# 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). **Is**<br> **CEPT TENT CONDITE 15**<br> **CEPT COPYTE CONDITE CONDITE CONDITM**<br> **CEPT AT ALOT MATERIAL CONDITE COPT COPT AT ALOT CONDISIS and lack the cell wall thickening layers of collenchy<br>
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### 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. **Table 1.1** Plant cell types.

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

**Table 1.3** Plant tissues.



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.



**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.\*

\*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.

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  $\alpha$ -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 clathrincoated 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



**(b)**

**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.



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<sup>++</sup>, 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.



**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.



**Table 1.8** Toxic metals and metalloids.

**Table 1.9** Effects of environmental pollutants on organelles.



of  $\mathrm{CO}_2$  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





\*Other effects of elevated temperature are on photosynthetic activities (Weis and Berry, 1988) and the plant immune response (Franklin and Wigge, 2014).

> Biotic stress – chemical, humidity, mechanical, radiations, temperature and water Abiotic stress – competition, herbivory, infection ROS levels increase superoxide, hydrogen peroxide, hydroxyl radical, singlet oxygen, Nitric oxide involving cell wall, chloroplasts, mitochondria, phagosomes Oxidative damage

> > Programmed cell death

**Figure 1.12** Reactive oxygen species (ROS) and plant cell death.

affect organelle structure and function are radiation (Parida *et al*., 2002; Mokobia and Anomohanran, 2005; Borzouei *et al*., 2012) and salinity (Bennici and Tani, 2009; Kumar *et al*., 2013).

# Cell death

In certain mammalian systems, there appear to be two apoptotic pathways: extrinsic and intrinsic. Whereas the extrinsic pathway involves death receptor liquids, in the intrinsic pathway a variety of factors act upon mitochondria to promote loss of mitochondrial membrane potential. Whether these two pathways are significant in plant apoptosis remains to be established with certitude. Programmed cell death in plants (Bryant *et al*., 2000) is viewed as a normal phase of development (Gray, 2004; Lam, 2008). These authors state that little is known about how plant cell death occurs and is regulated. However, reactive oxygen species (ROS) seem to be involved (Karuppanapandian *et al*.,  $2011$  – Figure 1.12). Fragmentation of nuclear DNA, involvement of  $Ca^{++}$ , alterations in protein phosphorylation, increases in nuclear heterochromatin and involvement of ROS seem to occur. Beers *et al*. (2000) conclude that proteases may possess a role in programmed cell death. In animals, caspases are significant components of programmed cell death. Although caspase attributes have been

detected in plants, a role for these proteases in plant cell death is unclear (Lam, 2006). Lastly, van Doorn (2011) distinguished between ureolytic and non‐ ureolytic cell death. Whereas the former involves tonoplast rupture and subsequent destruction of the cytoplasm, the latter includes tonoplast rupture but not cytoplasmic destruction.

Finally, aspects of plant cells can be found in the following general plant cell biology textbooks: Batra (2009), Dashek and Harrison (2006), Gupta (2004), Pandian (2008), Pickett‐Heaps and Pickett‐Heaps (1994) and Wayne (2009).

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