts. Reproduced with permission of University of Rhode Island.

development is discussed in Fosket (1999), Moore and Clark (1995), Greenland (2003), Leyser and Day (2003) and Rudall (2007).

What is the composition of cells?

Certain plant components exhibit polar growth, for example, the tip growth of pollen tubes (Hepler *et al.*, 2001). The tubes elongate via the fusion of Golgi-derived vesicles with the plasmalemma and subsequent deposition of the vesicles' contents into the cell wall (Taylor and Hepler, 1997; Parton *et al.*, 2001 and others as reviewed in Malho (2006a, 2006b)). In 2007, Dalgic and Dane (2005) published a diagram depicting the now known tube-tip structural elements and physiological processes that facilitate tube elongation. The diagram represents a

Table 1.2 Meristems and their derivatives.*

Meristems	Derivatives
Primary	
Protoderm	Epidermis
From tunica (Evert, 2006)	
Procambium (provascular)	Primary xylem and phloem
From corpus (Evert, 2006)	Vascular cambium
Ground	Ground tissue: pith and cortex
Lateral	
Vascular cambium	
Fusiform initials	Secondary xylem Secondary phloem
Ray initials (Evert, 2006)	Ray cells
Cork cambium	
Phellogen Periderm (Evert, 2006)	Replaces the epidermis when cork cambium initiates stem girth increase; composed of 'boxlike' cork cells which are dead at maturity; protoplasm secretes suberin; some cork cells that are loosely packed give rise to lenticels which function in gas exchange between the air and the stem's interior. http://www.Biology-online.org, Evert (2006), http://www.vebrio.Sceince.vu.nl.en/virut
Phelloderm	Parenchyma cells produced on the inside by the cork cambium

* Meristems are discussed by Steeves and Sussex (1989).

Table 1.3 Plant tissues.

Tissue system			
Meristematic	Ground	Vascular	Dermal

significant advance over the early studies of pollen tubes as it assigns function to ultrastructural components, for example, signalling molecules, the Rho family of GTPases and phosphatidylinositol 4,5 bisphosphate appear to be localized in the apical plasma membrane. Besides pollen tubes, root hairs exhibit polar growth.

Cell organelles – an introduction

Organelles are required for plant growth, development and function (Sadava, 1993; Gillham, 1994; Herrmann, 1994, Agrawal, 2011). These organelles (Figure 1.7) are the loci for a myriad of physiological and biochemical processes (Tobin, 1992; Daniell and Chase, 2004 – see individual chapters).

There are many diagrams of a generalized plant cell. Some of these are available at www.explorebiology.com, http://www.daviddarling.info/images/plant_cell.jpg

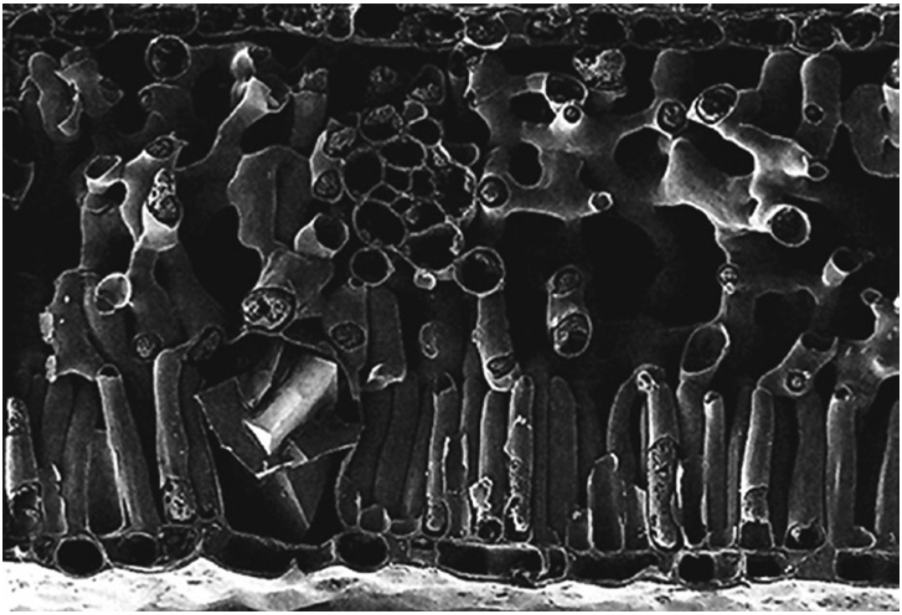
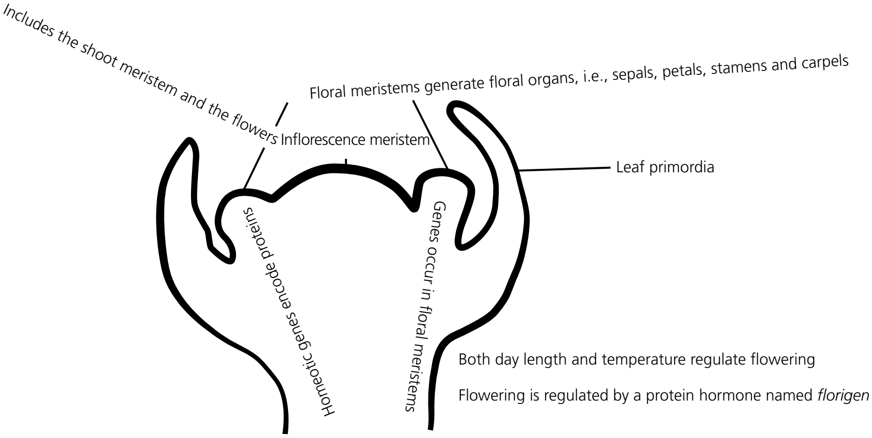


Figure 1.4 SEM of a pecan leaf. Diagram of a leaf's interior is available at http://pics4learning.com. Source: Reproduced with permission of Asaf Gal.



Includes the shoot meristem and the flowers

Floral meristems generate floral organs, i.e., sepals, petals, stamens and carpels

Homeotic genes encode proteins

Genes occur in floral meristems

Both day length and temperature regulate flowering

Flowering is regulated by a protein hormone named *florigen*

Figure 1.5 Schematic of the floral meristem.

and http://micromagnet.fsu.edu. The organelle contents of plant and animal cells in common and those unique to plant cells are depicted in Table 1.4. The dimensions of plant organelles are presented in Table 1.5. A plant organelle database (PODB) has been reviewed by Mano *et al.* (2008).

To enter a plant cell, molecules must traverse both the cell wall and the fluid mosaic plasmalemma (Singer and Nicolson, 1972; Leshem *et al.*, 1991; Larsson and Miller, 1990). In contrast to the fluid mosaic model (Figure 1.8) of the plasmalemma,

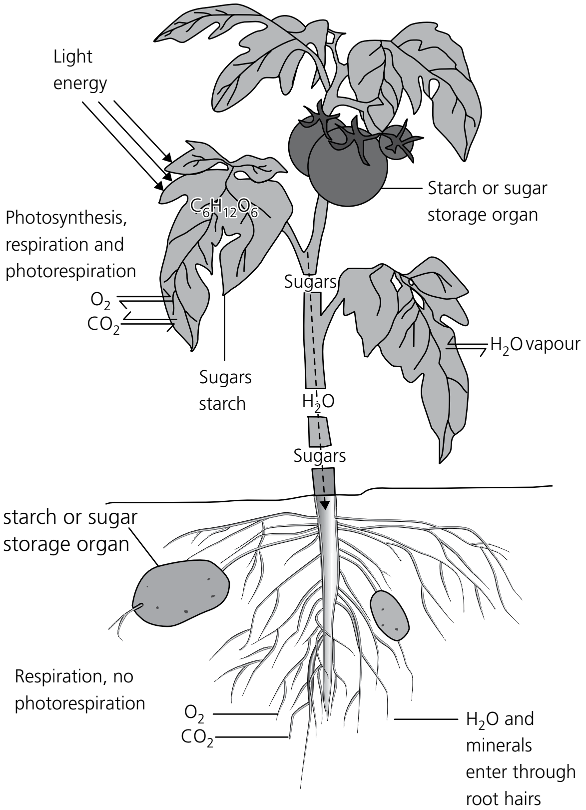


Figure 1.6 Diagram of angiosperm plant body. Source: From http://www.msu.edu/course/te/8021/science08plants/foods.html.

Figure 1.7 Electron micrograph of a plant cell and its organelles. Source: Reproduced with permission of H.J. Horner.

Table 1.4 Comparison of organelle contents of plant and animal cells.*

Organelle	Animal cell	Plant cell
Cell wall	Absent	Present
Centrioles	Present	Absent
Endoplasmic reticulum	Present	Present
Glyoxysomes	Absent	Present
Golgi apparatus	Present	Present
Microfilaments	Present	Present
Mitochondrion	Present	Present
Nucleus	Present	Present
Peroxisomes	Present	Present
Plastids	Absent	Present
Protein bodies	Absent	Present
Spindle	Present	Present
Vacuoles	Sometimes small	Present (mature cell – large central)

* Early discussions of plant cell organelles occur in Hongladarom *et al*. (1964), Pridham (1968), Reid and Leech (1980) and Tobin (1992).

Table 1.5 Dimensions of subcellular organelles.

Organelles	Dimension
Chloroplast	4–6 μm in diameter
Golgi apparatus	Individual cisternae, 0.9 μm Coated vesicles 50–280 μm in diameter
Microbodies	0.1–2.0 μm in diameter
Microtubules	0.5–1.0 μm in diameter
Mitochondria	1–10 μm
Nuclear envelope pores	30–100 μm in diameter
Nucleus	5–10 μm in diameter
Peroxisome	0.2–0.7 μm
Plasmodesmata	2–40 μm in diameter
Primary wall	1–3 μm
Protein bodies	2–5 μm in diameter
Vacuoles	30–90% of cell volume

the picket–fence model proposes the accumulation of membrane protein anchored in an actin network beneath the membrane (Kusumi *et al.*, 2012).

The plasmalemma is composed of water, protein and lipids. There are both integral and peripheral proteins (Leshem *et al.*, 1991). The integral proteins may be simple (classical α-helical structure that traverses the membrane only once) or complex (globular – composed of several α-helical loops which may span the membrane several times). Peripheral proteins can be easily isolated by altering

Fluid mosaic model of the plasmalemma

Consists of a lipid bilayer in which globular proteins are embedded; There are two types of proteins: integral and peripheral. Oliogsaccharides (2–20 monosaccharides) can be attached to the integral proteins. Phospholipids from the bilayer with a polar head on the outside and non-polar tails on the inside.

Fence model of the plasmalemma

There is a membrane skeleton with skeleton-anchored proteins and transmembrane proteins projected outwards into the cytoplasm. Cytoplasmic domains of proteins collide with the actin skeleton, yielding temporary confinement of the transmembrane proteins. The membrane can contain lipid rafts and related caveolae invaginations. The rafts are combinations of proteins and the lipids which may function in signalling. sphingolipids are prevalent in the rafts.

Picket model of the plasmalemma

Phospholipids can also be confined by the membrane skeleton. Some investigators combine the fence and picket models.

Figure 1.8 Top: Fluid mosaic model of the plasmalemma. Middle: Fence model of the plasmalemma. Bottom: picket model of the membrane.

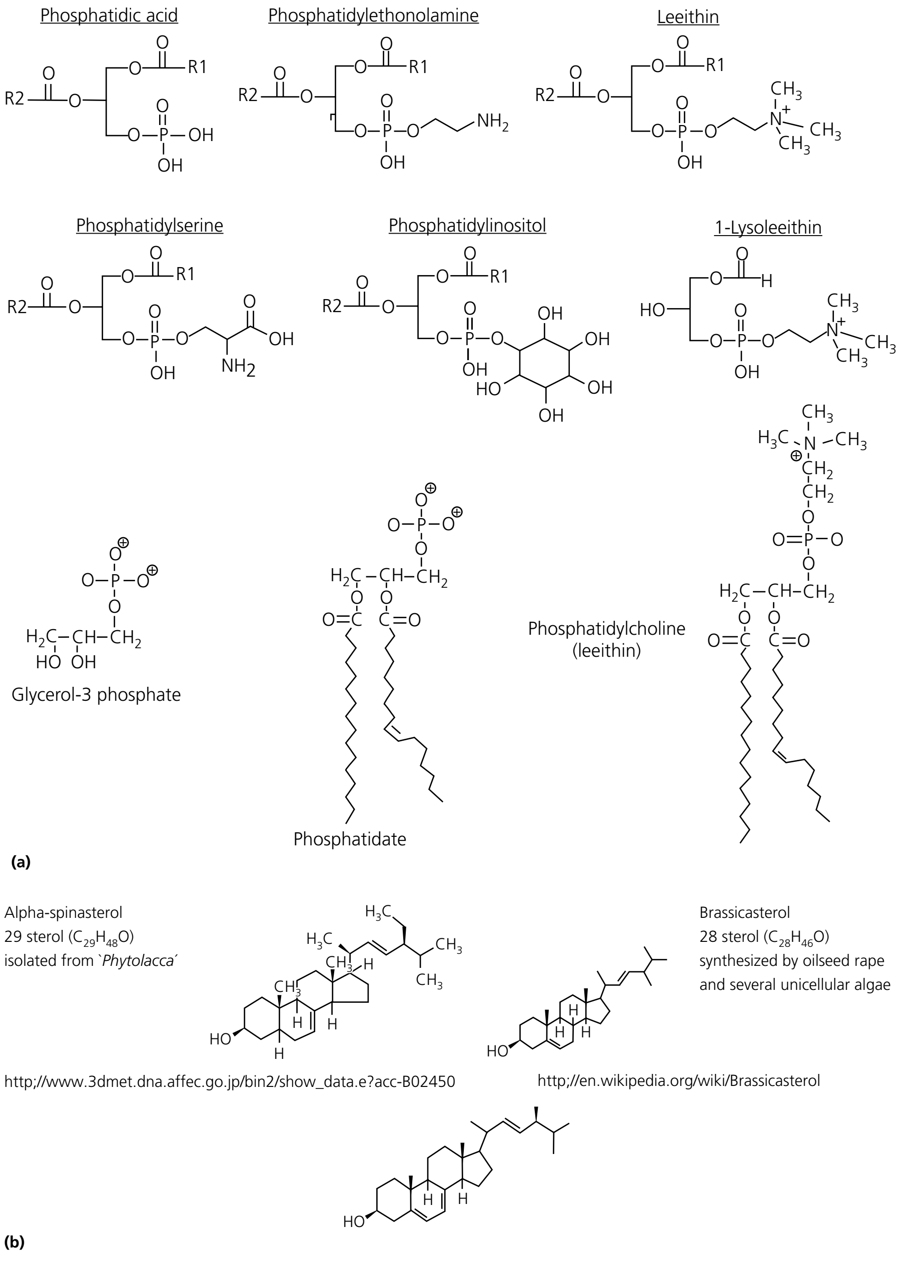
the ionic strength or pH of the encasing medium. The transport proteins are pumps, carriers or chemicals (see section on membrane transport). The lipids are electro-negative and anionic phospholipids, sphingolipids (Figure 1.9), chloroplast-specific glycerolipids and sterols (Table 1.6).

Lipid rafts are specialized phase domains containing sterols and sphingolipids which may be important in signal transitions (Gray, 2004; Furt *et al.*, 2007; Grennan, 2007; Mongrand *et al.*, 2004). Caveolae, which give rise to clathrin-coated vesicles (Brodsky *et al.*, 2001), are anchored multifunctional platforms in lipids (Van Deurs *et al.*, 2003; Patel and Insel, 2009).

The organization of the caveolae (Bastani and Parton, 2010) in the plasmalemma and clathrin-coated vesicles (Samaj *et al.*, 2005) is presented in Figure 1.10. The current discussion focuses on membrane transport mechanism. Plants can internalize certain molecules by endocytosis via invaginations of the plasmalemma yielding clathrin-coated vesicles (Figure 1.11, Holstein, 2003) which become the endosome (Low and Chandra, 1994; Battey *et al.*, 1999; Šamaj *et al.*, 2006). Proteins involved in clathrin-dependent endocytosis appear to be clathrin, adaptor proteins and two adaptins (Pearse and Robinson, 1990; Šamaj *et al.*, 2006). Plant endocytosis and endosomes (Contento and Bassham, 2012) seem to be significant in auxin-mediated cell–cell communication, gravity responses, stomatal movements, cytokinesis and cell wall morphogenesis (Šamaj *et al.*, 2006).

Ion channels

Plasma membranes contain potassium (K^+), calcium (Ca^{++}) and anion channels (Roberts, 2006). Voltage-gated ion channels are transmembrane ion channels activated by changes in electrical potential. Gating is the precise control of ion channel opening (Krol and Trebacz, 2000). An example of an ion channel is the K^+ the



Alpha-spinasterol
29 sterol ($C_{29}H_{48}O$)
isolated from `*Phytolacca*´

http;//www.3dmet.dna.affec.go.jp/bin2/show_data.e?acc-B02450

Brassicasterol
28 sterol ($C_{28}H_{46}O$)
synthesized by oilseed rape and several unicellular algae

http;//en.wikipedia.org/wiki/Brassicasterol

Figure 1.9 Structures of (a) phospholipids and (b) sphingolipids.

inwardly potassium channel. This type of channel possesses a positive charge in the cell. Stomatal pore movements are mediated by a rise in intracellular K$^+$ and anion contents of guard cells (Schroeder and Hagiwara, 1989). Another example is the adenosine triphosphate (ATP) binding cassette transporter or ABC transporter. These transport toxic substances from the cell or into the vacuole. These

Table 1.6 Composition of certain cellular membranes.

Chemical composition	
Fatty acyl groups in membrane lipids 16:0, 16:1, t-16:1, 16:3, 18:0, 18:1, 18:2, α18:3, δ18:3, 18:4, 22:0, 22:1, 24:0, 24:1	
Electroneutral phospholipids	Phosphatidylcholine, phosphatidylethanol, phosphatidylethanolamine
Anionic phospholipids	Phosphatidylserine, phosphatidylglycerol, phosphatidylinositides
Lyo-phospholipids	Cerebrosides
Sphingolipids	Galactolipids, sulpholipids
Chloroplast-specific glycerolipids	Diphosphatidylglycerol and monophosphatidylglycerol
Mitochondrial phospholipids	
Sterols	Sitosterol Campesterol Stigmasterol Unusual sterols Cycloartenol Cholesterol, minute quantities
Sterol glycosides	
Lanosterol	Pathogenic fungal membranes
Water	
Extramembrane water	Membrane is a bilayer sandwiched between two layers of water
	Water located within the bilayer which is attached to or in approximate contact with the expanses of membrane constituents
Proteins	May cross the membrane once or several times and are linked either electrostatically or by means of biophysical lipophilicity to the inner domains of the bilayer
Integral proteins	
Simple integral proteins	Classic α-helical structure that traverses the membrane only once
Complex integral proteins	Globular – comprised of several α-helical loops that may span the membrane several times
Peripheral proteins	Associated with only leaflet–easily isolated by altering ionic strength or pH of the encasing medium
Transport proteins	Pumps, carrier and channel

Source: From Leshem *et al.* (1991).

transporters are composed of four core domains, two cytosolic nucleotide-binding proteins and two transmembrane domains (Malmstrom, 2006).

Besides cation channels there are anion channels regulated by voltage, but their activity is also influenced by Ca^{++}, ATP, phosphorylation or membrane stretching (Tyerman, 1992). Anion plasma membrane channels function as efflux channels when they are open.

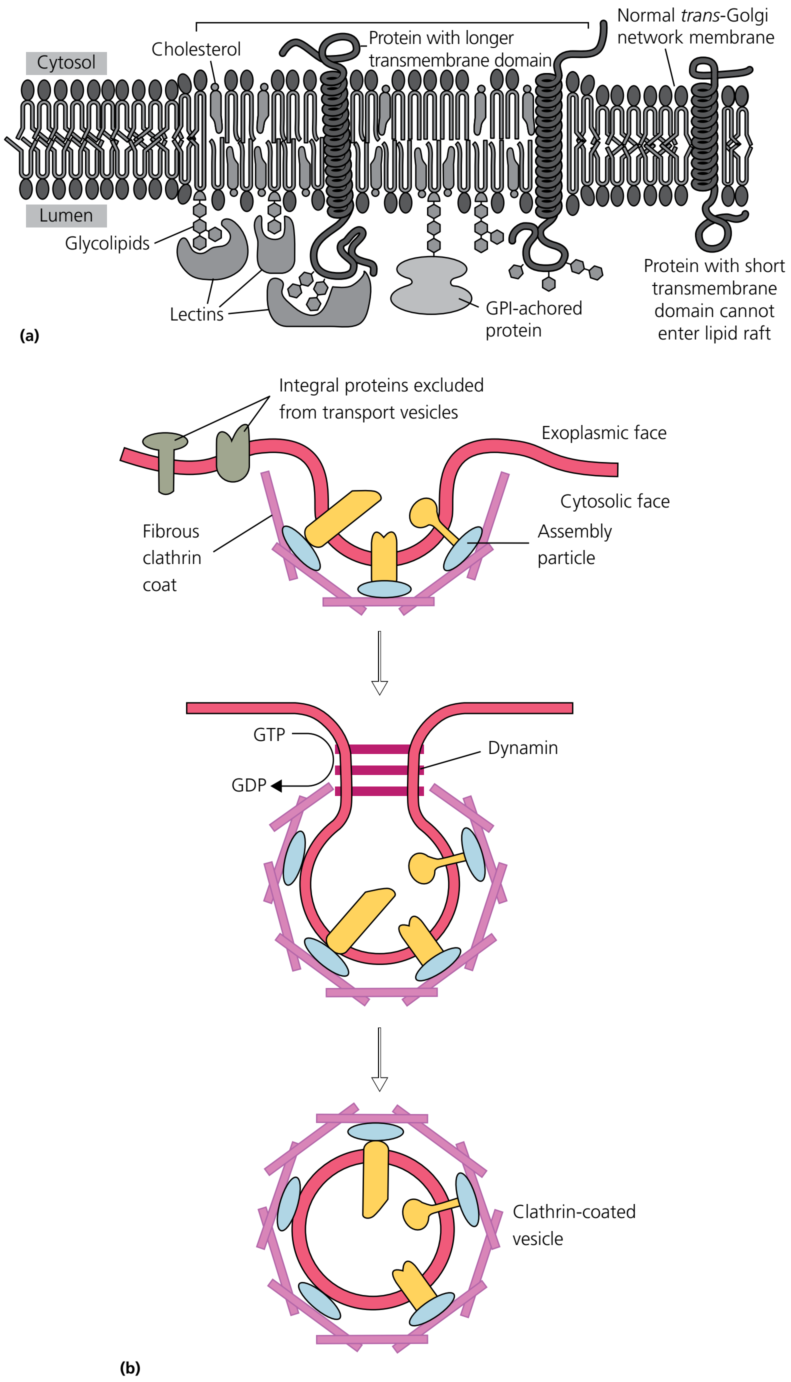
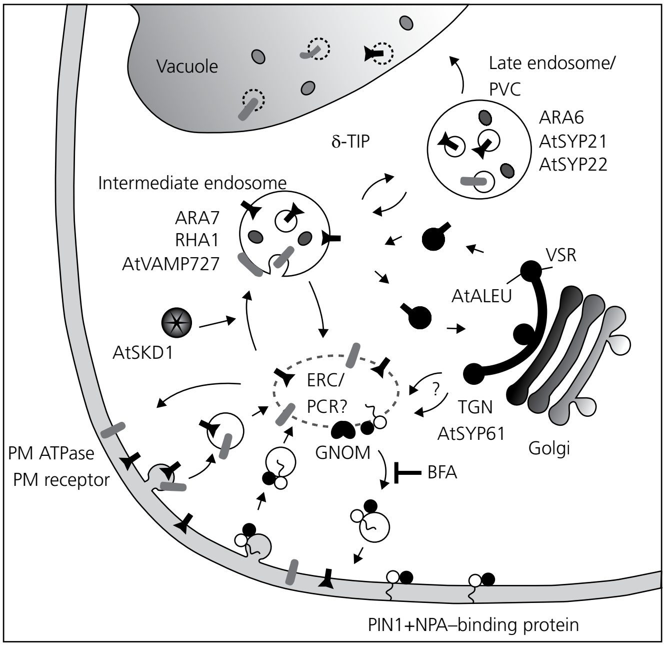


Figure 1.10 Depictions of a (a) lipid raft, (b) caveolae and a clathrin-coated vesicle. Source: Reproduced with permission of Caveolae and Clathrin Vesicle.



SVP – a syntaxin
GNOM – Plant-specific protein that participates in ADP-ribosylation
ESCRT – protein endosomal sorting complex
RHA – a member of the Rab GTPases function in trafficking pathways
ARA6 – a member of the Rab GTPases
SYP – a SNARE component of the late endosome
VSR – vacuolar sorting receptor
SKD – vacuolar protein suppressor
Ubiquitylation – signal that regulates the cell surface expression

Figure 1.11 Diagram of plant endocytosis. Source: Reproduced with permission of M. Otegui, University of Wisconsin.

Proton pumps

The transport of a substance against its electro channel gradient requires energy generated by ATP-proton pumps (Briskin and Hanson, 1992; Evert, 2006). One such pump is the V-ATPase found in both the plasmalemma and the tonoplast (Barkla and Pantoja, 1996; Vinay *et al.*, 2009). The H^+-ATPase in the plasmalemma is the P-ATPase which forms electrochemical gradients (Elmore and Coaker, 2011). Mitochondria and chloroplast membranes possess F-ATPases.

Water channels

Aquaporins are channel proteins which exist in the plasmalemma in intracellular spaces (Maurel *et al.*, 2008). These proteins permit water to move freely but exclude ions and metabolites (Chrispeels and Maruel, 1994; Muller *et al.*, 2007), providing for buffering osmotic fluctuations in the cytosol. Aquaporins are major intrinsic membrane proteins which are composed of four subunits, each of which comprises six transmembrane-spanning helices. Aquaporins are encoded by multiple gene families (Johansson *et al.*, 1998).

Carriers

Carriers are unitransporters and co-transporters (Evert, 2006). Unitransporters transport only one solute from one side of the membrane to the other. On the contrary, co-transporters transfer one solute with the simultaneous or sequential transfer of another solute. A thorough discussion of membrane transport processes occurs in Malmstrom (2006).

Organelle structure and function can be influenced by a variety of environmental parameters which affect plant growth. A discussion of parameters is presented because of the increasing pollution of the earth's atmosphere and ecosystem. In addition, global climate change is a current issue of urgent concern (Dashek and McMillin, 2009).

Both major and minor elements are required for growth and development (Table 1.7). Metals and metalloids at elevated levels can result from mining (Dashek and McMillin, 2009). What effects do these levels have on the structure and function of cellular organelles? (See Lepp, 1981; Medioini *et al.*, 2008; Yusuf *et al.*, 2011; see also Table 1.8.)

Elevated levels of SO_2, CO_2, NO_2 and O_3 (Treshow and Anderson, 1989) can occur in the atmosphere as a result of industrial and contemporary activities. Table 1.9 presents the effects of certain gases (Bell and Treshow, 2002) on the structure and function of organelles. Of special interests are the increasing levels

Table 1.7 Major and minor elements required for plant growth and development.

Element		mg/kg	Minor or major
Nitrogen	N	15 000	Major
Potassium	K	10 000	Major
Calcium	Ca	5 000	Major
Magnesium	Mg	2 000	Major
Phosphorus	P	2 000	Major
Sulfur	S	1 000	Major
Chlorine	Cl	100	Minor
Iron	Fe	100	Minor
Boron	B	20	Minor
Manganese	Mn	50	Minor
Zinc	Zn	20	Minor
Copper	Cu	6	Minor
Molybdenum	Mo	0.1	Minor

Table 1.8 Toxic metals and metalloids.

Metal or metalloid	Toxic level effects	References
Aluminium	Affects root cells of plasmalemma	Mossor-Pietraszewska (2001)
Arsenic	Pale green to yellow lesions on leaves and necrosis of leaves Defoliation Impaired nitrogen metabolism Needle abscission	Treshow and Anderson (1989)
Cadmium	General chlorosis Reduced photosynthesis Reduced transpiration; toxic effects – changes in proline levels; changes in lipid peroxidation and seed germination	Treshow and Anderson (1989), Saadati *et al*. (2012) and Khateeb (2014)
Copper	Interference with normal metabolic reactions Blocks specific enzymatic reactions	Treshow and Anderson (1989) and Shah *et al*. (2001)
Chromium	Contamination Can promote white dead patches on leaves	Treshow and Anderson (1989) and Antonovics *et al*. (1971)
Lead	Condensation of nuclear chromatin; decrease in germination of two *Brassica* cultivars	Rout and Das (2003) and Hosseini *et al*. (2007)
Nickel	Dilution of nuclear membrane	Seregin and Kozhernikova (2006)
Zinc	Disruption of cortical cell	Rout and Das (2009)

Table 1.9 Effects of environmental pollutants on organelles.

Elevated CO_2		
	Stomatal openings reduce as CO_2 increases	Woodward *et al*. (1991)
	Affects both primary and secondary meristems of shoots and roots; alternation of leaf size and anatomy; increased branching and stem diameter	Pritchard *et al*. (1999)
	Increase in the number of mitochondria and amount of chloroplast stroma thylakoid membranes	Griffin *et al*. (2001)
	Stomatal densities decrease in two species of *Spartia*	Lammertsmaa *et al*. (2011)
Acid rain	Leaching of nutrients on tree needles; damages surfaces of needles and leaves and reduces a tree's ability to withstand cold	Godbold and Hüttermann (1994), Schulze *et al*. (2000) and White and Terninko (2003)
Nitric oxide	Necrotic lesions, marginal chlorosis	Lamattina and Polacco (2007)
Ozone and its derivatives	Changes in metabolism	Roshchina and Roshchina (2003)

of CO_2 in the atmosphere, which many scientists believe causes global warming (Dashek and McMillin, 2009). Table 1.10 offers the effects of sublethal and lethal temperatures on organelles. Franklin and Wigge (2014) discuss the effects of temperature on plant development. Other environmental parameters which can