

Root Anatomy and Poiseuille's Law for Water Flow in Roots

We now turn to water movement in plant roots. We shall apply Poiseuille's law for the flow through the xylem. But first let us review root anatomy and the cell types that make up the xylem.

15.1 ROOT ANATOMY

15.1.1 The Four Regions of an Elongating Root

Elongating roots usually possess four regions: the root cap, the meristematic region, the region of cell elongation, and the region of differentiation and maturation ([Figure 15.1](#)). But these regions are not always clearly delimited ([Kramer, 1983](#), p. 122). The root cap is composed of loosely arranged cells and is usually well defined. Because it has no direct connection with the vascular system, it probably has little role in absorption. It is the site of perception of the gravitation stimulus. Higher plants sense their orientation with respect to gravity in the columella cells of the root cap ([Silady et al., 2004](#)). The columella is the central part of a root cap in which the cells are arranged in longitudinal files ([Esau, 1977](#), p. 505). [In this chapter and in subsequent chapters where we talk of stem anatomy (Chapter 17), leaf anatomy (Chapter 23), and stomatal anatomy (Chapter 24), we shall rely on the books by [Esau \(1965, 1977\)](#) for descriptions and figures. Even though other books since her death in 1997 have been published on plant anatomy ([Bowes, 2000](#); [Simpson, 2006](#); [MacAdam, 2009](#)), her books remain the standard and should be consulted for information on plant anatomy. They are illustrated with line drawings that represent anatomical parts with accuracy. Recent plant anatomy books mainly use photographs to illustrate plant parts. One cannot point out in a photograph what can be depicted in a drawing. Botanical illustration is a lost art. Draftsmen are no longer available to make

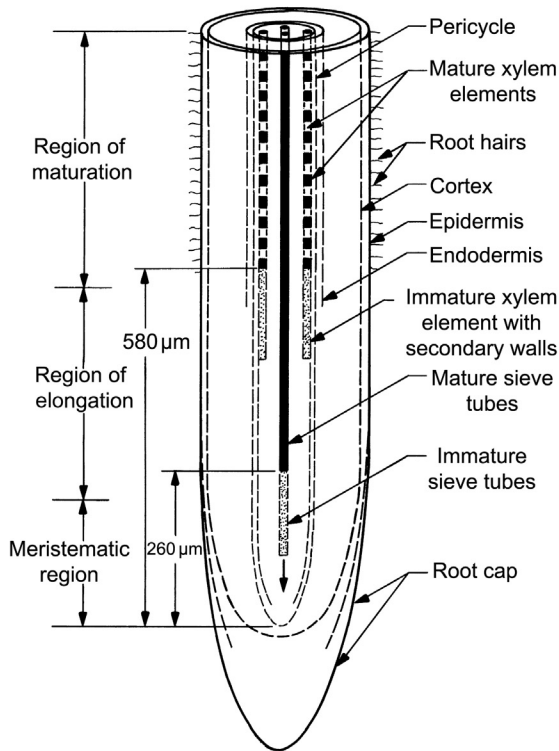


FIGURE 15.1 Diagram of a tobacco root tip showing relative order of maturation of various tissue. The distance from the tip at which the various tissues differentiate and mature depends on the kind of root and the rate of growth. From [Kramer, 1983](#), p. 123. Reprinted by permission of Academic Press.

drawings for textbooks. The diagrams in early textbooks are masterpieces ([Hayden, 1986](#); [Desmond, 1989](#); [Lack, 2001](#)). See Appendix, [Section 15.8](#) for a biography of Esau.]

Plant roots need gravity to grow into soil. In space, roots grow in any direction, including upward. It is felt that statoliths (amyloplasts, which contain starch, a product of photosynthesis) are gravisensors, and they are capable of responding swiftly when the organ that houses them (e.g., a root) is displaced relative to the gravity vector ([Barlow, 1995](#)). The response is rapid ([Esau, 1977](#), p. 226), taking place in <2 min ([Kimbrough et al., 2004](#)). See [Esau, 1977](#) (p. 227, her Figure 14.11) for diagrams

illustrating the response to gravity of statoliths in root caps oriented vertically and horizontally. How the statoliths maintain straight growth downward remains an unsolved puzzle. Information suggests they contact the cell membrane (plasma membrane), which contains gravity receptors. Hormones are then produced that cause the root to grow down and the shoot to grow up (Kirkham, 2008).

The meristematic region typically consists of numerous small, compactly arranged, thin-walled cells almost completely filled with cytoplasm. Relatively little water or salt is absorbed through this region, largely because of the high resistance to movement through the cytoplasm and the lack of a conducting system (Kramer, 1983, p. 122).

Usually there is a zone of rapid cell elongation and expansion, a few tenths of a millimeter behind the root apex. It is difficult to indicate a definite zone of differentiation because various types of cells and tissues are differentiated at different distances behind the root apex (Kramer, 1983, p. 122). Typically, sieve tubes of the phloem differentiate before the xylem elements (Esau, 1965, p. 498). As the newly enlarged, thin-walled cells at the base of the zone of enlargement cease to elongate, they become differentiated into the epidermis, cortex, and stele, which constitute the primary structures of roots.

15.1.2 Root Hairs

Root hairs appear when the epidermis differentiates. The epidermis has specialized cells that are root hair cells. Much attention has been given to root hairs because of their presumed importance as absorbing surfaces. The epidermis is usually composed of relatively thin-walled, elongated cells that form a compact layer covering the exterior of young roots. Sometimes a second compact layer, the hypodermis, lies beneath the epidermis. In some plants, including citrus and conifers, root hairs can arise not only from the epidermis, but also from the layer of cells beneath the epidermis, or even from deeper in the cortex (Kramer, 1983, p. 125).

15.1.3 Dicotyledonous Roots

The arrangement of the principal tissues in a dicotyledonous root is shown in Figure 15.2. The conductive tissues form a solid mass in the center, instead of being dispersed in bundles around the periphery of the pith, as in stems of most herbaceous, dicotyledonous plants (Kramer, 1983, p. 124) (We will study stem anatomy in Chapter 17.). The primary xylem in the roots of dicots usually consists of two to several strands extending radially outward from the center, with the primary phloem located between them. The outermost layer of the stele is the pericycle. The stele comprises pericycle, the vascular system, and the associated

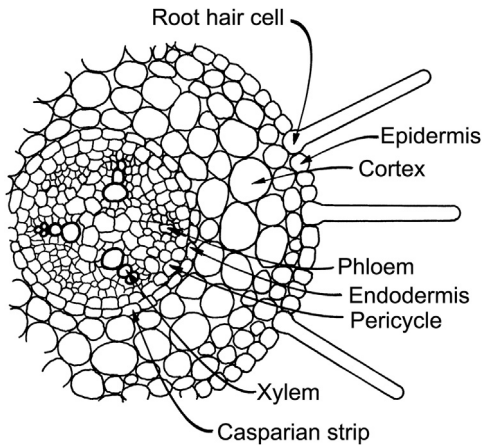


FIGURE 15.2 A dicotyledonous root (a squash root). Note the central stele of vascular tissue. From *Kramer, 1983, p. 12. Reprinted by permission of Academic Press.*

ground tissue (*Esau, 1977, p. 527*). The cells of the pericycle retain their ability to divide, and they give rise not only to branch roots but also to the cork cambium, if secondary growth occurs. The endodermis usually consists of a single layer of cells and forms the inner layer of the cortex. The endodermis has the casparian strip, which is a band-like wall formation within primary walls that contains suberin and lignin. It occurs on the radial and transverse walls in the endodermis (*Esau, 1977, p. 504*).

15.1.4 Monocotyledonous Root

In monocotyledonous plants, a variable number of xylem vessels are arranged in a circle around a pith (*Figure 15.3*). However, in some monocotyledonous roots such as wheat (*Figure 15.4*), a single vessel occupies the center and is separated by nontracheary elements from other vessels (*Esau, 1965, p. 496*). The large central xylem vessel is part of the metaxylem. The metaxylem is part of the primary xylem that differentiates after the protoxylem and before the secondary xylem, if any secondary xylem is formed in a given species. Protoxylem is the first-formed element of the xylem in a plant organ. It is the first part of the primary xylem. The protoxylem gets crushed as the metaxylem develops. Although most monocotyledons lack secondary growth from a vascular cambium, they can undergo a type of “secondary growth” by an intense and protracted thickening growth. Large trees can result, such as palm trees (*Esau, 1965, p. 400*), which are monocotyledons.

15.1.5 Movement of Water and Solutes across the Root

The structure of the root is of particular interest with regard to the movement of water and the dissolved salts in it from the absorbing cells to

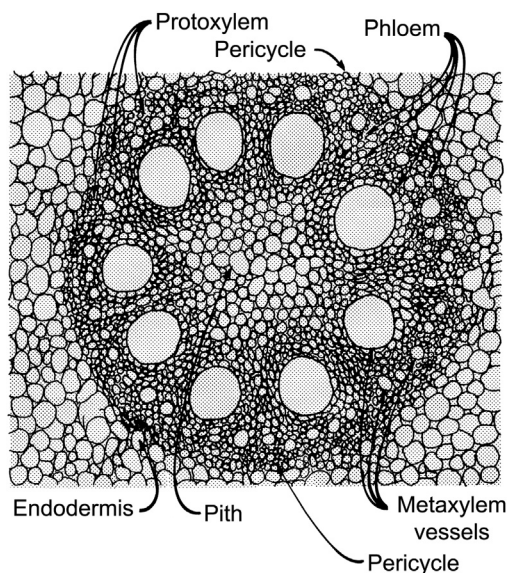


FIGURE 15.3 A monocotyledonous root (a corn root). Note the central pith. From [Esau, 1965](#), p. 713. This material is used by permission of John Wiley & Sons, Inc.

the conducting tissues, and their release from the living cells of the vascular cylinder into the nonliving tracheary elements. [Figure 15.5](#) illustrates the pathway of the soil solution in the wheat root ([Esau, 1965](#), pp. 516–517). The arrows indicate the direction of movement in certain selected cells. The living cells among these are stippled. The most notable features of this pathway are: (1) the presence of abundant intercellular spaces in the cortex, (2) the lack of such spaces in the vascular cylinder,

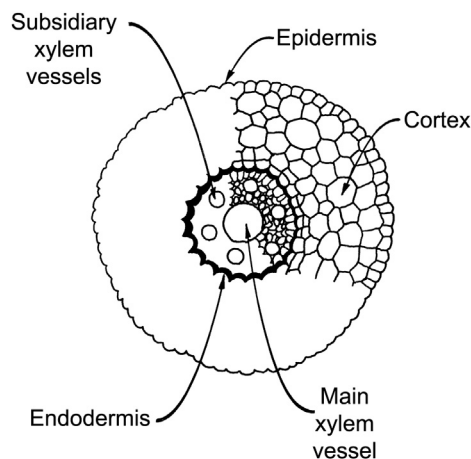


FIGURE 15.4 A monocotyledonous root (a wheat root). Note the central large xylem vessel, part of the metaxylem. From [Richards, R.A., Passioura, J.B., p. 250, 1981a](#). *Crop Science Society of America*. Madison, Wisconsin. Reprinted by permission of the Crop Science Society of America.

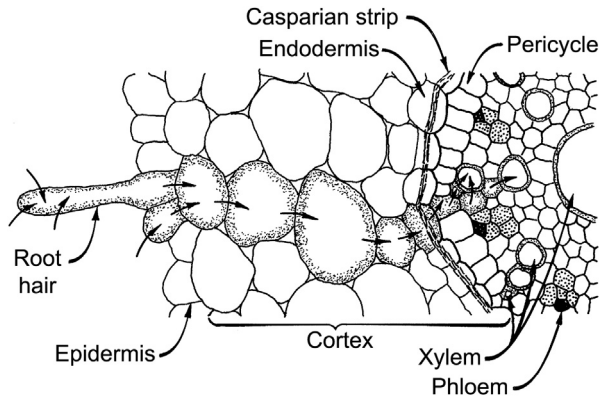


FIGURE 15.5 Part of a transection of a wheat root, illustrating the kinds of cells that may be traversed by water and salts absorbed from the soil before they reach the tracheary elements of the xylem. Arrows indicate the direction of movement through a selected series of cells. Among these, the living cells are partly stippled. The casparian strip in the endodermis is shown as though exposed in surface views of end walls. From *Esau, 1965, p. 517*. This material is used by permission of John Wiley & Sons, Inc.

and (3) the presence of a specialized endodermis between the two systems. The endodermis between the two distinct systems (cortex and vascular cylinder) acts as a barrier that facilitates the development of hydrostatic pressure in the vascular cylinder by preventing a leakage of solutes from the vascular cylinder into the cortex.

15.1.6 Endodermis

Let us consider the endodermis and its casparian strip in more detail. A prominent feature of the primary structure of most roots is the endodermis, the inner layer of cells of the cortex which separates it from the stele. The endodermis is not part of the stele. The stele comprises the vascular system (xylem and phloem) and the associated ground tissue (pericycle; interfascicular regions, and pith, if it occurs). Early in the development of the endodermis, suberin (a fatty substance) is deposited in bands on the radial walls and transverse walls in the longitudinal direction, forming the casparian strip (*Figure 15.6*). It renders them relatively impermeable to water and presents a barrier to inward movement of water and solutes in the apoplast (*Kramer, 1983, p. 128*). The apoplast is the supposedly dead part of the plant tissue, including the cell walls. The symplast or symplasm is the continuum of communicating cytoplasm, which is created by the intercellular connections. Plasmodesmata are fine, cytoplasmic threads that pass from a protoplast through a cell wall directly into the protoplast of a second cell (*Nobel, 1974, p. 37*).

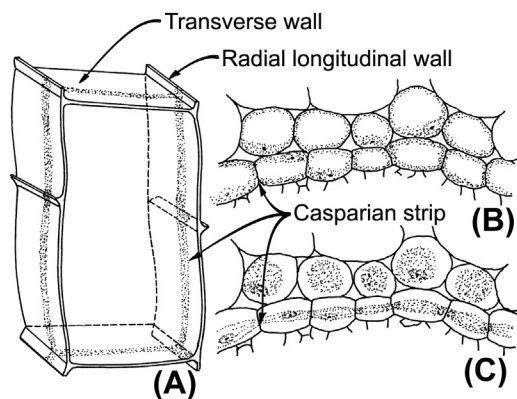


FIGURE 15.6 Endodermal cells. (A) Entire cell showing location of casparian strip. (B and C) Effect of treatment with alcohol on cells of endodermis and of parenchyma. (B) Cells before treatment and (C) after treatment. (B, C) The casparian strip is seen only in the sectional views. From *Esau, 1965, p. 489, 1965*. This material is used by permission of John Wiley & Sons, Inc.

The endodermis characterized by casparian strips is almost universally present in roots (*Esau, 1965, p. 489*). It is made up of both suberin and lignin (*Esau, 1977, p. 504*). The strip is formed during the early ontogeny of the cell and is a part of the primary wall. It varies in width and is often much narrower than the wall in which it occurs. The incrustation of the cell wall by the material constituting the casparian strip presumably blocks the submicroscopic capillaries in the wall and hinders the movement of substances through the walls (*Esau, 1965, p. 517*). Moreover, the cytoplasm of the endodermal cells is relatively firmly attached to the casparian strip, so that it does not readily separate from the strip when the tissue is subjected to the effects of plasmolytic or other agents normally causing a contraction of protoplasts (*Figure 15.6*). Thus the casparian strip appears to form a barrier at which the soil solution is forced to pass through the selectively permeable cytoplasm (the symplasm) rather than through the cell wall (apoplast) (*Grebe, 2011*). When the casparian strip is broken down, which may occur when herbicides or chelating agents are added to the soil, free passage of ions into the stele occurs (*Nowack et al., 2006*). When the root cells are so damaged and there is uncontrolled inflow of soil solution into the stele, the plant dies (Brett H. Robinson, Soil and Physical Sciences, Lincoln University, Christchurch, New Zealand, personal communication, June 17, 2012). For an assessment of the endodermis using molecular data from *Arabidopsis*, see *Petricka et al. (2012)* and *Geldner (2013)*.

15.1.7 Cell Types in Xylem Tissue

Xylem is a tissue that is composed of four cell types (*Table 15.1*): tracheids and vessel members, which make up the tracheary elements, fibers, and parenchyma cells (*Esau, 1977, p. 103*). The tracheary elements

TABLE 15.1 The Four Cell Types in Xylem Tissue: Tracheids, Vessel Members, Fibers, and Parenchyma Cells

Cell Types	Principal Function
<ul style="list-style-type: none"> ● Axial system <ul style="list-style-type: none"> ✓ Tracheary elements <ul style="list-style-type: none"> ● Tracheids ● Vessel members ✓ Fibers <ul style="list-style-type: none"> ● Fiber-tracheids ● Libriform fibers ✓ Parenchyma cells ● Ray system <ul style="list-style-type: none"> ✓ Parenchyma cells (Tracheids in some conifers) 	<ul style="list-style-type: none"> Conduction of water Support; sometimes storage Storage and translocation of ergastic substances

From Esau, 1977, p. 106, ©1977. This material is used by permission of John Wiley & Sons, Inc.

are the most highly specialized cells of the xylem and are concerned with the conduction of water and substances in water. They are nonliving cells at maturity. They have lignified walls with secondary thickenings and a variety of pits.

The two kinds of tracheary cells, the tracheids and the vessel members, differ from each other in that the tracheid is an imperforate cell, whereas the vessel member has perforations, one or more at each end and sometimes also on a side wall (Esau, 1977, p. 106). The longitudinal series of vessel members interconnected through their perforations are called *xylem vessels* or simply, *vessels*. The perforated part of a wall of a vessel member is called the *perforation plate*. A plate may be simple, with only one perforation, or multiperforate, with more than one perforation.

The fibers are long cells with secondary, commonly lignified, walls (Esau, 1977, p. 108). The walls vary in thickness but are usually thicker than the walls of tracheids in the same wood (wood is secondary xylem, which we discuss in the next paragraph). Two principal types of xylem fibers are recognized—the fiber-tracheids and the libriform fibers. If both occur in the same wood, the libriform fiber is longer and has thicker walls than the fiber-tracheid. Fibers give support to the xylem.

Parenchyma cells of the primary xylem occur in interfascicular regions and are considered to be part of the ground tissue (Esau, 1977,

pp. 112–113). In the root, the primary xylem forms a core with parenchyma (as in some monocotyledonous roots) or a core without parenchyma (as in dicotyledonous roots). In secondary xylem, the parenchyma cells make up the axial and ray parenchyma. These parenchyma cells store starch, oils, and many other ergastic substances. Ergastic substances are products of protoplasts such as starch grains, fat globules, crystals, and fluids. They occur in the cytoplasm, organelles, vacuoles, and cell walls (Esau, 1977, p. 509). Rays are important in plants that undergo secondary growth (e.g., trees). We shall consider them when we discuss the anatomy of stems (Chapter 17). Rays extend radially in the secondary xylem (called the *wood*) and the secondary phloem (the *bark*) (Esau, 1977, p. 531, 503), and they are shown in the wood in Figure 17.3, which illustrates secondary vascular tissue. Ray parenchyma cells function as a radial route for nutrient distribution in woody plants. Wood rays are known to play an important role in tree development and may allow some trees to live more than 1000 years (Larisch et al., 2012).

We can list the characteristics of tracheids, vessel members, fibers, and parenchyma cells as follows:

Tracheids

- More primitive (in angiosperms, gymnosperms, and lower vascular plants)
- Tapered ends
- Long cells
- Thin cells
- Lignified secondary cell walls
- No protoplasts at maturity (dead)

Vessel members

- Present only in angiosperms (more evolved than tracheids)
- Short cells
- Broad cells
- Flat ends
- Perforated end walls with perforation plates
- Lignified secondary cell walls
- No protoplasts at maturity (dead)
- Several together form a continuous tube, which is called a xylem vessel
- A xylem vessel is a low-resistance circuit
- Width varies from 10 to 800 μm ; an average diameter is about 40 μm
- Length of a xylem vessel varies from few hundred microns (μm) to a few millimeters. Long and wide xylem vessels occur in tropical plants such as vines (e.g., kiwifruit) and rattans (climbing palms). Fisher et al (2002) of the Fairchild Tropical Garden in Miami, Florida, found a vessel in a rattan that was 3 m long and 532 μm in diameter.

Fibers

- For structural support
- Long cells
- Thin cells
- Heavily lignified cell walls
- No protoplasts at maturity (dead)

Parenchyma cells

- For storage
- For lateral movement of water and solutes into and out of conducting cells (the ray system in secondary xylem) ([Table 15.1](#)).

15.2 POISEUILLE'S LAW

Poiseuille, a French physiologist, discovered the law on velocity of flow of a liquid through a capillary tube (For a biography of Poiseuille, see the Appendix, [Section 15.6](#)). He found that the volume of fluid moving in unit time along a cylinder is proportional to the fourth power of its radius and that the movement depends on the drop in pressure. Poiseuille's law applies to cylindrical, capillary tubes. Even though the soil can be considered to consist of cylindrical tubes, Poiseuille's law is usually not applied to water movement in soil. Darcy's law is used. As noted in Table 7.1, Darcy's law is a linear-flow law (Poiseuille's law is not), and Darcy's law applies to an area-averaged section of the soil. Darcy's law does not consider water movement at the small scale of a capillary tube.

Poiseuille's law states ([Weast, 1964](#), p. F-62):

$$v = (\pi pr^4)/(8X\eta), \quad (15.1)$$

where

v = volume (cm^3) escaping per second

p = difference of pressure at the ends of the tube (dyn/cm^2)

r = radius of the tube (cm)

X = length of tube (cm)

η = coefficient of viscosity (poise or $\text{dyn-s}/\text{cm}^2$).

The volume will be given in cm^3/s if X and r are in cm , p in dyn/cm^2 , and η in poises or $\text{dyn-s}/\text{cm}^2$.

We take a moment here to consider viscosity ([Weast, 1964](#), p. F-62). All fluids possess a definite resistance to change of form and many solids show a gradual yielding of forces tending to change their form. This property, a sort of internal friction, is called *viscosity*. It is expressed in $\text{dyn-s}/\text{cm}^2$ or poises. The unit is named after Poiseuille. Remember that poise also can be expressed as $\text{g}/\text{cm}/\text{s}$ if we replace dyne by $(\text{g cm})/\text{s}^2$ using Newton's law, $F = ma$.

We present the Poiseuille equation in the form that Nobel (1974, p. 392; 1983, p. 494; 1991, p. 508; 1999, p. 375; 2005, p. 448; 2009, p. 471) gives

$$v = -(\pi r^4/8\eta)(\partial P/\partial X), \quad (15.2)$$

where

- v = rate of volume movement (e.g., in units of cm^3/s)
- r = radius of the capillary tube (cm)
- η = viscosity of the solution (poise)
- $-(\partial P/\partial X)$ = the negative gradient of the hydrostatic pressure.

Hydrostatics (construed as singular) is the branch of physics having to do with the pressure and equilibrium of water and other liquids. Statics is the branch of mechanics dealing with bodies, masses, or forces at rest or in equilibrium. Henceforth, instead of saying “hydrostatic pressure”, we simply will say “pressure”. Because positive flow occurs in the direction of decreasing pressure [$(\partial P/\partial X)$ is <0], the minus sign is necessary in Eqn (15.2).

In Eqn (15.2), we use partial derivatives. When a quantity is a function of more than one independent variable, it is necessary to use partial derivatives when discussing differentials or derivatives. For example, if $u = f(x, y)$, the partial derivative of u with respect to x , $(\partial u/\partial x)_y$, is the rate with which u changes with a change in x at a constant value of y . A subscript is used on the partial derivative when it is important to emphasize which variable is held constant (Daniels and Alberty, 1966, p. 740). See Appendix 6 of Nobel, 1974, (pp. 435–450) for a discussion of calculus, including partial derivatives. Note that v depends both on P and X .

In Poiseuille's law, we are concerned with the volume flowing per unit time and area, often represented by J_v and called *flux*. For flow in a cylinder of radius r , and hence area πr^2 , J_v is

$$v/\pi r^2 = J_v = -(r^2/8\eta)(\partial P/\partial X), \quad (15.3)$$

where J_v has units of length/time. This is the form of Poiseuille's law that we shall use in our calculations (Section 15.4).

15.3 ASSUMPTIONS OF POISEUILLE'S LAW

Before we use Poiseuille's law, we need to consider the assumptions used in deriving it. These assumptions are important to know so we can apply the law correctly.

Poiseuille's law assumes two things. First, it assumes that the fluid in the cylinder moves in layers or laminae, each layer gliding over the adjacent one. In laminar flow, two particles of water moving will describe

paths (streamlines) that will never cross each other (Kirkham, 1961, p. 47). Such laminar movement occurs only if flow is slow enough to meet a criterion deduced by Reynolds in 1883 (Nobel, 1974, p. 392) called the Reynolds number, Re , which is the dimensionless quantity:

$$Re = (\rho J_v r) / \eta. \quad (15.4)$$

The symbols in Eqn (15.4) are the same as those defined above and ρ is the solution density (Reynolds did not call the number “the Reynolds number”; his students started to refer to it as “the Reynolds’s number”. It is usually called the Reynolds number and the possessive form is not used. For a biography of Reynolds, see the Appendix, Section 15.7.). Re must be < 2000 to have laminar flow. Otherwise, a transition to turbulent flow occurs and Eqn (15.3) is no longer valid. In turbulent flow, whirls and eddies develop. An eddy is a current of water or air running contrary to the main current, especially, a small whirlpool. For an article on turbulence, see Moin and Kim (1997). Turbulence is still one of the great unsolved problems of classical physics (Nelkin, 1992). The number 2000 is not exact and other numbers in this range are cited in the literature as the Reynolds number at which turbulence takes over.

Second, Poiseuille’s law assumes that the fluid in Poiseuille (laminar) flow is actually stationary at the wall of the cylinder. The velocity of solution flow increases in a parabolic manner to a maximum value in the center of the tube. Thus the flux in Eqn (15.3) is actually the mean flow averaged over the entire cross-section of cylinder of radius r .

Poiseuille’s law requires advanced mathematics for its proof. For a proof, see Childs, 1969 (pp. 194–196). For a discussion of Poiseuille velocity distribution in a circular tube, see Bird et al., 1960 (pp. 123–130).

15.4 CALCULATIONS OF FLOW BASED ON POISEUILLE’S LAW

Following the analysis of Nobel (1974, pp. 391–395; 1983, pp. 493–498; 1991, pp. 508–513; 1999, pp. 375–378; 2005, pp. 448–453; 2009, pp. 471–476), we now shall use Poiseuille’s law to estimate the pressure gradient in different parts of the pathway that water takes when it goes from outside the root and through the apoplast to the endodermis, where it is forced into the living part of the plant (symplast) because of the casparian strip. The region of a plant made up of cell walls and the hollow xylem vessels is part of the apoplast. Water and the solutes that it contains can move fairly readily in the apoplast. But they must cross a membrane to enter the symplast, the living part of the cells (Nobel, 1974, p. 395). The role of the apoplast in water transport is not fully understood and is an area of active investigation (Steudle and Frensch, 1996; Schreiber et al., 1999).

Nobel first calculates the pressure gradient that occurs in the xylem vessels of diffuse-porous wood. Before we continue with his analysis, we review wood anatomy. There are two types of wood (secondary xylem): diffuse-porous wood and ring-porous wood (Esau, 1965, 1977). In diffuse-porous wood, the xylem members have more or less equal diameters in the spring and summer wood. Esau, 1977 (p. 508) defines diffuse-porous wood as secondary xylem, in which the pores (vessels) are distributed fairly uniformly throughout a growth layer or change in size gradually from early to late wood. Examples of diffuse-porous wood are *Acer* (maple), *Betula* (birch), and *Liriodendron* (tulip tree). In ring-porous wood, the vessel members are large in diameter in the spring wood and are small in diameter in the summer wood. Esau, 1977 (p. 524) defines ring-porous wood as secondary xylem in which the pores (vessels) of the early wood are distinctly larger than those of the late wood and form a well-defined zone or ring in a cross-section of wood. Examples of ring-porous wood are *Castanea* (chestnut), *Fraxinus* (ash), *Robinia* (locust), and some *Quercus* (oak).

We note that Nobel's analysis is for wood, which can occur in woody stems or woody roots. His calculations for Poiseuille-law flow, therefore, are not confined to roots.

Nobel assumes, based on experimental data, that the velocity of sap ascent in the xylem of a transpiring tree with diffuse-porous wood is 0.1 cm/s. This is the value for J_v . For a tree with ring-porous wood, he assumes J_v is 10 times faster (1.0 cm/s). He assumes that the radius of the vessel member in the diffuse-porous wood is 20 μm and the radius of the vessel member in the ring-porous wood is 100 μm . Nobel also assumes that the xylem sap is a dilute aqueous solution, so the volume flow (flux) (J_v) is essentially the same as the volume of water flow, and the viscosity of the solution is the same as that for water.

We now use Eqn (15.3) to solve for the pressure gradient in a tree with diffuse-porous wood:

$$J_v = -(r^2/8\eta)(\partial P/\partial X)$$

$$0.1 \text{ cm/s} = -(20 \times 10^{-4})^2/8(0.010 \text{ dyn-s/cm}^2)(\partial P/\partial X)$$

or

$$(\partial P/\partial X) = -2 \times 10^3 \text{ dyn-s/cm}^3.$$

We know that 1 bar = $1 \times 10^6 \text{ dyn-s/cm}^2$. Therefore, $-2 \times 10^3 \text{ dyn-s/cm}^3 = -2 \times 10^{-3} \text{ bar/cm}$ or -0.2 bar/m . Remember this number. We will come back to it.

We digress to calculate Reynolds number for water movement in diffuse-porous and ring-porous wood. We use a density for the sap in the xylem of 1 g/cm³ (same as water at 20 °C). We now change the units of

density to $\text{dyn-s}^2/\text{cm}^4$. Remember $F = ma$; $1 \text{ dyn} = 1 \text{ g} \times 1 \text{ cm/s}^2$; so $1 \text{ g} = \text{dyn-s}^2/\text{cm}$. Substituting into the formula for density, ρ , we get units for density of $\text{dyn-s}^2/\text{cm}^4$. We find the Reynolds number, Re , for diffuse-porous wood with a radius of $20 \mu\text{m}$ for the vessel members and a velocity of sap flow of 0.1 cm/s to be

$$\text{Re} = (\rho J_v r) / \eta$$

$$\begin{aligned} \text{Re} &= [(1 \text{ dyn-s}^2/\text{cm}^4)(0.1 \text{ cm/s})(2 \times 10^{-3} \text{ cm})] / 0.010 \text{ dyn-s/cm}^2 \\ &= 0.02 \text{ (unitless)}. \end{aligned}$$

For a ring-porous tree with a radius of $100 \mu\text{m}$ for the vessel members and a velocity of sap flow of 1 cm/s , Re is

$$[(1 \text{ dyn-s}^2/\text{cm}^4)(1 \text{ cm/s})(0.01 \text{ cm})] / 0.010 \text{ dyn-s/cm}^2 = 1 \text{ (unitless)}.$$

The value of $\text{Re} = 1$ for the ring-porous tree is still far less than the value of 2000, where turbulence generally starts. Therefore, we can be assured that Poiseuille's law applies even to plants with large-diameter vessel members.

Let us get back to the main problem of determining the pressure gradient in different parts of the pathway that water takes as it crosses a root. We have calculated the pressure gradient that occurs in the xylem vessels. Now let us calculate the pressure drop in the cell walls, again following Nobel's (1974, 1983, 1991, 2005, 2009) analysis.

The interfibrillar spaces in a cell wall have diameters of about 10 nm . Let us assume that the average radius of these interstices is 5 nm . We are forgetting tortuosity and we are assuming that the cell walls are tubes where Poiseuille's law applies. Let us assume the same J_v that we used previously ($J_v = 0.1 \text{ cm/s}$). The pressure gradient in the cell walls is

$$J_v = -(r^2/8\eta)(\partial P/\partial X)$$

$$0.1 \text{ cm/s} = -(5 \times 10^{-7})^2/8(0.010 \text{ dyn-s/cm}^2)(\partial P/\partial X)$$

or

$$(\partial P/\partial X) = -3.2 \times 10^{10} \text{ dyn-s/cm}^3 = -3.2 \times 10^6 \text{ bars/m}.$$

A $(\partial P/\partial X)$ of only -0.2 bar/m is needed for the same J_v in the vessel member having a radius of $20 \mu\text{m}$. Thus, the $(\partial P/\partial X)$ for Poiseuille flow through the small interstices of a cell wall is over 10^7 times greater than for the same flux through the lumen of the vessel member. Because of the tremendous pressure gradients required to force water through the small interstices available for solution conduction in the cell wall, a solution cannot flow rapidly enough up a tree in the cell walls, as has been

suggested, to account for the observed rates of water movement (Nobel, 1974, p. 394).

Now let us calculate the pressure gradient for the cell membrane. The Poiseuille law no longer applies because we have no capillary tubes. We use the following equation for flux, J_v , through the plasmalemma (Nobel, 1974, p. 395 and p. 144):

$$J_v = L_p(\Delta P - \sigma\Delta\pi), \quad (15.5)$$

where

L_p = hydraulic conductivity coefficient of the cell membrane

ΔP = difference in pressure across the membrane

σ = reflection coefficient. This is a unitless number and varies between 0 and 1. If $\sigma = 1$, all solutes are reflected from the membrane and no solute gets across it. If $\sigma = 0$, all solutes can cross the membrane.

$\Delta\pi$ = osmotic pressure difference across the membrane.

We are considering a dilute solution. The xylem sap is very dilute and we can consider it to be like water. So we shall consider that $\Delta\pi = 0$ and the last term in Eqn (15.5) drops out.

So we have $J_v = L_p(\Delta P)$. Let us assume we are still studying plants with a J_v of 0.1 cm/s. A reasonable value to assume for L_p is 1×10^{-5} cm/s-bar (Nobel, 1974, p. 395). So,

$$\Delta P = (0.1 \text{ cm/s}) / 1 \times 10^{-5} \text{ cm/s-bar} = 10,000 \text{ bar} = 1 \times 10^4 \text{ bar}.$$

Now let us consider a vessel member before the plasmalemma has broken down (This is probably an unrealistic situation because in the mature vessel member, the cell membrane is broken down. But we continue with the analysis of Nobel, 1974 (p. 395), and compare flux through the vessel member, cell wall, and cell membrane.). Let us assume that the lumen in our vessel member is 1000 μm long and has a diameter of 20 μm and that the cell wall is 5 μm thick all the way around the cell. As water moves from below and up through this rectangular cell, it passes through the cell wall (5 μm), then the cell membrane, then goes into the lumen that is 1000 μm long, and then passes another membrane and finally another cell wall (5 μm). With these distances, we now can compare the pressure drop across the membrane, cell wall, and lumen. For the membrane, it is -2×10^4 bar. This value includes both ends of the cell (the water traverses the membrane two times—going into the cell and coming out of the cell).

Now let us consider the cell walls. Again, the water moves through one cell wall at the proximal end of the cell and another cell wall through the distal end. Taking the value for $(\partial P / \partial X)$, -3.2×10^6 bars/m, and multiplying it by 10×10^{-6} m (each end of the cell has a cell wall that is 5 μm

thick for a total cell wall thickness that the water must traverse of $10\text{ }\mu\text{m}$), we get

$$-3.2 \times 10^6 \text{ bar/m} \times 10 \times 10^{-6} \text{ m} = -30 \text{ bars (rounding off)}.$$

For the lumen, we found $(\partial P/\partial X) = -0.2 \text{ bar/m}$. If we multiply this by the length of the lumen, $1000\text{ }\mu\text{m}$ or $1 \times 10^{-3} \text{ m}$, we get $-0.2 \text{ bar/m} \times 1 \times 10^{-3} \text{ m} = -2 \times 10^{-4} \text{ bar}$.

Comparison gives the following:

Membranes: $-2 \times 10^4 \text{ bar}$

Cell walls: -30 bar

Lumen: $-2 \times 10^{-4} \text{ bar}$

The main barriers to water transport are the cell membranes. The interstices of the cell walls provide a much easier pathway for solution flow, while a hollow xylem vessel presents the least obstacle. The evolution of xylem, in particular, the vessel members in the angiosperms, provides a plant with a tube well suited for moving water over long distances.

15.5 AGRONOMIC APPLICATIONS OF POISEUILLE'S LAW

One of the first important agronomic uses of Poiseuille's law was in a pioneering paper by [Passioura \(1972\)](#) in Australia where wheat plants face *terminal drought*, as they do in other semiarid areas. This is a term that is used when plants are grown in dry land. If they are not irrigated, the crops often use up water stored in the soil by the time they reach flowering, and then no water is available for flowering, grain fill, and the remainder of the life cycle. So the drought at the end part of the life cycle is called "terminal".

[Passioura \(1972\)](#) suggested that when wheat is growing predominantly on stored water, it is an advantage for the plants to have root systems of high hydraulic resistance, so that they will conserve water during early growth and thus have more water available while filling their grain. The xylem of the seminal roots in wheat is dominated by one large metaxylem element (vessel member), the diameter of which (about $50\text{ }\mu\text{m}$ in diameter on average) probably determines the amount of water flowing through the wheat plant, and, thus, indirectly, its hydraulic resistance (Note: Poiseuille's law says nothing about resistance—only the flux in a capillary tube as it is related to the pressure drop.). [Passioura \(1972\)](#) suggested that the resistance to flow in the wheat root could be increased in one of the two ways: (1) by decreasing the size of the central metaxylem element, or (2) by reducing the number of seminal roots.

Passioura (1972) chose to reduce the number of seminal roots. He forced wheat plants to grow on one seminal root. The number of seminal roots that different cultivars (varieties) of wheat produce is under genetic control. Percival (1921) reported that the wheat plant may produce up to eight seminal roots. (Note: The words *cultivar* and *variety* are used interchangeably. A “cultivar” is a “cultivated variety”, i.e., a native variety cultivated for specific characteristics.)

Passioura (1972) grew wheat in two columns of soil in a greenhouse. The wheat plants in one column had only one seminal root because he cut off all the others. The wheat plants in the other column had their natural number of seminal roots (three seminal roots). He irrigated at the beginning of the experiment when the plants were young and then let the plants reach terminal drought. He applied Poiseuille's law to the central large metaxylem element for both treatments. His measurements and calculations showed the following:

	J_v (Measured) (mm/s)	$\partial P/\partial X$ (Pressure Gradient) (Calculated) (bar/mm)
1 seminal root	800	0.1
3 seminal roots	250	0.03

The single-rooted plants had double the available water at anthesis and produced double the grain yield. The plants with the one seminal root had a large pressure gradient. [Note, for comparison, Nobel, 1974 (p. 393) found for a diffuse-porous tree with a J_v of 0.1 cm/s the pressure drop was -0.2 bar/m or -0.0002 bar/mm.] However, the plant with one root could not sustain the large pressure drop and closed its stomata. Passioura (1972) concluded that it might be possible to conserve water by growing wheat plants with a single seminal root, and it may be possible to breed high root resistance into existing cultivars by breeding for smaller vessels. Passioura's (1972) classic paper showed that Poiseuille's law can be used to calculate the pressure drop in crops and that this value can be used to breed for drought-resistant varieties.

This idea was carried forward when Richards and Passioura (1981a,b) screened the world's wheat collection for the two factors that control resistance to water movement in the wheat root: number of axes (number of seminal roots) and central metaxylem vessel diameter. They screened about 1000 accessions in the collection, and they found that the number of axes varied between 3 and 5 and the central metaxylem vessel diameter varied between 35 and 75 μm . Because there was greater variability in the vessel diameter than in the number of axes, they said that the diameter was more important in determining resistance than the number of axes. One should breed for diameter, not for number of axes.

The wheat breeding program, as suggested by Passioura (breeding for small central metaxylem element), has been applied in Australia (Richards and Passioura, 1989). In field trials over 5 years in dry environments, narrow xylem vessel selections yielded between 3% and 11% more than unselected controls. However, many factors other than metaxylem vessel diameter and number of seminal roots determine the amount of water lost by a wheat plant. For example, even if the seminal roots are cut (or the wheat is bred for a small number of them), or if a small central metaxylem element diameter in the axes is bred for, the wheat plant develops adventitious roots. The large number of adventitious roots swamps the change in number of seminal axes or metaxylem vessel diameter. Nevertheless, the application of Poiseuille's law to a breeding program is important. Perhaps only a small amount of water can be saved through this breeding method. However, if applied over a large land area (dry land wheat is planted on huge acreages), then a large amount of water could be saved.

Meyer and Alston (1978) saw that the diameter of root vessels of wheat increased with depth. On average, a plant with metaxylem vessels that change in diameter from 30 μm at the soil surface to 45 μm at 1 m depth carries five times the water at 1 m depth as at the surface (Note: One metaxylem vessel would not be 1 m long.). This adaptation (wheat vessel diameter at depth is wider) might be valuable evolutionarily. If the soil surface is dry (as it often is under dry land conditions), then the vessel at depth, where more water might be, can have a higher flow rate and allow survival. But, at any one level in soil, we would like the diameter of the metaxylem vessels of a drought-resistant variety to be smaller in diameter than the metaxylem vessels of a drought-sensitive variety. This would allow water conservation in the drought-resistant variety.

Meyer et al. (1978) grew wheat that depended for moisture on subsoil water extracted below 45 cm. The plants had one, three, or five seminal roots. The size of the metaxylem vessel in the seminal axes affected water uptake. Using Poiseuille's law, they calculated that the flow rate at a subcrown potential of -15 bars would be increased by 30% in a plant with three axes without changing the root length, if the radius of each metaxylem vessel were increased by 3 μm .

Meyer and Ritchie (1980) also applied Poiseuille's law to sorghum. They suggested that cultivars with small vessels might have higher resistances and, therefore, be better adapted to dry conditions because they use less water.

The main limitations in the use of the Poiseuille equation to calculate pressure drop in the xylem (and indirectly resistance to water movement) are the inability to measure xylem vessel radii sufficiently accurately, lack of knowledge about effects of growth conditions on longitudinal variations in vessel radii, lack of knowledge about numbers of vessels that

carry water from one layer to another in field crops, and inability to account for water exchange along the vessel length (Klepper and Taylor, 1979, p. 61). The most serious of these limitations is that associated with vessel radii, especially in view of the fact that vessel radii enter the Poiseuille equation as r^4 . However, with improved scanning electron microscopes (e.g., Cooper and Cass, 2001), vessel member characteristics are being described with better resolution than in the past. Most investigators measure vessel diameter at one depth within the profile (Klepper and Taylor, 1979). To understand the hydraulics of the xylem vessels, their diameters at different depths in the root zone need to be known.

15.6 APPENDIX: BIOGRAPHY OF J.L.M. POISEUILLE

Jean Leonard Marie Poiseuille was a French physiologist born in Paris, France, on April 22, 1799. He got his M.D. in 1828 and practiced medicine in Paris. He received the Gold Medal of the French Academy of Sciences. He was the author of “*Sur la force du coeur aortique*” (1828) (*On the force of the aorta of the heart*) (The aorta is the main artery of the body; it carries blood from the left ventricle of the heart to all organs except the lungs.). Poiseuille also wrote “*Le Mouvement des liquides dans des tubes de petits diamètres*” (1844) (*The movement of liquids in tubes of small diameters*). In 1828, he was the first to use the mercury manometer for measurement of blood pressure, and this is still the most accurate method to measure blood pressure. In 1843, he discovered the law on velocity of flow of a liquid through a capillary tube, and in 1846, he studied the flow of viscous liquids. He invented the hemodynamometer for measuring blood pressure inside arteries and also invented the viscosimeter. He died in Paris on December 26, 1869 (Debus, 1968).

15.7 APPENDIX: BIOGRAPHY OF OSBORNE REYNOLDS

Osborne Reynolds (1842–1912), an English engineer and physicist, is best known for his work in the fields of hydraulics and hydrodynamics. He was born in Belfast (seaport and capital of Northern Ireland) on August 23, 1842. Gaining early workshop experience and graduating at Queens’ College, Cambridge, England, in 1867, he became in 1868 the first professor of engineering at Owens College, Manchester, England. He was elected a fellow of the Royal Society in 1877 and a Royal medalist in 1888. He retired in 1905 and died at Watchet, Somerset, England on February 21, 1912 (Priestley, 1971).

Reynolds's studies of condensation and the transfer of heat between solids and fluids brought radical revision in boiler and condenser design, and his work on turbine pumps laid the foundation for their rapid development. A fundamentalist among engineers, he formulated the theory of lubrication (1886), and, in his classical paper on the law of resistance in parallel channels (1883), he investigated the transition from smooth, or laminar, to turbulent flow. He later (1889) developed the mathematical framework that became standard in turbulence work. His name is perpetuated in the "Reynolds stress," or drag exerted between adjacent layers of fluid due to turbulent motion, and in the "Reynolds number," which provides a criterion for correct modeling in many fluid flow experiments. He developed corresponding criteria for wave and tidal motions in rivers and estuaries. Among his other work was the explanation of the radiometer and an early absolute determination of the mechanical equivalent of heat. Reynolds's *Scientific Papers* were published in three volumes (1900–1903) (Priestley, 1971).

15.8 APPENDIX: BIOGRAPHY OF KATHERINE ESAU

Katherine Esau (1898–1997), author of classic textbooks on plant anatomy and considered the greatest plant anatomist of the twentieth century, was born on April 3, 1898 in Yekaterinoslav, now called Dnepropetrovsk, in the Ukraine (Evert, 1992). Her family was Mennonite, descendants of German Mennonites invited to Russia by Katherine the Great to promote agriculture on the steppes of the Ukraine. After finishing high school, she enrolled at the Golitsin Women's Agricultural College in Moscow. In 1918, after 1 year of study, she, her parents, and brother fled the Bolshevik Revolution in Russia (Evert, 1997; Thorsch and Evert, 1997). At the time of their departure from Yekaterinoslav, Dr Esau's father, a mechanical engineer by profession, was the mayor of the city (Evert, 1992). They went to Germany where she enrolled in the Berlin Landwirtschaftliche Hochschule (Agricultural College of Berlin). In 1922, she completed her college education in Germany majoring in plant breeding (Mitchell et al., 1968). There she knew Professor Erwin Baur (1875–1933), a famous experimental geneticist who founded the Institut für Vererbungsforschung (Institute for Investigation of Heredity) (Encyclopaedia Britannica, 1971) and who was known for his work on chimeras (Jones, 1971). The Esaus left Germany for the United States in 1922. They settled in Reedley, California, a Mennonite community. In 1923, she took a job with Sloan Seed Company in Oxnard, California, but the company went bankrupt 1 year after she started work there (Thorsch and Evert, 1997). She then worked at Spreckels Sugar Company in Salinas, California, and bred strains of sugar beets for resistance to the virus causing curly-top

disease (Evert, 1997). She stayed at Spreckels until 1928 when she left to begin graduate studies at the University of California, where she studied the effect of curly-top virus on sugar beet. She completed her graduate work in December 1931, and the formal granting of the Ph.D. degree occurred on the campus of Berkeley in 1932 (Evert, 1992). Immediately after graduation she joined the staff at Davis to become, by 1949, Professor of Botany and Botanist of the Experiment Station (Mitchell et al., 1968). She studied the effect of disease on the anatomy of plants, an area called *pathological anatomy* (Evert, 1992). Her work on curly-top virus in tobacco showed the dependence of this virus on the phloem tissue for initiating infection and spreading it throughout the plant (Thorsch and Evert, 1997). During World War II, she became involved with a project to develop more productive rubber-yielding strains of guayule. After the war, she turned her attention to Pierce's disease in grapevine and studied the importance of the phloem in its infection (Evert, 1992).

In the 1950s, she began collaborating with Vernon I. Cheadle (1910–1995), who in 1952 had moved from Rhode Island State College to join the Botany Department at the University of California at Davis as Chair. They shared an interest in vascular tissues, especially the phloem (Evert, 1995). They studied the comparative structure of phloem in dicotyledons.

In 1963, 2 years before she was to retire, she moved to Santa Barbara, California, to continue her collaboration with Vernon Cheadle, who had been appointed in 1962 as Chancellor of the University of California at Santa Barbara (Evert, 1997). She had been introduced to electron microscopy at Davis in 1960, and her move to the University of California at Santa Barbara led to the development of electron microscopy in the biology department there (Evert, 1992). She applied this new tool to her anatomical research (Thorsch and Evert, 1997). She studied phloem and viruses including the tobacco mosaic virus and the beet western yellows disease that causes yellowing of sugar beet leaves (Evert, 1992). She reached the Emeritus status on June 30, 1965, but remained actively engaged in research into her late 80s and was working on a third revision of *Anatomy of Seed Plants* in her 90s. She was the oldest person to hold a National Science Foundation grant (Theodore M. Barkley, Professor of Biology, Kansas State University, personal communication, c.1985).

She is best known for her two classic textbooks: *Plant Anatomy* (first edition, 1953; second edition, 1965) and *Anatomy of Seed Plants* (first edition, 1960; second edition, 1977). In these books, she provided a standard terminology that is used in plant anatomy today (Thorsch and Evert, 1997). Each edition of *Anatomy of Seed Plants* has a glossary. Her two textbooks have been published in several languages including Russian (Evert, 1997). She had 15 Ph.D. graduate students, who got their degrees with her between 1950 and 1981 (Thorsch and Evert, 1997). One of her

students was Ray F. Evert. He got his Ph.D. with her in 1958 and spent his career at the University of Wisconsin. He became the leading plant anatomist in the USA after her. He said as a graduate student he was the recipient of Katherine Esau's "wisdom, knowledge, and insight" (Evert, 2002). When Ray Evert first met Dr Esau, she was riding a bicycle, which she did regularly to and from the Botany Department at the University of Davis. She set new standards for excellence. She told Dr Evert, "Ray, one can never be too careful" (Evert, 1997).

At many universities, including Kansas State University, plant anatomy is no longer taught. Teaching emphasizes molecular biology instead of taxonomy or anatomy. Therefore, Katherine Esau's textbooks are all more important, because students now must teach themselves plant anatomy, which they can do by reading her books.

Dr Esau received many awards for her accomplishments. She was elected to the American Academy of Arts and Sciences, the American Philosophical Society, the National Academy of Sciences, and the Swedish Royal Academy of Science (Evert, 1997). She was the President of the Botanical Society of America in 1951 (Mitchell et al., 1968). She received a Certificate of Merit on the Golden Jubilee Anniversary of the Botanical Society of America in 1956. The Certificate reads "Katherine Esau, plant anatomist and histologist, for her numerous contributions on tissue development of vascular plants and in particular for her outstanding studies on the structure, development, and evolution of phloem" (Evert, 1997). She received honorary degrees from Mills College, Oakland, California (1962), and the University of California (1966). In 1989, she was awarded the President's National Merit of Science. The citation accompanying the medal reads "In recognition of her distinguished service to the American community of plant biologists, and for excellence of her pioneering research, both basic and applied, on plant structure and development, which has spanned more than six decades; for her superlative performance as an educator, in the classroom and through her books; for the encouragement and inspiration she has given to a legion of young, aspiring plant biologists; and for providing a special role model for women in science".

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