Botany for arborists: Energy and trees

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Energy capture

The sun bathes the earth in waves of radiated energy. The waves of radiation occur along the electromagnetic spectrum that includes microwaves, radio waves, visible light, and infrared heat. The visible portion of that spectrum is the rainbow formed by sunlight passing through a prism. Solar energy is increasingly used to power our homes, offices, and businesses. Trees and other green plants have been using solar energy for many millions of years. Plants use that radiant energy to make and break chemical bonds that provide the energy needed for growth and survival. Much of the solar radiation that reaches the earth's atmosphere is reflected or diffused. Less than 0.1% is available for plants. Of the light that actually reaches the leaves, about 1.5% is used to fuel plant growth.

Leaves capture solar energy in the process of ***photosynthesis*** that converts radiant energy into chemical energy (**Fig. 1**). The end product of photosynthesis is the sugar *glucose*. Glucose is converted into other sugars, such as sucrose for translocation throughout the plant. These sugars are collectively known as ***photosynthate***. Other plant parts such as young branches or cortical cells just beneath the epidermis or thin bark can also photosynthesize (**Fig. 2**). In regions with very short growing seasons, such as subarctic forests and arid deserts, stem and branch photosynthesis may provide a significant share of total energy captured.

Photosynthate moves to the furthest root tip and eventually the soil immediately around the roots, feeding beneficial mycorrhizal fungi and free-living soil microorganisms. This transformed solar energy then becomes part of the soil matrix and the living web of soil organisms. In this way, trees energize the environment around them. Even in death, trees are a source of energy. As trees shed leaves, flowers, branches, and roots, or when the stem itself dies or falls, the energy bound in the plant parts becomes an energy source for saprophytic bacteria and fungi. As plant parts decompose, they provide food as well as habitat for many invertebrates and other animals.

The cellular machinery that performs photosynthesis is in ***chloroplasts*** — small green structures

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Figure 1. Closeup of the leaf surface of *Acer saccharum* (sugar maple)

Figure 2. Photosynthesis in bark furrows of *Ceiba speciosa* (floss silk tree).

within the photosynthetic ***parenchyma*** cells that comprise much of the leaf volume. Parenchyma cells are relatively small, thin-walled, and roughly uniform in size. Many parenchyma cells in the living tissues lack chloroplasts, and function to store energy, produce hormones, and defend against pathogens, insect pests, and mechanical damage.

Within the chloroplasts are highly ordered membrane structures that support various parts of the photosynthetic process. The collection of photosynthetic parenchyma within the leaf is the ***mesophyll***. The photosynthetic cells in the upper or ***palisade mesophyll*** are tightly packed in an upright orderly array and are primarily concerned with light interception. The cells in the lower ***spongy mesophyll*** layer are much less ordered and contain open spaces between some of the cells. They are primarily concerned with gas exchange.

Energy flow and element cycling

Let's take a closer look at the flow of energy and mineral elements in trees as well as the living world. Of the 92 chemical elements that naturally occur on earth, 16 are proven to be essential for all flowering plants, including trees. A few other elements have been proposed, but are not yet accepted as essential by the consensus of biological chemists. Advanced physics teaches us that ultimately, energy and matter are interconvertible. For living systems, it's convenient to think of ***matter*** as the physical arrangement of chemical elements, and ***energy*** as the property to perform the work of moving matter. For living systems, energy is contained within the bonds of chemical compounds. Organisms make use of these compounds to grow, reproduce, and survive.

Photosynthesis is the pathway for the capture of energy and the bulk of the physical matter in trees and other green plants. There are two parts, with the first involving the capture of solar energy to split the chemical bonds of water (H_2O) into hydrogen and oxygen, and to transfer that solar energy into short-lived high energy chemical compounds (**Fig. 3**). The second part uses those high energy compounds to split carbon from atmospheric carbon dioxide (CO_2) and to recombine the carbon with the oxygen and with the hydrogen from water to eventually form a molecule of glucose sugar ($C_6H_{12}O_6$). Energy is stored in the chemical bonds, particularly the bonds that link carbon to carbon. Oxygen released from H_2O during photosynthesis diffuses out of the leaf into the atmosphere. *Respiration* is the collection of biochemical pathways that release energy stored in those chemical bonds and cycles CO_2 back to the atmosphere. Some carbon compounds are sequestered for long periods in wood and organic matter in soil. Respiration occurs not only in trees as they use their sugars for metabolism, but in the soil as leaves and woody debris are decomposed by the microbial community, releasing bound energy. Humus, the organic matter that remains in the soil following decomposition, resists further degradation, and may persist in the soil for long periods. Humus serves to increase soil water-holding capacity and to store essential potassium, calcium, and magnesium.

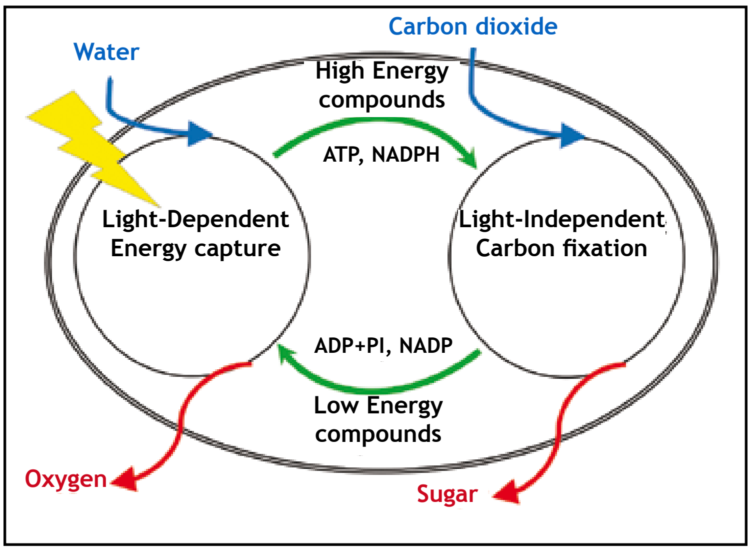

Figure 3. Sketch of photosynthesis showing the two sets of reactions (circles), the entry of solar energy (bolt), the uptake of water and carbon dioxide, and the production of oxygen and sugar.

The three dominant elements (carbon, hydrogen, and oxygen), comprising about 98% of a tree's dry weight, enter during photosynthesis. Carbon, which makes up about half of that weight, is obtained from the carbon dioxide in the atmosphere. Almost half of the remaining weight is composed of oxygen and hydrogen, derived from water. Just as essential for the living tree, but required in much smaller amounts, are nitrogen (about 1%) and the remaining dozen elements (collectively about 1%). In a simplistic way, the heat given off by the burning of leaves or wood demonstrates the energy contained within those plant parts. The residual ash after complete combustion contains the mineral elements that were not volatilized by the heat of burning, most of these derived from soil.

Metabolism and biosynthesis

The sugar from photosynthesis is the ultimate feedstock for all the structural and energy needs of trees. Those needs are met through *metabolism*, the chemical processes that occur within living organisms to sustain life. Traditionally, the term ***primary metabolism*** refers to processes of normal growth, development, and reproduction.

Secondary metabolism refers to additional chemical pathways with specific functions including tree defense. Both primary and secondary metabolism are essential for tree survival. The metabolic shifts result from "turning on" or "upregulating" portions of the genetic program to change the amounts and specific enzymes produced. Metabolism constructs all parts of the tree through ***biosynthesis***. The major products of biosynthesis are carbohydrates, proteins, lipids, and nucleic acids.

The transformations of sugar for structural growth and energy needs all involve chemical catalysts known as ***enzymes***. Enzymes often require small amounts of mineral elements such as phosphorous and magnesium as cofactors. Through enzymatic activity, photosynthate is converted into other simple sugars and more complex ***carbohydrates***. Carbohydrates include simple sugars (monosaccharides such as glucose and fructose), disaccharides made up of two simple sugars (e.g., sucrose), and polysaccharides made up of long chains or ***polymers*** of linked simple sugars (e.g., cellulose, starch).

The precise nature of the linkages in the sugar polymer can determine major differences in the function of the carbohydrates. For example, both ***starch*** and ***cellulose*** are unbranched polymers of glucose that differ in the orientation of the bonds that link adjacent glucose molecules. Starch is an energy storage material that can be coiled and packed into living cells. Starch is readily broken down for future release of energy as needed. Cellulose consists of long straight chains that are further combined into microfibrils that resist mechanical tension and that provide the structure for plant cell walls. Cellulose can only be broken down by a relatively small group of fungi and bacteria.

Enzymes are primarily chains of ***amino acids*** assembled into ***proteins***, a group of water-soluble compounds based on a sugar backbone with attached nitrogen. Enzymes are catalysts that help make and break chemical bonds and transport ions and other materials across membranes. Much of the nitrogen in trees is contained in enzymes. The precise structure of enzymes are determined by the genetic program, contained within living cells. The instructions of the genetic code are recorded in chains of *nucleic acids*. They, too, are comprised of a sugar backbone enriched with phosphorous and nitrogen.

Another group of metabolites derived from sugar are ***lipids***. Lipids include fats and are generally insoluble in water. Lipids perform important gatekeeper roles in cell membranes and cell walls. Lipids are involved in both normal growth and induced tree defense through the formation of waterproofing layers (*suberization*) in bark, leaves, stems, and roots.

In mature trees, the bulk of the dry weight is composed of *wood*. Wood is a composite material, largely composed of tightly packed and unbranched chains of cellulose entangled with chains of ***lignin***. Lignin is a complex and branched polymer that contains ***phenols***, rings of carbon molecules diverted away from amino acid biosynthesis. Lignin is even more difficult to degrade than cellulose and adds rigidity and compression strength to wood. Non-woody plants such as grasses and the non-woody foliage and bark of trees all contain cellulose and lignin in their cell walls. Although the structure of cellulose is the same for woody and non-woody plants, the chemical makeup of the building blocks for lignin vary among plant groups.

Plant defense frequently involves secondary metabolites. Some metabolic shifts are part of normal growth and maturation such as heartwood formation. Other shifts from primary to secondary metabolism result from challenges by pests, pathogens, or mechanical injury. Whether part of normal growth or induced by challenges, energy is diverted from normal growth processes and applied to produce ***plant hormones*** (natural growth regulators), ***phenols*** (such as tannins) and ***terpenes*** (the primary constituents of pine resin). Phenols are most abundant in broad-leaved trees while conifers rely primarily on terpenes. Both groups, though, produce these two classes of compounds. When tree energy reserves are low, production of secondary metabolites for induced tree defense may be sluggish or non-existent, increasing the vulnerability of the tree to pests, pathogens, and abiotic stress.

Evergreen and deciduous solar collectors

Leaves are collectively referred to as ***foliage***. Conifers and many tropical trees are typically evergreen and retain their foliage throughout the year. Broadleaved trees, with some exceptions, have deciduous foliage which is shed each year. In the temperate zone, foliage is shed in response to the shorter day lengths and cooling temperatures of autumn. Seasonal moisture stress frequently initiates foliage shedding in Mediterranean, monsoonal, and tropical species.

The leaf is the usual site of ***evapotranspiration***, where the liquid water within the internal transport system evaporates, providing the force to pull water (and dissolved essential elements) from the soil into and upward in the tree vascular system. The leaf surface contains pores or stomata which regulate the flow of gases including water vapor into and out of the leaves. The pattern of stomata in leaves varies with plant species. Stomata are usually more numerous on the lower surface than on the upper surface. This reduces the exposure of stomata to the drying effects of sunlight. Stomata open and close in response to environmental conditions, or as determined by plant metabolism. This represents a trade-off between growth and water conservation. The uptake of CO_2 for photosynthesis can only occur when the stomata are open. Open stomata also allow water to evaporate from the leaves, cooling the leaf surface. Evaporative cooling prevents leaf injury during hot weather, and is essential for photosynthesis in sunlit leaves in warm environments. Photosynthesis tends to slow down at temperatures greater than 90°F (32°C).

Because water loss occurs when the stomata are open, trees under moisture stress close their stomata during the day and only open them at night. The trade-off, though, is reduced CO_2 uptake. This is why trees under moisture stress capture less energy and exhibit less radial growth and shoot elongation. The total amount of CO_2 incorporated into sugar ("fixed") per unit of water lost is termed water use efficiency (WUE). The ratio of water molecules transpired to carbon dioxide molecules fixed is typically large, about 400 molecules of water per molecule of CO_2. Some weeds, grasses, and desert shrubs have modified some of the intermediate steps of photosynthesis to improve their WUE beyond that of more temperate trees. As global atmospheric carbon dioxide concentration rises, tree WUE may rise as well, because increased CO_2 favors normal photosynthesis.

Figure 4. Effective compartmentalization of drill wound in *Acer saccharum* (sugar maple).

Energy storage and compartmentalization

Photosynthate is usually transported by the phloem, from the foliage to where the energy is used or stored. In temperate zone trees, the energy translocated as sugar is stored as starch in sapwood parenchyma, particularly in the wood rays. Starch stored in woody branches, stems, and roots provides a ready reserve of energy to break bud dormancy and to fuel new cell divisions for root and cambial growth early in the growing season, and to sustain shoot elongation, leaf emergence, and maturation. Stored energy is also used for active plant defenses including the ***compartmentalization*** process.

Compartmentalization is a conceptual model of how trees grow and defend themselves from injury and infection. Compartmentalization is a boundary-setting process that resists the loss of normal tree function and the spread of infection. Energy stored as starch in wood parenchyma is critical for effective compartmentalization. After injury from, say, the breakage of branches, stems or root severance, waterproofing and antimicrobial compounds are synthesized from locally stored starch that help to seal off the wounded area from the living sapwood (**Fig. 4**). Wood formed by the vascular cambium after injury is structurally and chemically altered and becomes an effective "barrier zone" to resist the outward spread of infection towards the vascular cambium.

When energy runs out… Geriatric trees and energy flow

Old trees accumulate a lifetime of responses to injuries and insults. This is especially true for trees in urban environments. As trees age, branches, stems, and roots are injured from storms and human activity, including tree care practices. The foliage and woody parts of the tree are attacked by various insect pests. Microorganisms may cause cankers, blights, rots, and wilts. Soil may be washed away or compacted around the root system. Repeated injuries, root loss, defoliation or adverse environmental conditions result in trees with less foliage. Large trees may contain extensive decay and cavities. With fewer leaves, the tree draws energy from the remaining sapwood to support basic metabolic functioning. The sapwood is not easily replenished with starch because there are fewer leaves and more disrupted connections in the phloem between foliage and where the energy is needed or would be stored. Since basic metabolism has priority for stored energy, there may not be enough to support secondary metabolism to maintain natural defenses against insect pests and disease pathogens. This spiral of decline continues with shrinking amounts of foliage, and the tree may succumb to secondary pathogens or insect pests.

Figure 5. Nurse log and advanced regeneration of *Picea sitchenis* (Sitka spruce).

Some trees are able to maintain themselves by 'shedding' large branches followed by epicormic sprouting from the lower stem or other branches. In this manner, the tree develops a new, smaller crown. Because the tree is now smaller with reduced energy needs, the new but smaller crown can support the tree. In a stable, and reasonably favorable environment, such trees can survive and contribute to the landscape for decades. Stressful urban environments typically result in a steep decline spiral of reduced energy availability and increased vulnerability to pests, pathogens, and environmental stress. For trees that are severely stressed, even low levels of additional infection or increased stress can result in tree mortality. Weak pathogens have their chance to kill a tree.

In nature, the energy trees capture during their lifetime is used for growth, metabolism, and, to a lesser extent, the maintenance of their mycorrhizal partners. The leaf litter and fallen branches that accumulate under trees is an important source of energy for the soil microbes that quickly decompose the material, releasing bound minerals back to the soil. Fallen trees, however, take much longer to decompose, and, thus, are important because they gradually release nutrients to the soil, encouraging seedling development and survival. (**Fig. 5**). Nonetheless, the natural decomposition of woody debris or the application of wood chips or other organic matter to the soil is critical to maintain the health and diversity of the soil microbes that help sustain trees and other vegetation.

When a tree in a forest or grove dies, falls, or is removed, access to sunlight improves, allowing trees and other plant seedlings to germinate and capture enough light energy to become established. In this manner, the flow of energy and the cycling of matter continues to maintain the forest ecosystem.

Additional reading:

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