Primary and Secondary Growth

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1 Introduction

In the previous handout, you should have learned about the different types of cells, tissues, and organs in plants. Here, we'll delve into three specific organs — roots, stems, and leaves — and how they develop through primary and secondary growth. Both primary and secondary growth are essential processes in plant development and are driven by cell division, elongation, and differentiation from the apical and lateral meristems. **Meristems** are tissues containing undifferentiated cells that can divide.

- **Primary growth** is growth in length facilitated by **apical meristems** located in the tips of roots and shoots.
- **Secondary growth** is growth in width facilitated by **lateral meristems** — the vascular cambium and cork cambium — that only occurs in the roots and stems of woody plants.

In addition, all organs/organisms can be classified as growing indeterminately or determinately.

- **Indeterminate growth** is growth that occurs throughout an entire lifespan (e.g. roots and stems).
- **Determinate growth** is growth that stops after a certain size is reached (e.g. leaves and flowers).

2 Herbaceous and Woody Plants

Before discussing the specifics of primary and secondary growth, we have to understand the differences between herbaceous and woody plants. Both are types of vascular plants, but are differentiated by their ability to produce wood through secondary growth.

Herbaceous plants are characterized by having soft, flexible, and green stems. They lack the lateral meristems that facilitate secondary growth and therefore do not have woody tissue. Instead, almost the entire plant undergoes primary growth through the apical meristems, which involves the lengthening of roots and shoots, and therefore the development of new leaves, flowers, and fruits. Examples of herbaceous plants include grasses like wheats, and garden flowers, like irises.

Woody plants have hard, rigid stems that usually become thick trunks. These plants undergo both primary and secondary growth simultaneously, but do so in different regions. Similarly to herbaceous plants, woody plants experience primary growth in the younger, newer parts of the plant. The key difference, however, is that woody plants have lateral meristems that produce woody tissue such as secondary xylem. This growth in width occurs in the older parts of the roots and stem. Examples of woody plants include trees like oaks, maples, and pines, and shrubs like roses, azaleas, and yews.

3 Anatomy Review

This section reviews the plant anatomy covered in the previous handout and also introduces some new content. Familiarizing yourself with this information will help you better understand the growth and development processes in the following sections.

3.1 Root and Shoot Systems

- A plant's **root system** is composed of its roots.
- A plant's **shoot system** includes its stems and leaves, in addition to organs such as flowers, fruits, and thorns, if applicable.

3.2 Plant Tissues

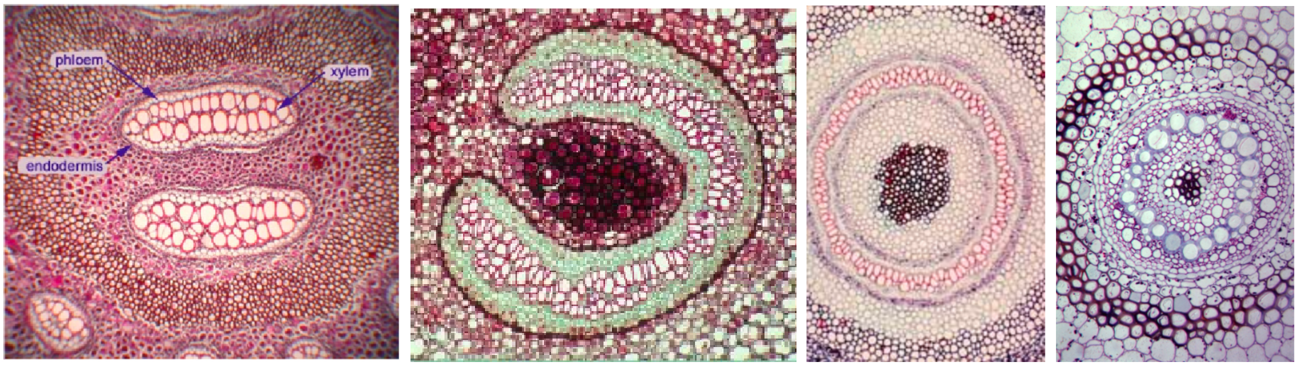
Roots, stems, and leaves are made up of three tissue types — dermal tissue, ground tissue, and vascular tissue. In this section, noteworthy terms made up of **dermal tissue** will be in blue, **ground tissue** in brown, and **vascular tissue** in purple.

Dermal tissue makes up a plant's outer protective layer while vascular tissue makes up the innermost layer and transports materials between the root and shoot systems. The vascular tissue of a root or stem is called the **stele** and is composed of xylem and phloem. Tissue that is neither dermal nor vascular is called ground tissue. Ground tissue outside of the vascular cylinder is called **cortex** and inside the vascular cylinder is called **pith**.

3.3 Root Anatomy

A root system consists of a primary root from which lateral roots branch out. In roots, the dermal tissue system is a single layer of tightly packed cells called the **epidermis**. The epidermal cells of many plants also have small, fine extensions called root hairs that increase the surface area for nutrient absorption. The root **stele** varies depending on the plant, but tends to be a vascular cylinder surrounded by ground tissue. Some examples are listed below.

- Angiosperms have a **vascular cylinder** surrounded by **cortex**.
  - The vascular cylinder of monocots tends to have a core of undifferentiated parenchyma cells surrounded by a **siphonostele** — a ring of alternating xylem and phloem tissues.
  - On the other hand, eudicots (dicots) have a **eustele** or **actinostele** — a core of xylem tissue with arms radiating outwards and phloem tissue in between the arms.
- Most gymnosperms have a **protostele** — a simple solid core of vascular tissues.
- Ferns and fern allies have a **dictyostele** or **polystele** — strands of vascular tissue dispersed in parenchyma tissue. These plants do not have a defined vascular cylinder.



(a) Dictyostele (b) Siphonostele (c) Amipholic (d) Ectopholic

Figure 1: Various fern root cross-sections. (Source: Zelmay)

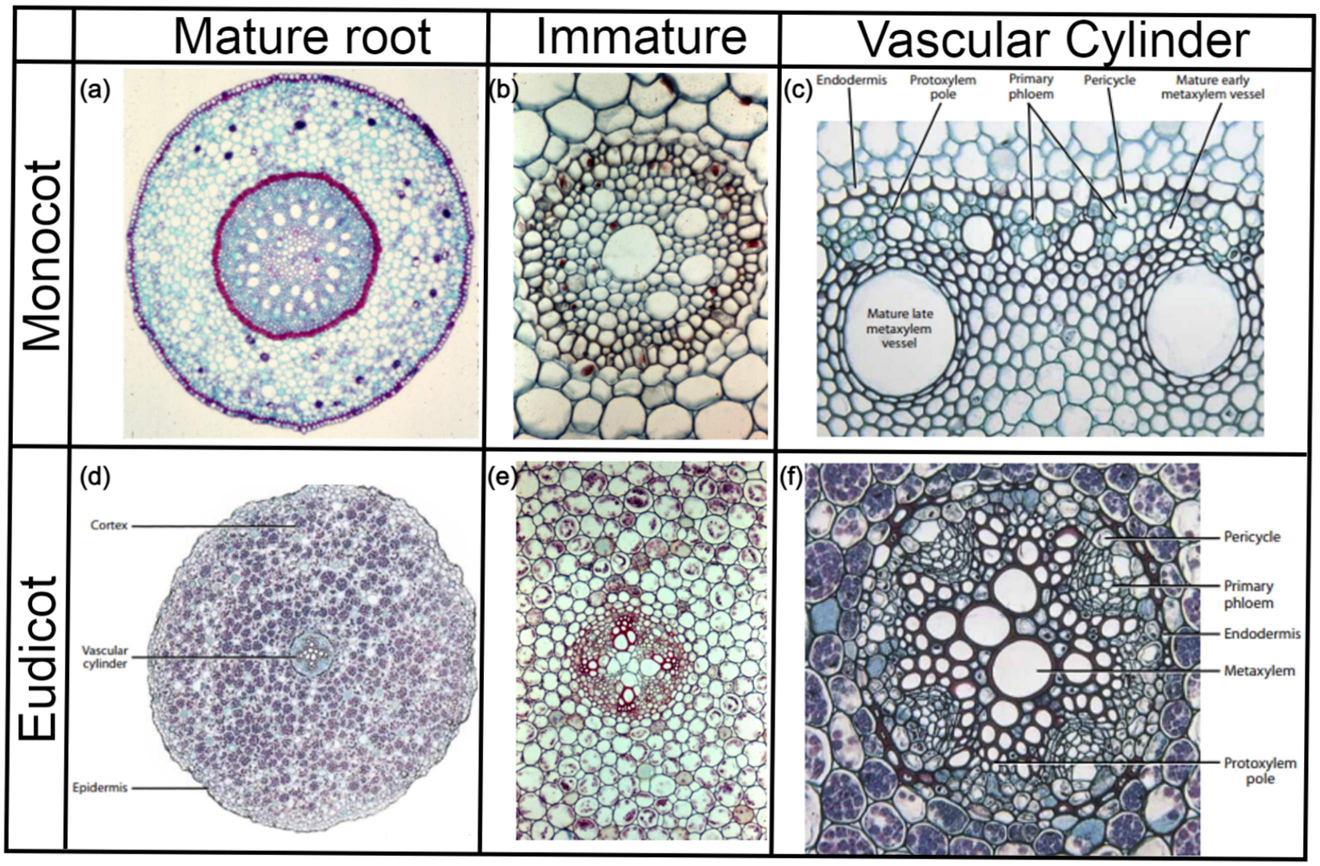


Figure 2: Cross-section comparison between monocots and dicots. Note how the xylem forms an X-shape in the center of the eudicot root. In monocots, the xylem appears as a ring of large holes, with the phloem being the smaller holes outside the xylem. The main difference between immature and mature cross-sections is that the mature root has more lignin in its cell walls, and thus the staining is stronger. **(a)** *Similax*, **(b)** *Triticum*, **(c)** *Zea Mays*, **(d-f)** *Ranaculus*. (Source: Raven Biology of Plants / EBC / Zelmay)

3.4 Stem Anatomy

In a shoot system, each stem has alternating **nodes** and **internodes**. Leaves are attached at nodes and an axillary (lateral) bud may be present in the **axil** — the upper angle formed by the leaf and stem. An axillary bud can form a flower or even a lateral branch. Internodes are the stem segments in between consecutive nodes. At the shoot tip, an **apical bud** (terminal bud) is present.

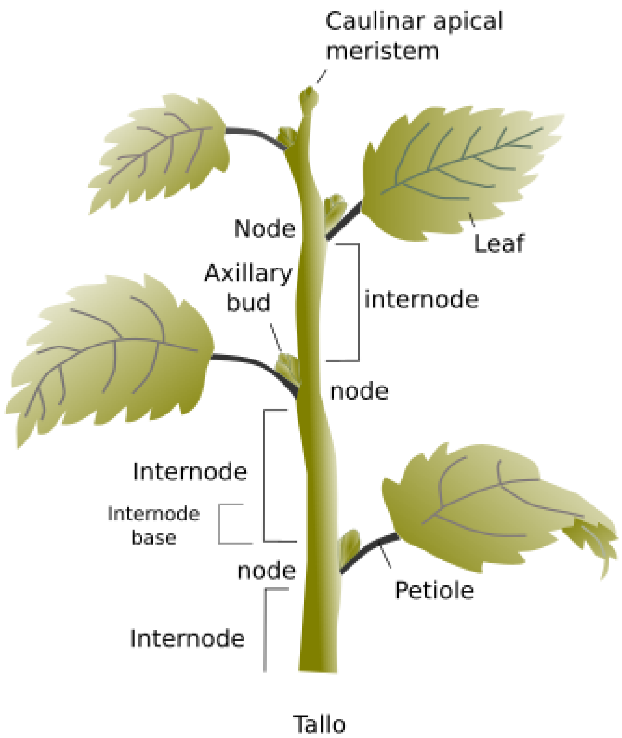
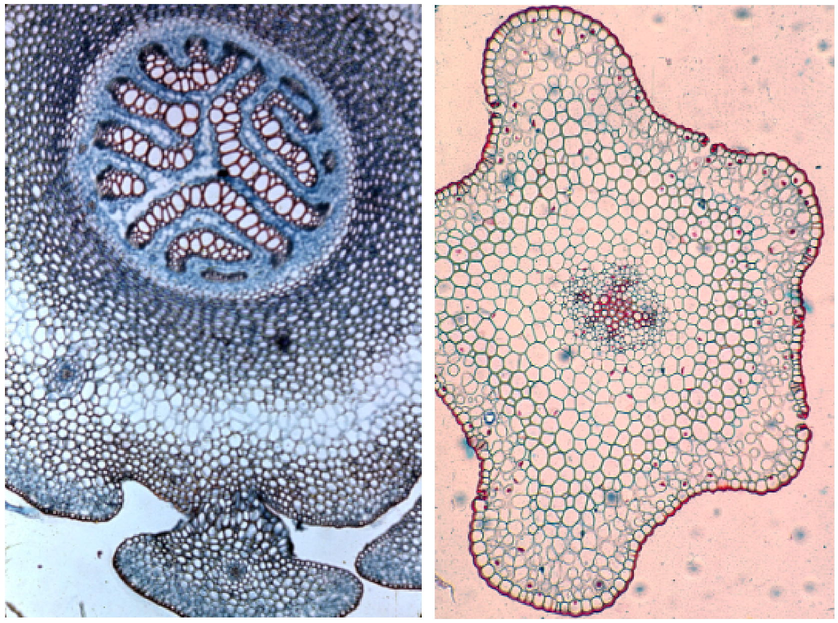


Figure 3: Stem structure. (Source: Atlas of Plant and Animal Histology)

In most stems, the dermal tissue system includes both an **epidermis** and a waxy **cuticle** that serves as the outermost layer and prevents water loss. The stem has specialized epidermal cells such as guard cells and trichomes. The ground tissue system is mostly parenchyma cells with additional collenchyma cells in regions undergoing primary growth and sclerenchyma cells where growth is finished. As in roots, the stem **stele** varies depending on the plant type. However, while roots tend to have vascular cylinders, stems tend to have vascular bundles. Each vascular bundle contains both xylem and phloem tissues and is surrounded by a layer of parenchyma cells called the **pericyle**. Two common arrangements are provided below.

- Monocots tend to have vascular bundles scattered throughout ground tissue. In this type of arrangement, ground tissue is not (cannot be) classified as cortex or pith.
- Eudicots (dicots) tend to have a ring of vascular bundles, which can therefore still classify ground tissue as cortex and pith.



(a) *Lycopodium* (plectostele) (b) *Psilotum* (actinostele)

Figure 4: Various fern stem cross-sections. (Source: Zelmay)

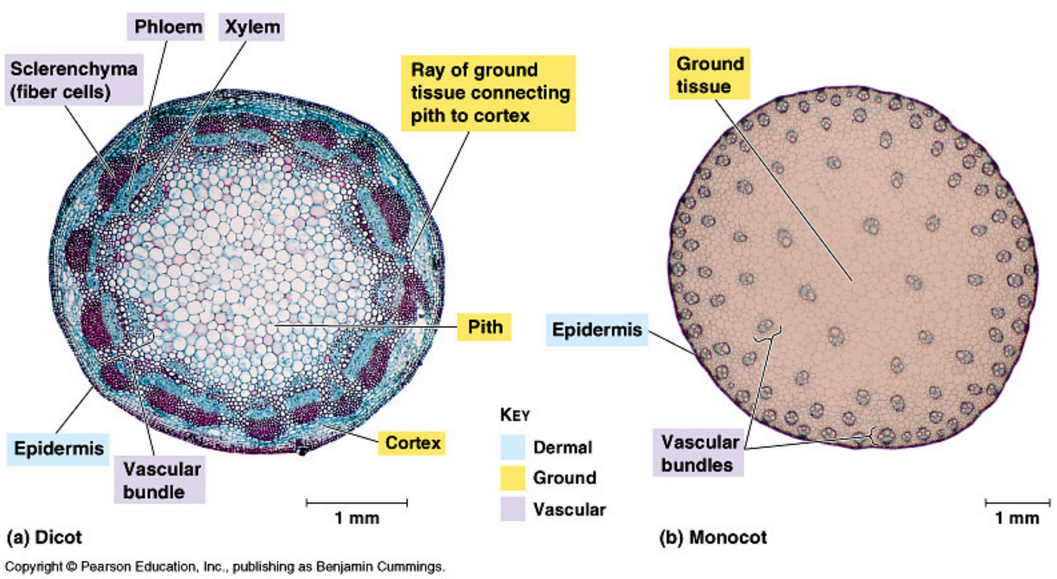
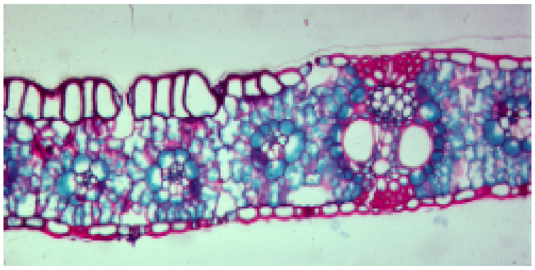


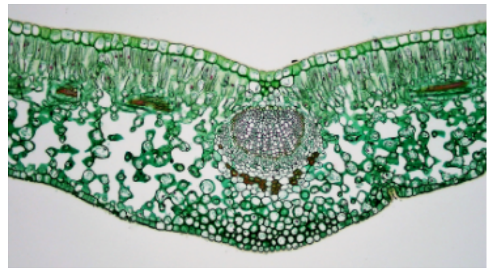
Figure 5: Comparison of dicot and monocot stem cross-sections. (Source: bio.miami.edu)

3.5 Leaf Anatomy

In leaves, the dermal tissue system is similar to stems in that the **epidermis** is also coated in a **cuticle**. In addition, **stomata** are dispersed throughout the cuticle layer to facilitate water evaporation and the exchange of gases needed in photosynthesis. The stomatal pore is flanked by two **guard cells** — specialized epidermal cells that open and close the pore. The guard cells themselves are surrounded by **subsidiary cells** that nourish them. Stoma are present on both the upper and lower epidermis, with ground tissue in between.



(a) Monocot Leaf (*Zea mays*)



(b) Dicot Leaf (*Ligustrum*)

Figure 6: Comparison of monocot (Kranz anatomy) and dicot leaf. (Source: Zelmay)

Ground tissue in leaves is called the **mesophyll** and usually has two layers in eudicots — the **palisade mesophyll** and **spongy mesophyll**. Both are composed of parenchyma cells, but the palisade layer on the upper half of the leaf has densely packed, elongated cells, while the spongy layer on the bottom has loosely arranged cells. This arrangement allows for efficient resource use and photosynthesis, as the palisade layer contains abundant chloroplasts, which maximize light absorption, while the spongy layer has gaps that facilitate gas exchange and diffusion.

The vascular tissue of each leaf connects to the vascular tissue in the stem. In the form of veins, vascular tissue branches throughout the mesophyll in order to bring xylem and phloem tissue closer to photosynthetic tissue. Veins are often protected by a **bundle sheath**, which regulates substances traveling between the vascular tissue and mesophyll.

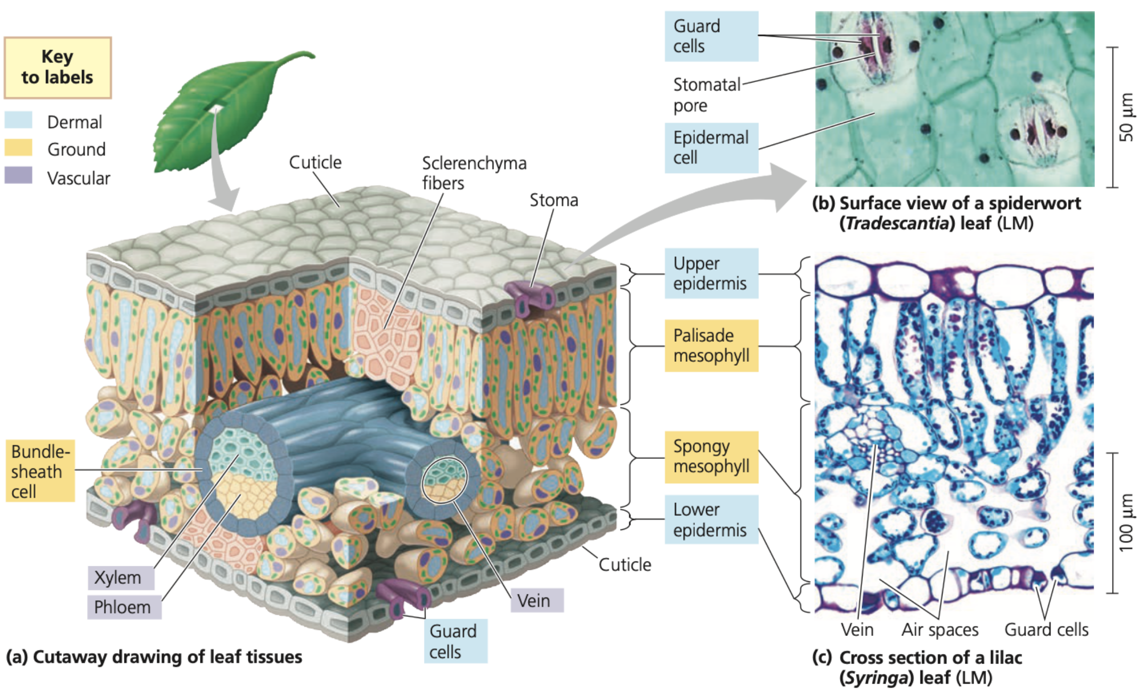


Figure 7: Leaf anatomy. (Source: Campbell's Biology 11th Edition)

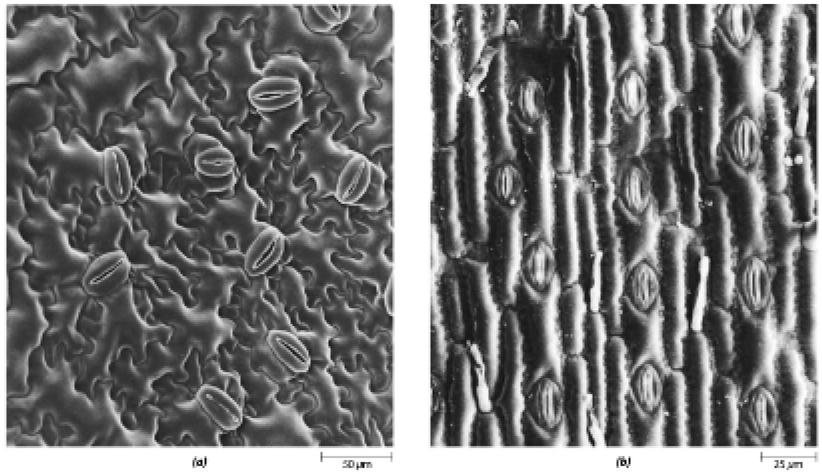


Figure 8: Comparison of dicot **(a)** and monocot **(b)** stomata. Dicot stomata are bean shaped and irregular, while monocot stomata are dumbbell shaped and arranged in rows. (Source: Raven)

4 Primary Growth

4.1 Primary Growth of Roots

As the apical meristems push downward through the soil, growth occurs in three successive zones: the zone of cell division, zone of elongation, and zone of differentiation. The zone of cell division is at the tip of the root while the zone of differentiation is further up and closest to the ground surface.

The **zone of cell division** includes the apical meristem and the cells it produces.

- The **root apical meristem** contains undifferentiated stem cells and rapidly produces new root cells, called meristematic activity.
- The apical meristem also produces cells that form the **root cap**; it surrounds and protects the meristem, secretes (through periphery cells) a polysaccharide slime called **mucilage** to lubricate the soil, and responds to environmental cues such as gravity (through columella cells in the center of the cap).

The **zone of elongation** is where root cells elongate and begin to differentiate. Note that the primary meristems are bolded in blue to follow their development in the zone of differentiation.

- Root cells elongate while the apical meristem continues adding cells to the younger side of the zone. This pushes the root further into the soil.
- While elongating, cells begin differentiating into three tissues called **primary meristems** — the protoderm, ground meristem, and procambium (from outermost to innermost layer).

The **zone of differentiation/cell maturation** is where cells of the primary meristems finish differentiating and become distinct cell types.

- The **protoderm** completes differentiation and becomes the **epidermis**, an outer, single-celled layer of cuticle-free cells with root hairs. These epidermal cells absorb water and nutrients.
  - In woody plants, the **periderm** replaces old regions of epidermis.
- The **ground meristem** becomes **mature ground tissue**, consisting mostly of parenchyma cells. Remember that ground tissue outside of the vascular cylinder is called the **cortex**. It stores, transports, and allows for extracellular diffusion of nutrients from the root hairs inwards.
  - The **endodermis** is the innermost layer of the cortex. It is a one-cell thick barrier that surrounds the vascular cylinder. It regulates the passage of substances from the soil into the vascular cylinder.
- The **procambium** becomes the **vascular cylinder**, which is surrounded by a cell layer called the **pericycle** and contains xylem and phloem tissue.

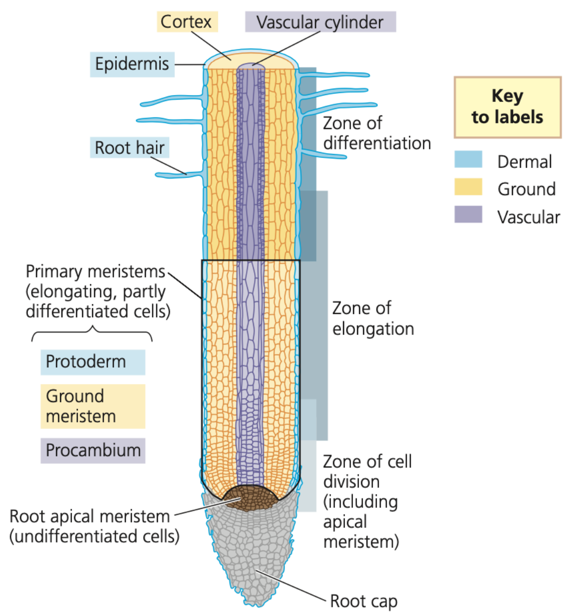


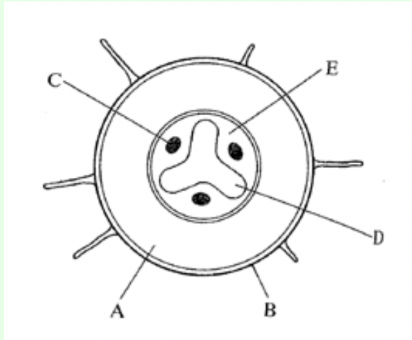
Figure 9: Primary growth of a eudicot root. (Source: Campbell's Biology 11th Edition)

In the diagram, you can see the zone of cell division at the bottom (tip of the root) with the apical meristem and root cap. A few centimeters above it is the zone of elongation with the primary meristems. In the zone of differentiation at the top of the diagram, each primary meristem becomes its fully differentiated counterpart.

4.2 Lateral Roots

The formation of lateral roots is also a type of primary growth. In a root system, lateral roots branch off of a primary root and may go on to branch further themselves. A lateral root begins in the **pericycle** — the outermost layer of the vascular cylinder — and then pushes through the cortex and stretches the epidermis.

Example 4.1 (Adapted from USABO Semifinal Exam 2013) The diagram below shows a cross-section of a plant root. Letters A through D point to different tissues.



(a) Which tissue will produce a lateral root?

(b) Which tissue transports sugar from the shoot to the root?

(c) Which tissue transports water from the root to the shoot?

(d) What type of plant is this root cross-section most likely from?

(A) Monocot
(B) Eudicot
(C) Gymnosperm
(D) Fern
(E) Moss or liverwort

(e) From which area of the root is the cross-section taken?

(A) Apical meristem
(B) Root cap
(C) Zone of cell division
(D) Zone of cell elongation
(E) Zone of cell maturation

Solution: Since lateral roots are produced in the pericycle, the answer to question **(a) is E** because it points to the outer layer of the vascular cylinder. The visible rim enclosing the vascular cylinder represents the endodermis, not the pericycle. We should know from previous handouts that the xylem transports water up and the phloem transports sugar down. In the diagram, we see a core of xylem tissue with arms and more phloem tissue in between. Therefore, the answer to question **(b) is C** and the answer to question **(c) is D**. The root stele structure in the diagram with a star-shaped xylem core is typical of eudicots so the answer to question **(d) is (B)** Eudicot. Finally, root hairs are present and the vascular cylinder is fully differentiated, so the answer to question **(e) is (E)**.

4.3 Primary Growth of Shoots

The process of primary growth in shoots is similar to the process in roots. At the tip of a shoot, the apical meristem is protected by the **leaf primordia** — the young leaves of the apical bud. Elongation occurs in the internode cells and the beginning of differentiation creates the three primary meristems. Just like in roots, these primary meristems fully differentiate to become the parts of the mature shoot.

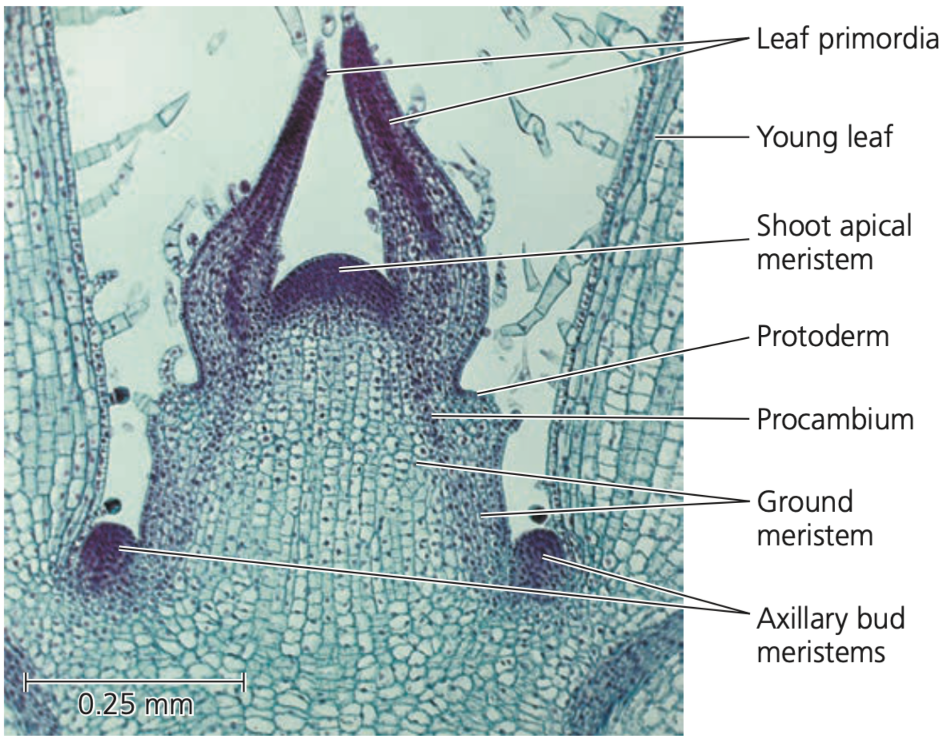


Figure 10: The shoot tip. (Source: Campbell's Biology 11th Edition)

4.4 Lateral Branches

Axillary buds have their own apical meristems and can form lateral branches once activated by environmental or hormonal signals. Once activated, the cells within the axillary bud start dividing rapidly and primary growth occurs. Since lateral branches originate from axillary buds, they do not disrupt interior tissue like lateral roots do.

4.5 Apical Dominance

If too close to the apical bud, an axillary bud may experience **apical dominance** — a phenomenon that occurs when a main shoot's apical bud suppresses the growth of axillary buds through auxin production. Auxin is a plant hormone responsible for regulating growth, development, and tropic responses. Therefore, if the chemical communication of an apical bud is interrupted, an axillary bud has the potential to be activated and grow a lateral branch.

5 Secondary Growth

As a reminder, secondary growth only occurs in woody plants. It is common in all gymnosperms and many eudicots but is infrequent in monocots. The process is similar in roots and stems.

As the apical meristems cause primary growth, the lateral meristems cause secondary growth and include the **vascular cambium** and **cork cambium**.

5.1 Vascular Cambium

The vascular cambium is a ring of meristematic cells located in between the primary xylem and primary phloem before secondary growth begins.

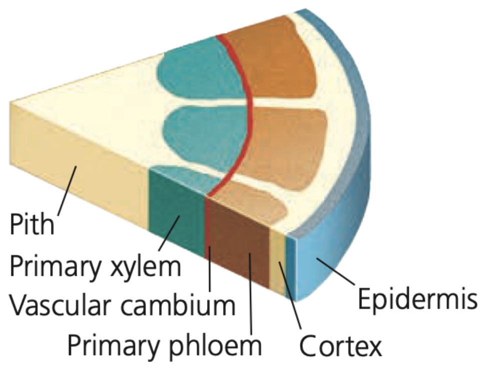


Figure 11: Cross-section of a woody eudicot before secondary growth occurs. (Source: Campbell's Biology 11th Edition)

In the diagram, the vascular cambium is represented by a thin red layer. As secondary growth begins, the vascular cambium will produce secondary xylem inwards and secondary phloem outwards. There are two different types of cells in the vascular cambium that serve to produce different structures.

- Elongated stem cells parallel to the stem/root produce mature, specialized cells such as tracheids, vessel elements, and fibers in the xylem and sieve-tube elements, companion cells, axially oriented parenchyma, and fibers in the phloem.
- Shorter stem cells perpendicular to the stem/root produce **vascular rays** — rays of parenchyma cells that connect and transport materials between the secondary xylem and phloem. A visualization of the rays can be seen in the diagram below.

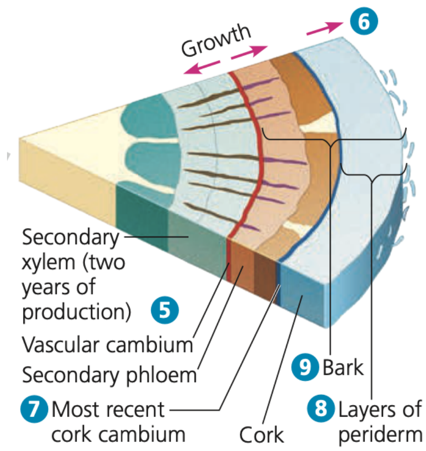


Figure 12: Cross-section of a woody eudicot after two years of secondary growth. (Source: Campbell's Biology 11th Edition)

In temperate regions, early wood develops during early spring and has secondary xylem cells with large diameters and thin cell walls. This structure optimizes the delivery of water to the leaves. As the growing season progresses, late wood is produced during the summer and has thick-walled, smaller cells that offer more support but transport less water. The distinct contrast between the large cells of the new early wood and the smaller cells of the late wood from the previous growing season results in the formation of annual **growth rings** visible in cross-sections of most tree trunks and roots.

In addition, the innermost, older layers of secondary xylem that cease to transport water and minerals (xylem sap) become known as **heartwood**. The newer layers that still transport xylem sap are known as **sapwood**. The presence of sapwood enables a large tree to continue surviving even if the center of its trunk becomes hollow. Though heartwood no longer transports water and nutrients, it may contain resins, oils, and other substances that make it more resistant to decay and insect damage. This is the reason why heartwood appears darker than sapwood.

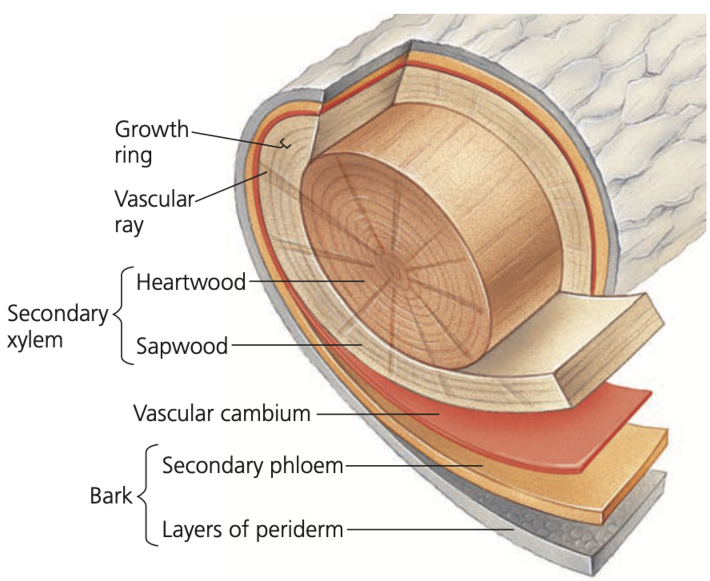


Figure 13: Anatomy of a tree trunk. (Source: Campbell's Biology 11th Edition)

As the vascular cambium expands in diameter, the cells in the secondary phloem, epidermis, and other tissues external to the cambium cease dividing. Consequently, these tissues become unable to keep up with the cambium's growth and eventually rupture. This allows for a second lateral meristem — the **cork cambium** — to develop from parenchyma cells in the cortex.

5.2 Cork Cambium

The cork cambium is also called **phellogen**. Like the vascular cambium, it also produces new cells both inwards and outwards. It produces **phelloderm** toward the inside and **phellem**, also known as cork, toward the outside. Cork cells are dead at maturity and have suberized walls, meaning they are impermeable and create a protective barrier against water loss, pathogens, and mechanical damage. Phellogen, phelloderm, and phellem are collectively known as **periderm**, which replaces the epidermis after it ruptures in secondary growth. **Bark** is the umbrella term that defines all tissues exterior to the vascular cambium. **Lenticels** are small, raised, horizontal slits on the surface of woody stems that allow for gas exchange.

As the stem or root's diameter increases, the outermost tissues beyond the cork cambium rupture and are shed. In some instances, the cork cambium re-establishes itself at a deeper position within the cortex. When there are no more parenchyma cells left in the cortex, the cambium arises from phloem parenchyma cells. Each cork cambium, along with the tissues it generates, contributes to the formation of a periderm layer.

Example 5.1 (USABO Semifinal Exam 2011) When an oak seedling is one year old, a small marker is inserted into its primary phloem tissue. Two years later, where would you expect to find this marker?

(A) External to the cork cambium
(B) Between the secondary phloem and the cork cambium
(C) Between the vascular cambium and the secondary phloem
(D) Between the vascular cambium and the primary xylem
(E) Internal to the primary xylem

Solution: After two years of growth in the oak seedling, the primary phloem tissue, including the inserted marker, would be pushed outward by the production of secondary phloem in the vascular cambium. At the same time, the cork cambium produces cork and forms the outer layer of the trunk. Therefore, the **answer is B**.

Example 5.2 (USABO Open Exam 2017) Which of the following statements about eudicot plant anatomy is most accurate?

(A) The phelloderm is a thin layer of parenchyma cells derived from the vascular cambium.
(B) Lateral roots arise from the pericycle and push through the cortex, endodermis, and epidermis during their growth.
(C) Secondary growth refers to growth of a branch once all primary growth along

that given branch has finished.
(D) One may distinguish leaves from the leaflets of a compound leaf by the absence or presence, respectively, of an axillary bud at the base of the structure in question.
(E) Secondary phloem develops along the outer circumference of primary phloem during secondary growth.

Solution: Phelloderm is derived from the cork cambium, so option A is incorrect. C is incorrect because primary growth and secondary growth often happen simultaneously. D is incorrect because an axillary bud is not an indicator for simple versus compound leaves. E is incorrect because secondary phloem develops along the inner circumference of primary phloem, not the outer circumference. The **answer is B**.

6 Conclusion

Plants are cool. Read Raven's for more coolness.

Good luck on USABO!! I'm rooting (lol) for you.

- Vivian Ye