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EC1268

Plant Growth Processes: Transpiration, Photosynthesis, and Respiration

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Knowledge of the basic plant growth processes, including photosynthesis, respiration, and transpiration, is important for gardeners and professional landscape managers to understand how the growing environment and management practices influence plant growth and development. Each of these plant growth processes relies on water to carry out their functions.

The Life Giving Properties of Water

Water is all around us! Most of the Earth's surface is covered in water. Plants and animals are mostly made of water and all the chemical reactions of life take place in aqueous solution inside plant and animal cells (*Figure 1*). Water has some unique properties; it resists temperate changes, dissolves molecules of life, and allows gas exchange. All of these characteristics are essential for life on earth and they all depend on one chemical property of water that few other liquids share: hydrogen bonding. Water molecules have positive and negative poles that make them bond to each

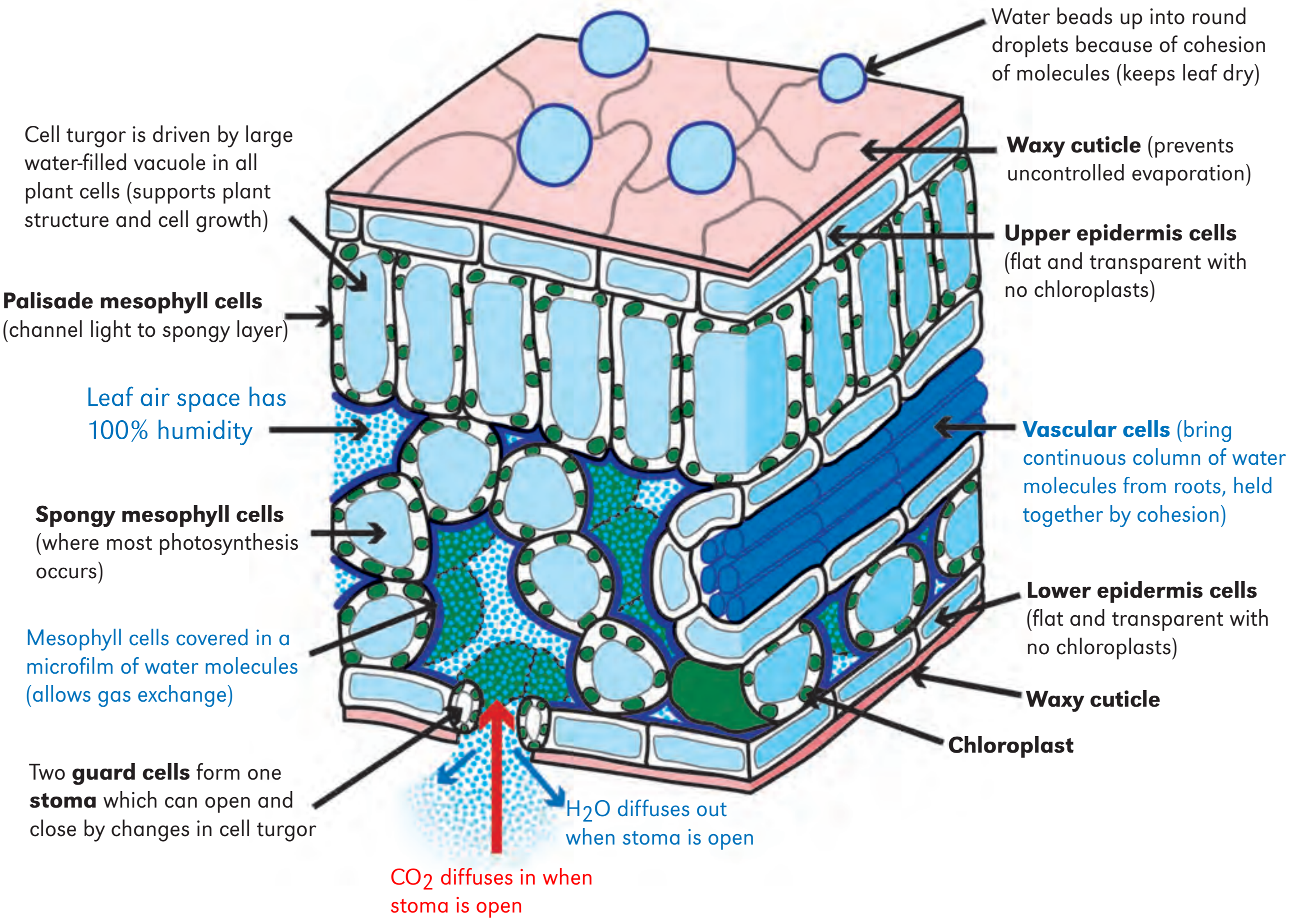

Figure 1. Cells are the fundamental unit of all living things. All plant cells contain the same basic makeup of a nucleus, cytoplasm, organelles, cell membrane, and a cell wall. Many water relationships exist within plant leaves.

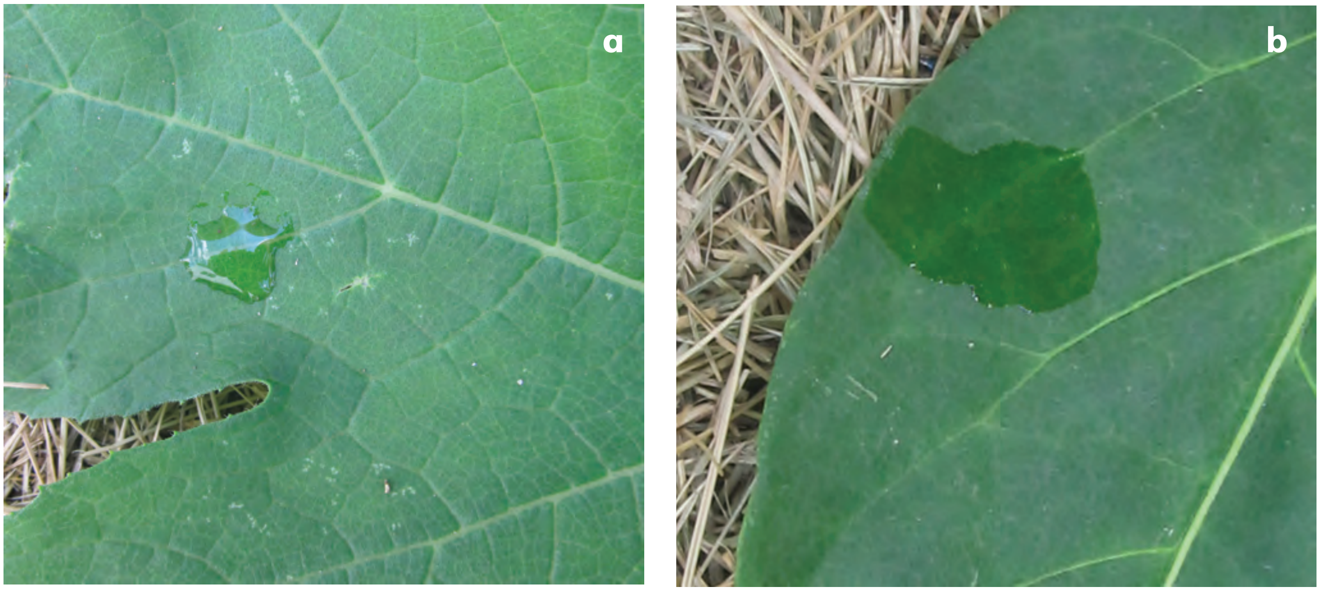

Figure 2. Water will bead up or form thin films depending on the nature of the surface. On hydrophobic surfaces, such as leaf surfaces, water beads up due to its cohesive characteristics (a). On hydrophilic or polar surfaces, such as the inner leaf surface of cells and root hairs, water spreads out to form a thin film. Products can be added to fertilizers and pesticides to lower surface tension of the water on the leaf and in the soil and increase adhesion. This flattens the droplet and allows for better absorption of the fertilizer, pesticide, or water, similar to what is observed on hydrophilic surfaces (b).

other temporarily in a process called hydrogen bonding. The unique physical properties of water allow it to do the following functions in plants:

- **Regulate Temperature.** Water is resistant to temperature changes and stays in the liquid form over a broad range (from 0°C to 100°C or 32°F to 212°F). Large bodies, like oceans, are the most stable and are able to resist extreme temperature changes; lakes, rivers, streams and puddles are increasingly less resistant. The same size ratio applies to living things; elephants and giant sequoia trees are very good at resisting temperature change, while mice and small plants have to work harder to keep a stable temperature. As water evaporates from the leaves of plants, heat energy is lost and the plant cools down.

- **Dissolve Molecules of Life.** Water is one of the most versatile solvents for dissolving the molecules of life. Most of the small and large molecules that plants and animals need for life are dissolved in water. Small molecules like carbon dioxide (CO_2) and oxygen (O_2) must dissolve in water to enter or leave plant or animal cells; mineral nutrients in the soil must dissolve in water to be taken up passively by plant roots; medium-sized molecules needed for plant growth, such as sugars, amino acids, ATP (adenosine triphosphate) and hormones, easily dissolve in the water making up plant and animal cells; and large macro-molecules, like DNA, protein and complex sugars, are covered in positive (+) and negative (–) charges and can be surrounded and dissolved by charged water molecules.

- **Allow Gas Exchange.** Cohesion, or sticking of water molecules to each other, combined with adhesion, sticking of water molecules to polar surfaces, allows water to form very thin films (*Figure 2*). This is essential for gas exchange between the air and the inner surface of leaf cells. **Mesophyll cells** in leaves are the primary location of photosynthesis. In the leaf air spaces, each mesophyll cell is covered in a thin film of moisture allowing water and oxygen to leave the cells and carbon dioxide to enter the cells.

Water and Transpiration

Transpiration is the movement of liquid water into, through, and out of the plant (*Figure 3*). Water lost through transpiration enters the plant through the roots, moves up through the stem in the xylem, and exits through openings in the leaf called **stomata**. Cohesion and adhesion create the property of capillarity, which allows water molecules to rise up against the forces of gravity. This works only as long as the water is constrained in tubes with a large surface area. Surface area is what the xylem tissue of plants provides, lots of very narrow interconnected tubes.

Environmental Change	Transpiration Response	Reason
↑ Light	↑ Transpiration	Light causes most stomata to open
↑ Temperature	↑ Transpiration	Warm air hold more moisture
↓ Soil water	↓ Transpiration	Less water enters the plant roots
↑ Wind	↑ Transpiration	Reduces humid boundary layer around the leaf
↑ Humidity	↓ Transpiration	Air moisture gradient is not as steep

Figure 3. The rate of transpiration is affected by several environmental conditions.

The xylem tissue of vegetative plants or the lignified (woody) tissue of trees is made of the cell wall remnants of elongated cells that the plant sacrificed through a process called programmed cell death. Transpiration is essential for:

- **Evaporative cooling.** Plants are able to keep cool when they are in direct sunlight through the evaporation of water that occurs in transpiration. As water changes from the liquid to gas phase, heat energy is lost and the plant is cooled. Plants rely on transpiration for evaporative cooling so that despite being exposed to direct sunlight, their tissues do not overheat. On which surface would you rather play soccer on a 100°F day — grass or artificial turf?

- **CO_2 acquisition.** All the carbon incorporated into carbohydrate through photosynthesis comes from atmospheric CO_2 entering through pores in the leaves called stomata. Water loss through the stomata is a continuous process that occurs as long as stomata are open. Plants are able to close their stomata to restrict water loss during times of drought or high temperature, but this directly reduces photosynthetic output because less CO_2 enters the leaves.

- **Maintaining turgor.** Since 90 percent of plant tissues constitute water, the structure of plant tissues depends on cell turgidity and since plant cells are leaky, water needs to be continually taken up (think of a plant cell like an inflated tire with a puncture). Cell expansion, a driving force of growth, is also driven by cellular water pressure.

- **Mineral nutrient uptake.** In addition to carbon assimilation from the air, plants incorporate mineral nutrients dissolved in water taken up from the soil. These are distributed throughout the plant by way of the transpiration process.

Figure 4. Photosynthesis uses water and mineral nutrients from the soil, CO_2 from the air, and light energy from the sun to create photosynthates (sucrose and starch) used in respiration or are stored. Oxygen is a byproduct of the light reactions in photosynthesis.

The Role of Photosynthesis and Respiration in Energy Generation in Plants

All life on earth depends on plants. Plants are **autotrophic**, meaning they can convert simple molecules like CO_2 from the atmosphere and minerals from the soil into the complex carbohydrates, proteins, and fats, forming the basis of living organisms. The most important set of chemical reactions in plants harness the energy of sunlight in the process of **photosynthesis** which generates sugar, oxygen, and a molecule called ATP (*Figure 4*). ATP is energy in its simplest form and powers the chemical reactions that support life in both plant and animal cells. Animals

Photosynthesis	Respiration
Occurs in chloroplasts	Occurs in mitochondria and cytoplasm
Uses light energy (sun)	Uses chemical energy (ATP, NADPH)
Uses low energy, unreactive CO_2	Uses high energy, reactive carbohydrate
Building process	Breaking-down process
Uses H_2O	Produces H_2O
O_2 is released from splitting of water	Uses O_2
Produces carbohydrate (sugar)	Produces CO_2
Occurs only under light (sun or artificial)	Occurs with and without light

Figure 5. Although the chemical processes of photosynthesis and respiration are very different and involve different parts of the cell, they can be thought of as essentially opposite reactions.

are **heterotrophic,** meaning that they must consume macronutrients, carbohydrates, proteins, and fats in their diets. Ultimately all these compounds are derived from plants. The ATP that animal cells use for energy comes from the process of **respiration** powered by the chemical energy of sugar, also derived from plants. Plant cells also use respiration to make ATP. This occurs all the time, day and night, even when the sun is not shining.

Although the chemical processes of photosynthesis and respiration are very different and involve different parts of the cell, they can be thought of as essentially opposite reactions (*Figure 5*). Photosynthesis uses sunlight to drive chemical reactions that are thermodynamically unfavorable (requires energy to occur), while respiration is a thermodynamically favorable set of reactions (releases energy). The carbohydrate is ‘burned’ in a controlled way to release the energy as ATP instead of just heat energy as would happen if it were just ignited in air. The classic chemical reaction ($CO_2 + H_2O \rightarrow C_6H_{12}O_6 + O_2$) commonly written for this reaction is just a summary of many different chemical reactions.

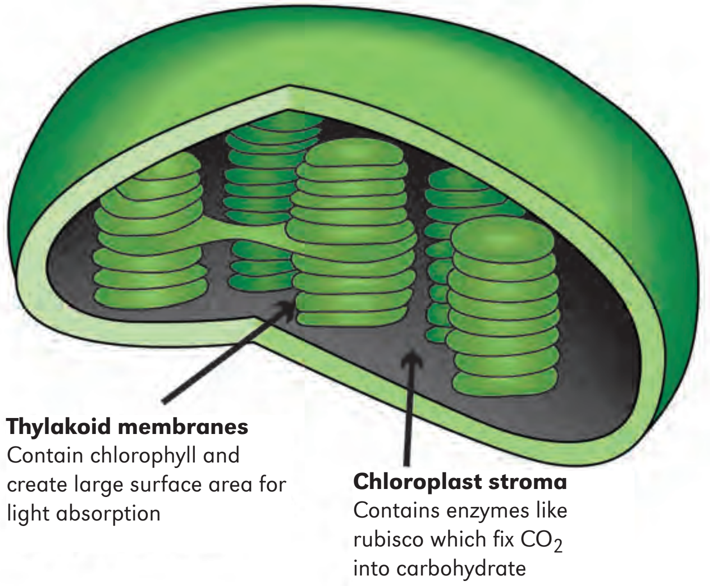

Figure 6. Photosynthesis occurs in the chloroplast; the light reactions in the thylakoid membranes and the carbon reactions in the stroma.

The Basics of Photosynthesis

Photosynthesis literally means “to put together with light.” All of the reactions of photosynthesis happen inside chloroplasts. Chloroplasts are small organelles that are green because they contain chlorophyll. Mesophyll cells in the leaves and stem contain many **chloroplasts,** each having a highly ordered array of membranes arranged in stacks (*Figure 6*). These stacks are called **thylakoid membranes** and are solar panels with a large surface area that organize chlorophyll and pigments called **carotenoids** that can collectively absorb and utilize light energy (*Figure 7*). Photosynthesis has two distinct parts:

- **Light reactions.** The light absorption part of photosynthesis is referred to as the light reactions. It relies on energy from the sun, so it

Figure 7. Chlorophyll (green) and other carotenoid pigments such as lycopene (red), carotene (orange), and zeaxanthin (yellow) are found in plants, and are used in the light reactions. The colors of the other pigments are seen only in plant tissues without chlorophyll, such as fruits or fall leaves after chlorophyll production has slowed or stopped and the colors of the other pigments are unmasked.

occurs only during the day in the thylakoid membrane of the chloroplasts. In the light reaction, water is split and oxygen released, but more importantly, it provides the chemical energy to fix CO_2 into carbohydrate in the carbon reactions.

- **Carbon or dark reactions.** The carbon reactions occur in the matrix of the chloroplast called the stroma and uses protein types called enzymes. The most important enzyme in this process is called rubisco. Rubisco is the most abundant protein in plants and therefore, the major consumer of nitrogen. This is why when plants are deficient in nitrogen, they are not productive and turn yellow because they stop photosynthesizing. The dark reaction creates three carbon sugar products that leave the chloroplast for use in respiration and sucrose (common table sugar) synthesis. The sucrose is converted to starch or shipped out to other parts of the plant for storage or growth through the phloem.

Photorespiration

In order to extract CO_2 from the air, rubisco needs to have a high affinity for it (CO_2 makes up only 0.04 percent of air). However, rubisco also binds significantly to O_2 gas which makes up a much higher percentage of air (21 percent). When rubisco binds O_2, a wasteful process called photorespiration (not to be confused with respiration) occurs. Photorespiration diminishes photosynthetic output because it actually produces CO_2 rather than fixing it into carbohydrate. The negative effects of photorespiration result from a plant's reduced ability to maintain a favorable CO_2 gradient into the leaf air spaces. Most types of plants (C3 plants, see below) respond to increased photorespiration by opening their stomata more to compensate for the unfavorable CO_2 gradient. This has severe consequences for C3 plants under hot or water restricted conditions.

Photosynthetic Variations of the Carbon Reactions

Plants are classified based on how they complete photosynthesis. The dark reactions described above are found in more than 95 percent of the plants on Earth. They are called **C3 plants** because the first organic molecule that CO_2 is incorporated into is a three-carbon molecule. Two variations of the carbon reactions have evolved in angiosperm plants as ways to get around the problem of photorespiration. They are:

- **C4 photosynthesis.** Plants with C4 photosynthesis include corn, buffalograss, and many weedy grasses including crabgrass (*Figure 8*). It is called C4 photosynthesis because the first organic molecule that CO_2 is incorporated into is a four-carbon malate molecule. These C4 plants minimize photorespiration and water loss through a specialized cellular architecture in the leaves: light reactions occur in one cell type and the carbon reactions occur in cells called bundle sheath cells not in direct contact with the air. Plants with C4 photosynthesis are able to achieve high rates of photosynthesis with their stomata only slightly open which minimizes water loss. They often look better than C3 plants during hot dry conditions because they are able to protect the plant from high water loss by closing their stomata.

- **CAM photosynthesis.** Plants with crassulacean acid metabolism (CAM) photosynthesis, such as cacti, all succulents, and purslane, minimize photorespiration and water loss by keeping their stomata completely closed during the day so no water is lost (*Figure 8*). This also means they cannot take in CO_2 during the day. To get around this, CAM plants take in CO_2 through the stomata at night and store it as a molecule called malate. Then during the day, with the sun shining and the stomata closed, rubisco coverts the malate to useful carbohydrate. Although this enables CAM plants to grow in extreme heat and be extremely water efficient, they have low photosynthetic productivity — they grow slowly!

Respiration

Respiration takes sugar either directly from photosynthesis or from breakdown of storage compounds like starch or lipids (oils), and uses its stored chemical energy to make energy currency (ATP). The whole process of respiration can be divided into several different steps. The first part is called glycolysis which literally means sugar splitting. This occurs in the cytoplasm of the cell and does not use oxygen and produces a small amount of ATP. Glycolysis also serves as the central primary metabolic pathway on which most other secondary metabolic pathways depend. This means that crucial plant biomolecules such as proteins, lipids, starch, cellulose, DNA, RNA, chlorophyll, other pigments, plant hormones, and many others are all intricately related with metabolic flux through glycolysis. The other parts of respiration occur in specialized organelles called mitochondria. This is where the bulk of the ATP is released in processes requiring oxygen.

Plant Productivity and Respiration

During seed germination, seed storage proteins, carbohydrates, and lipids must all be broken down to support the germinating seedling, and aerobic respiration is a crucial part of these processes. When seeds

Figure 8. CAM plants are very slow growers. Because they grow in water-limiting environments, they have adapted in other ways, outside of their CAM photosynthesis, to conserve water. These adaptions include reduced or no leaves, light gray or green color to reflect light, vertical stems and leaves, and thorns for protection from predators. As a result, cacti, aloe, agave, and other CAM plants can go weeks with little to no watering.

Figure 9. Most plants, except aquatic plants, can only survive short periods of time underwater. Extended periods of low or no oxygen in the soil results in anaerobic respiration, root death, and eventually plant death. The dead turf areas indicate locations where water had stood for less than 72 hours. (Photo courtesy of Zac Reicher.)

are planted in the spring, timing and temperature are important. First, planting time should be past the danger of frost damage. Second, soil temperatures should be sufficiently warm. The reason for this is that respiration increases substantially with increased temperature. If the soil temperature is too cold, respiration will be too low to metabolize seed storage reserves, and the seed cannot germinate (*Figure 9*).

The fact that respiration increases with temperature also has a profound effect on adult plant productivity. When it is very hot, many plants grow very slowly because of reduced productivity. This usually results from lack of water to support transpiration and CO_2 uptake. But it also results from an unfavorable balance between photosynthesis and respiration. As temperature and light availability increase, photosynthetic output eventually plateaus because the chloroplasts have a finite light absorption capacity. On the other hand, the rate of respiration keeps increasing as it gets hotter, which burns more and more carbohydrate. The more respiration increases, the less net photosynthetic product there is. The effect of high temperature on respiration is most severe at night when there is no photosynthesis. If nighttime temperatures are very high, all the carbohydrate made by the plant during the day can be used up in respiration and there may be no net growth (*Figures 10* and *11*).

Summary

Plant growth and development relies on water for transpiration, photosynthesis, and respiration. The unique ability of water to regulate temperatures, dissolve molecules of life, and allow gas exchange, is essential for all life on earth. Transpiration is essential for evaporative cooling, CO_2 acquisition, maintaining plant turgor, and mineral nutrient uptake. Photosynthesis converts CO_2 into simple carbohydrates. Respiration releases energy obtained from photosynthesis. Respiration also acts as a central metabolic hub, ultimately resulting in the complex organic molecules that form the basis of plants. In addition to carbon derived from CO_2, many of these complex carbon molecules also incorporate mineral nutrients acquired from the soil.

Figure 10. Cultural practices, such as scalping or mowing at lower than recommended mowing heights, will reduce photosynthetic rates because of the lack of green tissue available for photosynthesis. This practice will reduce the amount of carbohydrates stored because they will be directed toward new growth to repair the damaged turf. This will put unneeded stress on a turfgrass stand and may result in thinning or weed encroachment. Most turfgrasses in Nebraska should be mowed no lower than 2.5 inches. (Photo courtesy of Zac Reicher.)

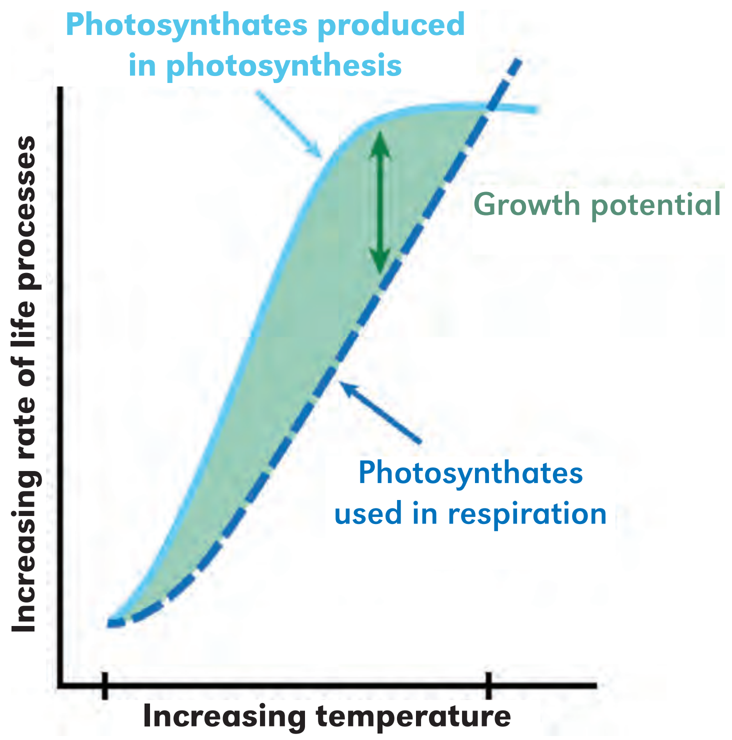

Figure 11. The rate of photosynthesis and respiration generally increase as temperature increases. When the rate of photosynthesis exceeds the rate of respiration, plants grow. If respiration exceeds photosynthesis, then growth declines, photosynthate reserves are used, and plants become more susceptible to biotic and abiotic stresses. Optimal growth temperatures vary; cool-season plants, such as Kentucky bluegrass, tall fescue, broccoli, and radish prefer temperatures between 40-75°F. Warm-season plants, such as buffalograss, peppers, and tomatoes prefer temperatures between 65-90°F.

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