

Text for ‘**Transpiration – Water Movement through Plants**’

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Overview and Objectives

Overview:

Transpiration is the loss of water from a plant in the form of water vapor. Water is absorbed by roots from the soil and transported as a liquid to the leaves via xylem. In the leaves, small pores allow water to escape as a vapor. Of all the water absorbed by plants, less than 5% remains in the plant for growth. This lesson will explain why plants lose so much water, the path water takes through plants, how plants might control for too much water loss to avoid stress conditions, and how the environment plays a role in water loss from plants.

Objectives:

At the completion of the lesson, students will be able to:

1. Define transpiration and explain why it occurs in plants.
2. Follow the pathway that water takes through plants from root uptake to evaporation at leaf cell surfaces.
3. Describe how the driving force for water movement and any resistances to its flow through the plant are the two major components controlling rates of transpiration.
4. Describe how environmental conditions alter rates of transpiration.
5. Explain how the plant is able to alter rates of transpiration.

INTRODUCTION

Welcome to a lesson that will examine how water moves through plants. Plants lose gallons of water every day through the process of transpiration, the evaporation of water from plants primarily through pores in their leaves. Up to 99% of the water absorbed by roots is lost via transpiration through plant leaves. How and why do they do it? How do the plants avoid losing too much water? What environmental conditions control water loss? The animation in the lesson will provide a visual tool for you to understand these processes as well. The animation contains the text below.

POP-UP - Did you know that an acre of corn can transpire up to 400,000 gallons of water in one growing season?

POP-UP – Because water molecules stick together so well due to hydrogen bonding, water can be pulled up trees 100 meters tall (that's over 300 feet or three times the height of most shade trees!).

What is transpiration? In actively growing plants, water is continuously evaporating from the surface of leaf cells exposed to air. This water is replaced by additional absorption of water from the soil. Liquid water extends through the plant from the soil water to the leaf cell surfaces where it is converted from a liquid into a gas through the process of evaporation. The cohesive properties of water (hydrogen bonding between adjacent water molecules) allow the column of water to be 'pulled' up through the plant as water molecules are evaporating at the leaf surface. This process has been termed the **Cohesion Theory of Sap Ascent** in plants.

Why do plants transpire?

Evaporative cooling: As water evaporates or converts from a liquid to a gas at the leaf cell and atmosphere interface, energy is released. This exothermic process uses energy to break the strong hydrogen bonds between liquid water molecules; the energy used to do so is taken from the leaf and given to the water molecules that have converted to highly energetic gas molecules. These gas molecules and their associated energy are released into the atmosphere, cooling the plant.

Accessing nutrients from the soil: The water that enters the root contains dissolved nutrients vital to plant growth. It is thought that transpiration enhances nutrient uptake into plants.

Carbon dioxide entry: When a plant is transpiring, its stomata are open, allowing gas exchange between the atmosphere and the leaf. Open stomata allow water vapor to leave the leaf but also allow carbon dioxide (CO₂) to enter. Carbon dioxide is needed for photosynthesis to operate. Unfortunately, much more water leaves the leaf than CO₂ enters for three reasons:

- 1) H₂O molecules are smaller than CO₂ molecules and so they move to their destination faster.
- 2) CO₂ is only about 0.036% of the atmosphere (and rising!) so the gradient for its entry into the plant is much smaller than the gradient for H₂O moving from a hydrated leaf into a dry atmosphere.
- 3) CO₂ has a much longer distance to travel to reach its destination in the chloroplast from the atmosphere compared to H₂O which only has to move from the leaf cell surface to the atmosphere.

This disproportionate exchange of CO₂ and H₂O leads to a paradox. The larger the stomatal opening, the easier it is for carbon dioxide to enter the leaf to drive photosynthesis; however, this large opening will also allow the leaf to lose large quantities of water and face the risk of dehydration or water-deficit stress. Plants

that are able to keep their stomata slightly open, will lose fewer water molecules for every CO₂ molecule that enters and thus will have greater water use efficiency (water lost/CO₂ gained). Plants with greater water use efficiencies are better able to withstand periods when water in the soil is low.

Water uptake: Although only less than 5% of the water taken up by roots remains in the plant, that water is vital for plant structure and function. The water is important for driving biochemical processes, but also it creates turgor so that the plant can stand without bones.

How fast does water move through plants? Transpiration rates depend on two major factors: 1) the driving force for water movement from the soil to the atmosphere and 2) the resistances to water movement in the plant.

Driving force: The driving force for transpiration is the difference in water potential between the soil and the atmosphere surrounding the plant. This difference creates a gradient, forcing water to move toward areas with less water. The drier the air around the plant, the greater the driving force is for water to move through the plant and the faster the transpiration rate. The following section, FACTORS AFFECTING RATES OF TRANSPIRATION, expands on how changes in the environment alter this driving force and thus transpiration.

Description of water potential and how to measure it –Link to the Powerpoint Presentation in the Lesson.

Resistances: There are three major resistances to the movement of water out of a leaf: cuticle resistance, stomata resistance and boundary layer resistance. These resistances slow water movement. The greater any individual resistance is to water movement, the slower the transpiration rate. The following section, FACTORS AFFECTING RATES OF TRANSPIRATION, expands on how changes in the plant alter these resistances and thus transpiration.

A simple equation describing how these factors alter transpiration is:

$$\text{Transpiration} = \frac{[\text{Water potential}_{(\text{leaf})}] - [\text{Water potential}_{(\text{atmosphere})}]}{\text{Resistance}}$$

The units for this equation are mols of water lost per leaf area per time (mol/cm²/s). This equation makes predicting rates of transpiration easy. For example, any time the numerator (the value for the driving force) is increased, the rate of transpiration becomes faster and vice versa. Similarly, if the denominator (the value for resistance) increases, this means there is greater resistance and thus, slower transpiration.

MAJOR PLANT HIGHLIGHTS:

Root Detail – The major path for water movement into plants is from soil to roots. Water enters near the tip of a growing root, the same region where root hairs grow. The surface of the root hairs needs to be in close contact with the soil to access soil water. Water diffuses into the root, where it can take at least three different pathways to eventually reach the xylem, the conduit located at the interior of the root that carries the soil water to the leaves. View the next level of this animation to see the possible pathways that water can take across a root.

What path does water take to reach the leaf from the root hair? Once water has entered a root hair, it must move across the cortex and endodermis before it reaches the xylem. Water will take the path of least resistance through a root to reach the xylem. Water can move across the root via three different pathways. One path is the **apoplastic path** where the water molecule stays between cells in the cell wall region, never crossing membranes or entering a cell. The other two routes, called cellular pathways, require the water molecule to actually move across a membrane. The first cellular pathway is the **transmembrane path** where water moves from cell to cell across membranes; it will leave one cell by traversing its membrane and will re-enter another cell by crossing its membrane. The second cellular path is the **symplastic path** which takes the water molecule from cell to cell using the intercellular connections called the plasmodesmata which are membrane connections between adjacent cells. Regardless of the pathway, once the water molecule has traversed the cortex, it must now cross the endodermis. The endodermis is a layer of cells with a waxy inlay or mortar called the Casparian strip that stops water movement between cells. At this point, water is forced to move through the membranes of endodermal cells, creating a sieving effect. Once in the endodermal cells, the water freely enters the xylem cells where it joins the fast moving column of water or transpiration stream, headed to the leaves.

Xylem Details – The xylem is probably the longest part of the pathway that water takes on its way to the leaves of a plant. It is also the path of least resistance, with about a billion times less resistance than cell to cell transport of water. Xylem cells are called tracheids (cells with narrower diameters) or vessels (cells with wider diameters). Their cell walls contain cellulose and lignin making them extremely rigid. Xylem cells contain no membranes and are considered dead. These cells overlap to create a series of pathways that water can take as it heads to the leaves. There is no single column of xylem cells carrying water.

Cavitation – Cavitation is the filling of a xylem vessel or tracheid with air. It is also known as an ‘embolism’ or ‘air-lock’. Remember that during transpiration, the column of water is being pulled out of the plant by evaporation at the leaf cell surface. When this ‘pulling’ of water out of the plant becomes greater than the ability of the water molecules to stay together, the column of water will break. Using sound-sensing equipment, one can actually hear a ‘click’ when the water molecules split from one another. Unique structural characteristics help the plant

contain the air bubble so that it does not totally disrupt water movement up the plant.

Plants are particularly sensitive to cavitation during the hottest part of the day when there is not enough water available from the soil to keep up with the demand for water while it is evaporating off the leaf surface. Cavitation also occurs under freezing conditions. Because the solubility of gas in ice is very low, gas comes out of solution when the xylem sap freezes. Freezing of xylem sap is a problem in the spring when the ice thaws, leaving a bubble in a xylem vessel. These bubbles can block water transport and cause water deficit in leaves.

Plants avoid cavitation or minimize its damage through several mechanisms:

- 1) Xylem cells possess pits or tiny holes that allow liquid water transport, but do not allow the gas bubble to escape; this structural characteristic helps keep the gas bubble in one cell, so the other xylem cells can continue to transport water up the plant.
- 2) Water will detour around any xylem cell containing an air bubble through the pits as well.
- 3) The gas bubble will re-dissolve into liquid water when the pulling of water through the xylem is reduced, such as during the night when water is not being pulled out of the leaf via transpiration because the stomata are closed.
- 4) Xylem cells with narrower diameters (tracheids) compared to those with wider diameters (vessels) avoid cavitation because the column of water in a cell with a narrow diameter is better able to resist bubble formation or rupture.

POP-UP – Plants are most susceptible to cavitation when transpiration rates are extremely high.

Stomata Details – The stomata are the primary control mechanisms that plants use to reduce water loss and they are able to do so quickly. Stomata are sensitive to the environmental cues that trigger the stomata to open or close. The major role of stomata is to allow carbon dioxide entry to drive photosynthesis and at the same time allow the exit of water as it evaporates, cooling the leaf. Two specialized cells called ‘guard cells’ make up each stoma (stoma is singular for stomata). Plants have many stomata (up to 400 per mm²) on their leaf surfaces and they are usually on the lower surface to minimize water loss.

POP-UP – Webster’s Dictionary says a stoma (singular form of stomata) is a small, simple opening.

How do stomata open? Stomata sense environmental cues, like light, to open. These cues start a series of reactions that cause their guard cells to fill with water. Let’s follow a scenario where the sun is rising and a cotton plant is signaled to open its stomata.

1. Signal received: The blue light at dawn is the signal that is recognized by a receptor on the guard cell.
2. The receptor signals the H⁺-ATPases on the guard cell's plasma membrane to start pumping protons (H⁺) out of the guard cell. This loss of positive charge creates a negative charge in the cell.
3. Potassium ions (K⁺) enter the guard cell through channels in the membrane, moving toward its more negative interior.
4. As the potassium ions accumulate in the guard cell, the solute potential is lowered.
5. A lower solute potential attracts water to enter the cell.
6. As water enters the guard cell, its hydrostatic pressure increases.
7. The pressure causes the shape of the guard cells to change and a pore is formed, allowing gas exchange.

SIDE VIEW OF STOMATA – Environmental cues that affect stomata opening and closing are light, water, temperature, and the concentration of CO₂ within the leaf. Stomata will open in the light and close in the dark. However, stomata can close in the middle of the day if water is limiting, CO₂ accumulates in the leaf, or the temperature is too hot.

If the plant lacks water, stomata will close because there will not be enough water to create pressure in the guard cells for stomatal opening; this response helps the plant conserve water.

If the leaf's internal concentration of CO₂ increases, the stomata are signaled to close because respiration is releasing more CO₂ than photosynthesis is using. There is no need to keep the stomata open and lose water if photosynthesis is not functioning. Alternatively, if the leaf's CO₂ concentration is low, the stomata will stay open to continue fueling photosynthesis.

High temperatures will also signal stomata to close. High temperatures will increase the water loss from the leaf. With less water available, guard cells can become flaccid and close. Another effect of high temperatures is that respiration rates rise above photosynthesis rates causing an increase of CO₂ in the leaves; high internal CO₂ will cause stomata to close as well. Remember that some plants may open their stomata under high temperatures so that transpiration will cool the leaves.

POP-UP - Why do plants waste all this water!?! Transpiration helps the plant by providing evaporative cooling, nutrient uptake, and carbon dioxide entry.

TOP VIEW OF STOMATA –

OPEN STOMATA – When stomata are signaled to open, potassium ions (K⁺) enter the guard cells. This causes water to enter down its water

potential gradient, creating a hydrostatic pressure in the guard cell that changes the shape of the stoma. Guard cells expand on the outer edges of the stoma, but not on the inner side, resulting in kidney-shaped cells and an opening or pore between the two guard cells for gas exchange.

The shape taken by the guard cells is dependent on cellulose microfibrils that fan out radially from the pore, somewhat similar to radial tires. The cellulose microfibrils are rigid and do not stretch when water has entered the cell. The cell walls surrounding the stomatal opening are thickened, preventing that side of the guard cell from expanding. Therefore, when pressure in the cell increases due to water entry, guard cell does not widen, but rather the outer edge stretches disproportionately more than the inner edge. This unequal stretching allows the pore to form between the two guard cells.

POP-UP – Cellulose microfibrils keep the guard cells from expanding into sphere-shaped cells because the fibrils are rigid rings around the guard cell, restricting cell expansion other than the outer edge.

CLOSED STOMATA – Stomata must be open for the plant to photosynthesize; however, open stomata present a risk of losing too much water through transpiration. Stomata close when the guard cells lose water and become flaccid. This occurs because potassium ions move back out of the guard cell, followed by water that lowers the pressure in the guard cell.

POP-UP – Many plant leaves have stomata only on their lower surface to help avoid water loss.

FACTORS AFFECTING RATES OF TRANSPIRATION:

Plant Parameters – These plant parameters help plants control rates of transpiration by serving as forms of resistance to water movement out of the plant.

Stomata – Stomata are pores in the leaf that allow gas exchange where water vapor leaves the plant and carbon dioxide enters. Special cells called guard cells control each pore's opening or closing. When stomata are open, transpiration rates increase; when they are closed, transpiration rates decrease.

POP-UP – Stomata are the only way plants can control transpiration rates in the short-term.

Boundary layer – The boundary layer is a thin layer of still air hugging the surface of the leaf. This layer of air is not moving. For transpiration to occur, water vapor leaving the stomata must diffuse through this

motionless layer to reach the atmosphere where the water vapor will be removed by moving air. The larger the boundary layer, the slower the rates of transpiration.

Plants can alter the size of their boundary layers around leaves through a variety of structural features. Leaves that possess many hairs or pubescence will have larger boundary layers; the hairs serve as mini-wind breaks by increasing the layer of still air around the leaf surface and slowing transpiration rates. Some plants possess stomata that are sunken into the leaf surface, dramatically increasing the boundary layer and slowing transpiration. Boundary layers increase as leaf size increases, reducing rates of transpiration as well. For example, plants from desert climates often have small leaves so that their small boundary layers will help cool the leaf with higher rates of transpiration.

POP-UP – Did you know that hairs on a leaf surface increase the boundary layer and thus, reduce rates of transpiration?

Cuticle – The cuticle is the waxy layer present on all above-ground tissue of a plant and serves as a barrier to water movement out of a leaf. Because the cuticle is made of wax, it is very hydrophobic or ‘water-repelling’; therefore, water does not move through it very easily. The thicker the cuticle layer on a leaf surface, the slower the transpiration rate.

Cuticle thickness varies widely among plant species. In general, plants from hot, dry climates have thicker cuticles than plants from cool, moist climates. In addition, leaves that develop under direct sunlight will have much thicker cuticles than leaves that develop under shade conditions.

POP-UP – Sun leaves have much thicker cuticles than shade leaves causing slower rates of transpiration.

Environmental Conditions – Some environmental conditions create the driving force for movement of water out of the plant. Others alter the plant’s ability to control water loss.

Relative humidity – Relative humidity (RH) is the amount of water vapor in the air compared to the amount of water vapor that air could hold at a given temperature. A hydrated leaf would have a RH near 100%, just as the atmosphere on a rainy day would have. Any reduction in water in the atmosphere creates a gradient for water to move from the leaf to the atmosphere. The lower the RH, the less moist the atmosphere and thus, the greater the driving force for transpiration. When RH is high, the atmosphere contains more moisture, reducing the driving force for transpiration.

POP-UP – The drier the atmosphere, the larger the driving force for water movement out of the plant, increasing rates of transpiration.

Temperature – Temperature greatly influences the magnitude of the driving force for water movement out of a plant. As temperature increases, the water holding capacity of that air increases sharply. The amount of water does not change, just the ability of that air to hold water. Because warmer air can hold more water, its relative humidity is less than the same air sample at a lower temperature, or it is ‘drier air’. Because cooler air holds less water, its relative humidity increases or it is ‘moister air’. Therefore, warmer air will increase the driving force for transpiration and cooler air will decrease the driving force for transpiration.

POP-UP – Warmer air holds more water, creating a larger driving force for water movement out of the plant, increasing rates of transpiration.

Soil water – The source of water for transpiration out of the plant comes from the soil. Plants with adequate soil moisture will normally transpire at high rates because the soil provides the water to move through the plant. Plants cannot continue to transpire without wilting if the soil is very dry because the water in the xylem that moves out through the leaves is not being replaced by the soil water. This condition causes the leaf to lose turgor or firmness, and the stomata to close. If this loss of turgor continues throughout the plant, the plant will wilt.

Light – Stomata are triggered to open in the light so that carbon dioxide is available for the light-dependent process of photosynthesis. Stomata are closed in the dark in most plants. Very low levels of light at dawn can cause stomata to open so they can access carbon dioxide for photosynthesis as soon as the sun hits their leaves. Stomata are most sensitive to blue light, the light predominating at sunrise.

POP-UP – Light levels as low as one thousandth of the sun can cause stomata to open.

Wind – Wind can alter rates of transpiration by removing the boundary layer, that still layer of water vapor hugging the surface of leaves. Wind increases the movement of water from the leaf surface when it reduces the boundary layer, because the path for water to reach the atmosphere is shorter.

POP-UP – Windier conditions increase transpiration because the leaf’s boundary layer is smaller.

SUMMARY

Transpiration is the evaporation of water from the surface of leaf cells in actively growing plants. This water is replaced by additional absorption of water from the soil leading to a continuous column of water in the plant's xylem. The process of transpiration provides the plant with evaporative cooling, nutrients, carbon dioxide entry and water to provide plant structure. Rates of transpiration depend on the water potential gradient from the soil to the atmosphere and the resistances to its movement through the plant. Water enters the root and travels through the cortex and endodermal layers of cells to reach the xylem where water ascends to the leaf where, if not used in the plant, evaporates. If water loss is greater than water uptake, air bubbles can form in the xylem. Plants reduce water loss by closing their stomata, developing thick cuticles, or by possessing leaf hairs to increase the boundary layer. Stomata are quick to respond to environmental cues to protect the plant from losing too much water, but still allowing in enough carbon dioxide to drive photosynthesis.

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