Leaves are the primary photosynthetic organs of trees and other vascular plants. They are essential for nearly all trees. Some desert trees, though, drop their leaves to minimize water loss, but the bark of their green stems takes over that function. Leaves, collectively referred to as the foliage, function primarily to produce sugar from carbon dioxide and water in the presence of sunlight. The energy contained in the sugar can be used directly to sustain their living cells or stored as starch until needed in the parenchyma cells of the roots, trunk and branches. Starch can be converted back to various sugars when there is metabolic or other demand. Small openings in leaves (stomata) allow for the entry (and absorption) of carbon dioxide, an essential building block for the manufacture of sugar, and the release of oxygen and water vapor, into the atmosphere.

Trees can be divided into two broad categories; those that are deciduous or evergreen. Tree leaves are highly variable in size and shape, for example the leaves of cypress, juniper, incense cedar, giant sequoia, etc., are scale-like and those of trees like pines and other conifers are needle-like (Figs. 1, 2). In some species they are minute and in others quite large. Leaf size and shape also vary based on the leaf’s age and position in the tree (Fig. 3). Leaf shape is quite variable between taxa, yet their role is the same...to collect sunlight in the most efficient way possible. Both leaf shape and size have evolved in each species in response to environmental conditions, for example: heat, wind, humidity, exposure to sunlight, etc. Furthermore, each species has a strategy to maximize leaf efficiency. Leaf design appears to be a compromise between carbon gain, thermoregulation, and water loss, as well as the effects of gravity and wind.

Even in death, leaves enrich the soil when they fall as litter on the soil’s surface. In this manner, critical minerals bound within them can be recycled back to the tree. Fallen leaves and other woody debris are essential to maintain the health and natural diversity of the soil microbial community within the root zones of trees that sustains trees (Fig. 4). Having a greater understanding of why leaves are so important, from leaf flush to abscission, we can better understand how excessive pruning or defoliation by insect or disease pathogens can reduce a tree’s energy production, and how we can manage trees in urban landscapes more pru...

**Figure 1.** (Left) Incense cedar (*Calocedrus decurrens*), an example of a tree with scale-like leaves. Each twig segment has four tiny leaves. *Photo: B. Hagen*

**Figure 2.** (Right) Douglas fir (*Pseudotsuga menziesii*), an example of a tree with needle-like leaves. *Photo: B. Hagen*

**Figure 3.** The leaves of date palms can reach 20 feet long. *Photo: B. Hagen*
that fall off after the leaf expands are called deciduous, and those that remain on the leaf for its lifetime are referred to as persistent. Stipules may be modified into teeth, spines, hairs or tubes. Although their function is unknown, it’s possible that they protect the leaf attachment.

Leaf shapes are incredibly diverse. Simple leaves are typically oval in shape, sometimes lobed but not divided into leaflets at the midrib (Fig. 6), or palmate (Fig. 7). Compound leaves are those that are completely divided to the midrib (rachis), forming separate leaflets or pinnae. Those that are arranged linearly along a central axis (rachis) in a feather-like manner, are said to be pinnately compound (Fig. 8). The term bipinnately compound is used to describe leaves that have a second rachis and rank of leaflets. While generally rare, some trees form leaves with three ranks of pinnae. Leaves that are divided into pinnae that originate from a central point are considered palmately compound. (Fig. 9) Compound leaves are common in tropical and desert ecosystems. In deserts, leaflets of common
Compound leaves are often quite reduced in size (microphyll) (Fig. 10). Compound leaves are a likely adaptation to reduce transpirational water loss since the pinnae can be folded against one another during times of drought. The pinnae of compound leaves can move along multiple axes to track the movement of the sun, and thereby maximize photon capture.

Leaf edges can be entire (smooth edged) or serrated (toothed), lobed, or some variation in between (Figs. 11, 12). Generally laminae are larger in wetter (temperate and tropical) climates and smaller in arid climates. Leaf veins are also arranged in pinnate and palmate configurations (Fig. 13). The main vein is called the midrib. Dicotyledenous trees (those with two cotyledons in their embryos (seeds), are largely net-veined or have reticulate venation (Fig. 14). Monocotyledonous trees have parallel venation in their leaves (Fig. 15). In a few trees like Ginkgo the veins fork evenly and progressively from the leaf base to its tip and edges are said to have dichotomous venation. (Fig. 16).

Some leaves are modified to form other structures, such as tendrils that can curl around other plants or objects to provide support or aid in climbing. Another example are spines of desert plants that provide protection. In some trees like locust and mesquite, the stipules are modified into stout spines at the base of the leaf. Thorns, short projections from the axil of leaves, are modified stems.

Leaf color is another variable characteristic especially in deciduous trees. While leaves can be yellow, orange, red, copper-toned, dark purple or many shades of green, all leaves contain chlorophyll, even though the green color may be masked by other pigments. Deciduous trees often change color in the fall, sometimes quite dramatically. (Fig. 17). Some species, particularly those in tropical areas, have red new growth which is thought to discourage herbivory (Fig. 18). Chlorophyll breaks down in autumn—it is not known why, but appears related to signals from shortening day length. Fall color is revealed as the anthocyanins and carotenoid pigments that were previously masked by chlorophyll, become visible as chlorophyll degrades. Sometimes leaves are variegated with green, light green or white tissues. These are often genetic ‘sports’, or in some cases, the result of viral infections. Trees with variegated leaves are usually shade-loving or less able to withstand full sun exposure.

Even the tips and bases of leaves are variable in shape, and often used...
in species identification. Other features used for identification include texture. For example, thick leathery leaves are typically found on species adapted to hotter and dryer climates, and coastal or windy locations. Leaves of trees native to warm and moist locations tend to be thin and membranous. The epidermis can be highly modified with hairs, glands or extracellular waxes to help leaves survive harsh environments. Hairiness is an important characteristic that ranges from smooth (glabrous) and glossy to woolly, or even silky. Plant hairs are called trichomes and are commonly found on most leaves (Fig. 19). Texture can also be smooth or quite rough. Some leaves are described as “glaucous” or covered by a waxy material that increases light reflection and decreases water loss (Fig. 20). All of these modifications to leaves are part of the species strategy to survive in its native habitat.

Leaf anatomy
Most leaves, with the exception of those of conifers, are thin, flat and blade-like with an upper and lower surface. If you examine a cross-section through a leaf with the upper surface facing up, there are several distinct layers. Inside the upper and lower epidermal layers are the mesophyll layers. The uppermost mesophyll layer is called the palisade mesophyll and the lower layer is called the spongy mesophyll (Fig. 5). The two mesophyll layers have different purposes, but are composed of the same kinds of cells (parenchyma cells). Chloroplasts in the palisade mesophyll are responsible for capturing energy (photons) needed to drive the photosynthesis reaction. Although the cells in the spongy mesophyll also contain chloroplasts, they are important for gas exchange. Stomata (pores), primarily in the lower epidermis of leaves, open and close in response to light, humidity, and water availability. They regulate gas exchange between the atmosphere and the intracellular spaces within the leaf. Water vapor and oxygen within the intracellular spaces of leaves diffuse out through the stomata when they’re open. In the same manner, carbon dioxide (CO₂), the primary building block for photosynthesis, diffuses into the leaf and the photosynthetic reaction can proceed. Transpiration and photosynthesis occur primarily when stomates remain open.

The veins of cells running between the pallisade and spongy mesophyll layers are the ultimate extensions of xylem and phloem from the roots up into the stem, branches and leaves. Each vein contains strands of xylem that supply water to the leaf, and phloem that transports photosynthate (sugars) from the leaf to other living cells throughout the tree. The veins of most leaves branch out covering the entire surface of a leaf so that water can be delivered and sugars withdrawn from all the cells.
containing chloroplasts.

The epidermis is covered by a thin, waxy cuticle that limits water loss from the leaf surface. The cuticle is generally thicker on leaves from arid climates, than those of species adapted to temperate climates or that grow as understory species in tropical forests. The epidermis of leaves may also be highly specialized. Stomatal densities vary from none above and many below to relatively even distributions on both surfaces. Epidermal cells may have trichomes with diverse structures and functions. For example, trichomes may change the reflective value of leaves, minimize water loss by retaining higher humidity around leaves, or secrete oils and resins that slow water loss and repel insects (Fig. 21).

Leaf structure varies on the basis of tree water adaptations. Trees adapted to moist and relatively humid conditions are called mesophytes. Those adapted to arid climates are known as xerophytes. As you might expect, the leaves of each of these plant types vary dramatically based on plant water requirements. Only a few tree species are considered hydrophytes: most though, are aquatic or herbaceous plants. Mesophytes, in general, have leaves with few unique adaptions compared to xerophytes. They are pretty much as described above and have similar epidermal layers. Xerophytic trees on the other hand, have developed many ways to limit water loss, allowing them to thrive in arid climates. Their leaves are typically highly modified. For example, their leaves:

- tend to be smaller and compound.
- both upper and lower surfaces are often covered by trichomes that help retain the water vapor, released by the leaf, close to its surface.
- have thick cuticles
- secrete waxy or resinous materials that serve to inhibit water loss.
- have sunken stomatal chambers, and a much reduced spongy mesophyll layer. Both of which effectively reduce water loss.
- have a variety of trichomes that are wax encrusted making them more reflective to sunlight, and prevent heat damage to their mesophyll layers.
- have developed isobilateral mesophyll that takes the place of spongy mesophyll layer. Both of which effectively reduce water loss.
- are strengthened with sclerenchyma cells (sclereids) that prevent wilting and leaf collapse during severe drought. Sclerids are highly lignified cells that impart strength to the structures they occur in.

**Light reactions, photosynthesis and transpiration**

Plants have various kinds of photosynthesis (biochemistry). In trees, carbon is typically captured and converted into a 3-carbon sugar (C3 pathway). This reaction is facilitated by an enzyme—RUBISCO (-ribulose bisphosphate carboxylase-oxygenase). It is the most abundant enzyme in the world and mediates the formation of chemical bonds that change carbon dioxide and water into a simple three carbon sugar.

Leaves contain over 80% of the tree’s chloroplasts. Within the chloroplasts are molecules of chlorophyll, a complicated ring structure with an atom of Mg at its center. There are two basic kinds of chlorophyll (a and b) that absorb light from slightly different spectra. Photosynthesis is broken down into two processes: the light-dependent and light-independent (sometimes called the dark) reactions. The light dependent reactions involve the splitting of water into oxygen and hydrogen ions as well as formation of free electrons. The high energy electrons help form energetic phosphorous compounds that drive other biochemical reactions. Oxygen diffuses out of the leaf as a by-product of the light-dependent reactions. The electrons captured from splitting the water molecule are attached to compounds used in the light independent

---

**Figure 19.** A photomicrograph of trichomes on the epidermis of a leaf. *Photo: Louisa Howard: Dartmouth electron microscope Leaf_epidermis*

**Figure 20.** (Left) An example of leaf with a glaucous or waxy bloom that, in this case, gives the tree a bluish cast. The leaves are those of the blue oak (*Q. douglasii*), a very drought resistant oak, native to California. *Photo: B. Hagen*

**Figure 21.** (Right) When numerous, trichomes increase leaf reflectance, reducing leaf temperature and conserving water. *Photo: Veryhuman (Solanum scabrum)*
transpiration is a non-stop process when sunlight is driving photosynthesis. Carbon dioxide cannot enter the leaf unless the stomates are open. So the plant always loses water vapor during photosynthesis. Assimilation efficiency is the amount of carbon that can be captured per unit of water lost. In times of drought, plants have reduced photosynthetic output and, thus, overall growth is retarded. Transpiration also keeps leaves cool. The absorbed energy from water making its phase change from liquid to vapor keeps leaves from burning up in full sunlight conditions. A tremendous amount of water is required for this cooling effect, which is why only about 1-3 percent of water entering the leaf actually participates in photosynthetic reactions.

**Phyllotaxy**

Phyllotaxy, the arrangement of leaves along a stem, is not determined by the leaves (see BFA on stems: Spring 2019) but is a result of the buds and how they are arranged. There are three basic phyllotaxies: opposite, alternate and whorled (Fig. 22). But phyllotaxy also considers the arrangement in three dimensions as you move along a stem. Phyllotaxies are described in fractions such as 5/13, in which case 13 leaves would occur in five rotational cycles around the stem moving forward at a given angle (137.5°). Most plant phyllotaxies follow the Fibonacci series of numbers where the next number in the series is the sum of the previous two. The arrangement of leaves is also mirrored in the vascular strands that connect inside the stem which have their own similar arrangement. The phyllotactic arrangement of leaves is a natural way to optimize leaf locations for absorbing the most possible solar radiation.

Trees produce both sun and shade leaves depending on their canopy location, exposure to sun, and genetics. *Ficus benjamina* is infamous for being a touchy house plant when moved from a shady to a sunny location, because it has either sun or shade leaves and will shed them when it is moved to a location with higher or lower light intensity. The palisade mesophyll is laid down with multiple layers when light intensity is high and or a single layer of cells when it’s low.

**Leaf movements**

Although you don’t notice it, leaves move throughout the day to take advantage of available light. Generally, they turn in accordance to the movement of the sun to align with incoming photons. By optimizing their angle to the sun, the maximum number of photons are collected throughout the day. Leaves can also fold or turn downward when the tree is subjected to water deficits, to minimize solar exposure, reducing the water needed to cool the leaves. Cupping or folding also increases humidity around the leaves and reduces the transpirational water potential gradient, thus slowing water loss.

**Mineral accumulation and leaves role in tree mineral nutrition**

Over their lifespan, leaves transpire thousands of gallons of water. Solutes dissolved in water are taken up by the roots and moved upward within the sap stream to the foliage. These nutrients, once they reach the leaf mesophyll, can be used in photosynthesis and other metabolic processes. Most of the mineral salts in the transpiration stream are left behind when water evaporates, and is transpired through the stomates as water vapor. In time, leaves accumulate salt. Some of these minerals may be mobilized out of older leaves and utilized in the growth of new leaves. Macronutrients within plants are often mobile and can be extracted from the leaves before they die and are shed. Residual salts left behind in leaves become part of the soil mineral content as they decompose. It’s rare for trees to require fertilization because they are generally able to obtain adequate amounts of minerals and other nutrients from the soil. Trees are actually fertilized, if you will, by the dusts that accumulates on their foliage and stems, and air pollutants scavenged (adsorbed by the leaves) from the atmosphere. The composition of dust that settles on trees includes significant amounts of N, P and K that wash into the surrounding soil when it rains, becoming part of the soil minerals pool available for uptake.

**Leaf retention: deciduous vs evergreen**

The term deciduous is used to describe trees that shed leaves at the end of each growing season and replace them at the beginning of the next growing season (Fig. 23). Most broadleaf (hardwood) trees and a few conifers have deciduous canopies. Deciduous canopies confer advantages in temperate and northern climates. Deciduous trees survive freezing winters without damage to their leaves. Deciduous trees also reset the ‘internal clock’ with respect to leaf salt-levels. Thus, the new (regenerated) leaves can transpire and photosynthesize without the burden of high salinity inside them. Deciduous trees drop an enormous amount of
biomatter throughout the year especially in the fall, insulating the roots from freezing temperatures that will soon follow. Additionally, the lack of foliage minimizes the amount of heavy snow that can collect within the crown, greatly reducing snow loads that can break branches. Leaves damaged by environmental factors as well as insects and disease-causing pathogens are also replaced. Before leaves are naturally shed, some of the leaves’ mobile mineral nutrients are relocated to the stems for later use.

Evergreen trees maintain their leaves for a set number of years—usually 2 to 5 years. Their leaves are usually smaller, thicker, and waxier than those of deciduous trees. All leaves eventually senescence, and fall from the canopy. Many evergreen trees produce a series of flushes of new leaves, as they gradually lose older leaves throughout the year. Some evergreen trees constantly produce new leaves as the older ones die and fall away.

**Effect of leaves on the canopy**

As leaves photosynthesize, they lose (transpire) water to the atmosphere. To take in carbon dioxide, the stomata must be open, and water vapor escapes from the leaves during transpiration. The phase change of water going from a liquid to a vapor helps dissipate heat from exposure to the sun, keeping the leaves cool. The increases in water concentration in the atmosphere around the tree increases relative humidity, effectively reducing water loss from leaf surfaces. A full complement of leaves helps to maintain a cooler canopy, especially during the hottest part of the summer. Leaves also provide shade for the main stem and scaffolds, preventing sunburn damage to thin-barked species and keeping epicormic buds dormant during the growing season (Fig. 24). A full canopy of leaves will provide more energy for wound closure, particularly pruning wounds.

**Litterfall**

As leaves are shed in the fall or throughout the year, the remaining organic matter in the ‘litterfall’ comes to rest on the soil under the tree. Fallen leaves, twigs, flowers and fruit provide an important source of organic matter and mineral nutrients vital to normal tree health and function. Let’s not forget, though, that this litter is a critical carbon source for soil microorganisms that flourish within the root zones of perennial plants, particularly those where the litter is allowed to remain and decompose naturally. Much of the nutrients and energy contained in the organic matter are taken up by the soil organisms, but are released back to the soil when they die. Once that occurs, the minerals are released and can be absorbed by the roots of trees and other plants. The organic matter that gradually becomes incorporated in the soil, improves soil structure by separating clay colloids, and more indirectly through the activity of mycorrhizal fungi. These fungi, which commonly associate with tree roots to obtain sugar, can also access the carbon in leaf litter, causing the smallest soil particles to adhere to each other. This creates small voids between the aggregates which in turn, improve soil porosity. The accumulation, decomposition and gradual incorporation of organic matter into the soil ultimately improves soil porosity, aeration, gas exchange, water-holding capacity, and mineral content. The net effect is that the roots grow better, and the canopy is healthier. The take away message is: allow the litterfall to collect under trees, as much as possible. Let tree leaves remain under and around trees to decompose as nature intended.

**Reference:**


Dr. James Downer
Environmental Horticulture Advisor, UC Cooperative Extension, Ventura County

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You may receive one hour of Certified Arborist and/or WCISA Certified Tree Worker continuing education units (CEUs) for reading the following article and completing the test questions. Copy the question pages and use it to record your answers. Darken the correct letter choices and circle your choice for true and false or correct choice questions. Each question has only one correct answer. Passing score for this test is 24 correct answers (80%).

Next, complete the registration information on this form and send it to:

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2019 Regional Conference Schedule

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TRAQ Certification & Exam Schedule

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Fall courses coming soon
Home study for CEUs: Botany for arborists: Leaves

Summer: June 30, 2019 – Expiration date for submitting answer sheet is July 1, 2020. The CEUs from this article can only be applied to the 3-year current certification period.

1. Although the bark of some trees is green, photosynthesis is conducted solely in the leaves. T or F?

2. Sugar produced during photosynthesis is stored as? ___________________________ in living cells until needed.

3. Name the type of cells where the energy contained in the sugar is not needed immediately to sustain living cells is stored. ___________________________

4. Name the three distinct tissues found in leaves. ___________________________ ___________________________ ___________________________

5. Most leaves are attached to developing shoots via a? ___________________________

6. Leaves that are completely divided to the midrib (rachis), forming separate leaflets or pinnae are said to be? ___________________________

7. What term is used to describe leaves that have a second rachis and rank of leaflets? ___________________________

8. Leaves that are divided into pinnae that originate from a central point are referred to as? ___________________________

9. Generally leaves are larger in arid climates and smaller in wetter (temperate and tropical) climates. T or F?

10. Yellow, orange, red, or dark purple pigments often mask the green color imparted by chlorophyll. T or F?

11. Species adapted to hotter and dryer climates, and coastal or windy locations typically have thick leathery leaves. T or F?

12. What term is used to describe a waxy coating on leaves that serves to increase light reflection and decrease water loss? ___________________________

13. Stomata (pores), are found primarily in the upper epidermis of leaves. T or F?

14. Name the small natural opening (pores) found in leaf surfaces that regulate gas exchange between the atmosphere and the intracellular spaces within the leaf. ___________________________

15. These openings primarily in the epidermis of leaves, open and close in response to light, humidity, and water availability. T or F?

16. Trichomes, hairlike outgrowth from the epidermal cells of leaves, are known to increase leaf reflectance and minimize water loss. T or F?

17. The oxygen that diffuses out of the leaves during photosynthesis is produced when water is split into its basic components—oxygen, hydrogen ions, and free electrons. T or F?

18. Electrons released during the early phase of the photosynthesis process are combined into intermediary compounds in the later Calvin cycle process which involves the uptake of carbon dioxide and ultimately formation of glucose (energy). T or F?

19. Plants can only photosynthesize when their stomates are open and water is transpiring from the leaves. T or F?

20. Leaf veins contain strands of xylem that supply water to the leaf, and phloem that transports photosynthesize (sugars) from the leaf to other living cells throughout the tree. T or F?

21. When two leaves or buds are located at the same node on a twig or shoot, the arrangement is called? ___________________________

22. The uppermost mesophyll layer is called the? ___________________________

23. Name the three basic arrangements of leaves (phyllotaxies). ___________________________ ___________________________ ___________________________

24. Leaves move throughout the day to change their position with respect to the sun. T or F?

25. Macronutrients within leaves are often immobile and can’t be recycled before they die and are shed. T or F?

26. To take in carbon dioxide, the stomata must be open, allowing water vapor to escape from the leaves during transpiration. T or F?

27. The change of water going from a liquid to a vapor helps dissipate heat from exposure to the sun, keeping the leaves cool. T or F?

28. In general, thinning is a good practice to judiciously manage a tree’s canopy. T or F?

29. The removal of litterfall within the root zones of trees tends to have little or no influence on the soil and microorganisms that flourish within the root zones of plants. T or F?

30. Transpiration and photosynthesis occurs even if the stomates remain closed. T or F?