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Water Movement In Trees

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A tree allocates life-energy to survive and thrive in an environment which never has optimal resources. What essential resources are present are usually present in too low, too high, or unavailable concentrations. Trees continue to react to environmental changes with internal adjustments selected for efficient use of tree food and water, while minimizing energy loss to the environment. The more limiting essential resources become, (i.e. the larger tree energy costs), the greater tree stress.

Spell "Essentiality"

All tree life processes take place in water – food making, food transport, food storage, food use, and defense. Water is a reagent in chemical reactions, a chemical bath for other reactions, a transporter, a hydraulic pressure liquid, a coating, buffer, and binder. Water is a universal liquid workbench, chemical scaffold, and biological facilitator. Water comprises 80% of living tree materials. As such, water is aggressively gathered, carefully guarded, and allowed to slowly escape in exchange for work energy within a tree. Of all resource components of stress impacting tree survival and growth, water stress is the most prevalent. The largest single use of water in a tree is for transport of essential materials from roots to leaves.

Pulling Bonds

Water has an affinity for sticking closely to other water molecules. Because of electrostatic forces among oxygen and hydrogen atoms in water, one side of the water molecule carries a partial positive charge (the hydrogen side) and one side carries a partial negative charge (the oxygen side). These polar charges cause water to stick together unlike other molecules of similar size. This property allows drops of water placed on a wax (hydrophobic) surface to bead-up rather than flattening out and covering a surface. In this case, water would rather stick to other water molecules than to a waxed surface. Using your finger, you can "pull" water droplets over a waxy surface and consolidate them into larger drops.

Trees utilize water's special chemical features in many ways, most noticeably in transporting materials from soil, into roots, and then on to leaves. Water in a tree is pulled through thousands of long columns or tubes, located around the outside of a tree stem within the last few annual increments. These long columns of water (inside dead xylem cells) are functionally continuous between the source of water (soil) and leaves. Water is pulled in long chains into a root, up through narrow xylem columns or channels, and to leaf surfaces where it evaporates into perpetually dry air. Water evaporates as bonds between molecules are broken at the liquid water / air interface in a leaf.

Sticky Evaporation

As one water molecule is exposed at the wet internal surface of a leaf, it is still bound to surrounding water molecules. Because of temperature (sensible heat or energy) and humidity in the atmosphere, water molecules are pulled away from wet leaf cell wall surfaces. This is called evaporation. The pull (water demand or deficit) of air has enough energy to break water connections between water molecules, and at the same time pull neighboring water molecules onto the surface. These water molecules, in turn, evaporate into air generating an evaporative "pull" at the wet leaf surface measurable down through water columns to roots and into soil.

Water in a tree is a tightly connected stream moving from soil pores and surfaces, into the root, up the stem, out to leaf surfaces and into the atmosphere. Water molecules in a continuous line are held together by water's affinity for sticking to other water molecules. This "stickiness" allows water to be pulled to the top of the tallest of trees against gravity, conduit resistance, and pathway complexity. This transport pathway and process is called the "transpiration stream." Living cells surrounding this xylem pull (tension) system assist with monitoring the transpiration stream and making minor adjustments.

Holiday Traditions

The faster evaporation from leaf surfaces, the more energy exerted to pull water to a leaf. Too much exertion, and the continuous line of water molecules with billions of interconnections, break and are pulled apart. Water column breakage (cavitation) can be catastrophic for a tree because once broken, transport stops. Too much resistance in soil or too rapid (high energy) evaporation at a leaf, can quickly snap ascending water columns.

For example, many people bring cut trees and evergreen foliage into their house during Winter holiday observances. Most houses have relatively low humidity and indoors, a cut tree or foliage dries rapidly. Usually, after many well-meaning rehydration treatments (waterings), people give-up and finally discard these once living tissues. While a tree is in a house, faint clicks or pops can be heard on quiet nights coming from inside the tree crown. These noises are not caused by vermin brought in with a tree, but by water columns snapping inside the stem due to severe dryness. Some tree drought indices quantify severity using microphones to count snapping water columns.

Communicating Stress

As water moves from soil through roots and into leaves, it carries with it essential elements, nutrients, and chemical messages. As water and elements move from root to shoot, growth regulators (cytokinins) are added by roots and by neighboring cells along water columns. Through this chemical communication link, shoots of a tree can react to the status of roots. Shoots can then produce their own growth regulator (auxin) and ship it along living cells to the farthest root tips.

Organic growth materials are also added by roots to the transpiration stream. Any nitrogen captured by roots is processed into amino acids within roots using carbon captured by leaves. Amino acids are transported in the water stream to leaves. Shoots of a tree continually update growth processes in response to root functions, and roots continually modify life processes in response to shoot functions.

CO2 vs. H2O

In addition to growth regulation signals providing environmental supply and demand information in a tree, leaves have an additional environmental sensor. Leaves are the focus of the evaporative load on water columns throughout a tree. Leaves can close or open leaf valves (stomates) used for taking in carbon-dioxide gas required in photosynthesis to make food. A diagram of stomates on the underside of a broad leaf is shown in Figure 1.

Note the epidermis cells (leaf surface cells) are covered with a waxy cuticle to minimize water loss. When the stomates are closed, the cuticle and stomates have roughly the same resistance to water loss, assuring that neither stomate guard cell areas or cuticle is over-engineered. When stomates are open, resistance of the cuticle to water movement averages more than 25 times greater than the stomate.

When stomates are open, carbon-dioxide can move into a leaf, but water rapidly evaporates and escapes. For average conditions in a yard tree, theoretically 10 water molecules evaporate from a leaf for every one (1) carbon-dioxide captured. In reality, more than 300 water molecules are lost for each carbon-dioxide captured. In other words, a lot of water is transpired for small gains in food making carbon atoms. The more food made for the least water used is calculated as "water use efficiency" (WUE) and is used to compare water demand by different plants. As water availability declines, leaves sense and respond by closing down stomates and photosynthetic processes.

Measuring Potential

Water is measured inside tree cells using a construct called "water potential." Water potential is measured in many ways and using many different units of measure. Figure 2 provides a number of different water potential (pressure) measurement units found across the scientific literature. Here the use of bars of pressure will be used. Water potential is an estimate of energy in water to accomplish work, like moving materials or inflating cells in growth.

A simplified way of understanding water potential is illustrated in Figure 3. This figure shows a gradient of energies from water inside and surrounding a cell. Water brought into a cell causes it to either swell like a balloon and change volume, or as in tree cells with a solid cell wall, pressure inside the cell increases. Increasing pressure means increasing energy to do work (positive water potential or pressure). As water is removed from a cell, the cell membrane can either collapse away from the wall changing volume (deflating), or a cell can exert a pull on water in the area to move it into the cell. Increasing pull on water inside a cell generates a negative water potential or tension.

Swelling Or Drying

Water potential in trees has two primary components, an osmotic tension and a turgor pressure. The osmotic tension (negative pressure) is caused by water being attracted to and held around small compounds within cells. A clump of starch in a cell is large and has a relative small hydration sphere or coating layer of water. If individual components of starch are broken apart (sugars), the amount of water needed to form hydration spheres around each sugar is increased geometrically and is immense, demanding much more water. This process pulls water into a cell.

Turgor pressure in a cell is positive caused by outward pressure from within a cell. Cells use energy to bring in more water and hold it to generate internal pressure for cell growth or to keep a cell fully expanded. Turgor pressure in a fully turgid cell is at least equal to the osmotic tension in a cell. When turgor pressure is no longer positive, a cell can no longer fully occupy its cell wall space and is flaccid.

Example Potential

For example, in the morning of a bright sunny day during the growing season, water loss through transpiration begins. This causes a drop (becoming more negative) in leaf cell water potential. Turgor pressure drops causing total water potential to drop. This tension from lower water potential generated by transpiration in a leaf initiates a gradient of water potentials from the air surrounding a leaf through the tree to soil. Water will continue to move from higher pressure zones (more positive water potentials) toward lower pressure zones (more negative water potentials) by tension pulling water along. Figure 4.

Increasing Tension

As water potential concepts demonstrate, when water is pulled up to tree tops and resistance to soil-water movement increases (uptake slows), a tension or negative pressure develops in the water columns. Water continues to move from relatively low tension areas (like soil at field capacity), to high tension areas of rapidly evaporating leaf water. Because of the effectiveness of stomates in evaporating water, leaves can loose water faster than roots can pull water in from soil. As leaf water loss continues to exceed root water uptake, greater tension develops in water columns, and a water deficit begins to build.

When the water deficit becomes too great, stomates are closed until water uptake in roots catch-up. When stomates are closed, no carbon dioxide can get into a leaf and the tree cannot make food to feed itself. As water in soil becomes increasing scarce, the transpirational pull energy in a tree becomes greater. The whole tree dries as water is pulled away from various tissues. Cellular machinery is shut-down and damaged, as water loss becomes progressively greater. As soil dries, the tree water conduction system is under tremendous tension. Figure 5.

Rubber Bands

To visualize water movement and water column tension in a tree, think of a rubber band. The more you stretch one end of a rubber band, the tighter the band becomes, similar to water columns under transpirational pull. If you stop pulling on one end of the band and release the other end, energy in the band will snap it back. If you hold both end of the band and pull too hard, the band will break.

Transfer of the rubber band model to water movement in a tree is easy. As stomates lose water, water columns are pulled tighter and tighter down the tree and out into roots. If stomates close and stop adding more tension on the water column, roots will continue taking in water pulled by tension remaining in the water column. If soil is dry and transpirational pull too great, water columns snap or cavitate, preventing any more water movement in the cavitated water column. The only way to reduce water column tension in a tree is to close all stomates (and prevent any other surface evaporation), or to apply water to soil.

What A Drag

Water movement and evaporation is a function of temperature (energy) in the environment. Evaporative pull from leaf surfaces moves water from around soil particles and into roots. Water is not moved in a tree by "pumping," "suction," or "capillary action." Water in trees moves by sticking together and being dragged to leaf surfaces where evaporation through stomates (transpiration) generates a "pulling" force on the water columns. Water also evaporates from all other tree surfaces – buds, periderm, lenticels, fruit, etc. – but leaves have the only significant tree-controlled system for modifying water loss.

One way of thinking about water movement through evaporation is to visualize a tall glass of water with a wick or sponge. Water will be pulled into the sponge and into the air by evaporation across a large surface area. Open stomates provide a huge amount of moist, evaporative leaf surface area, open to the atmosphere.

Evaporative force to move water through a tree is generated by the dryness of air. The ability of air to evaporate water depends upon the water content gradient between air and leaf surface. A normal range of water content gradient over which tree growth occurs is -0.1 to -15 bars within a leaf. Drought conditions and damage occurs in a leaf as it approaches -15 to -20 bars.

Sultry

The gradient between internal leaf atmosphere at 100% relative humidity (0 bars) and the atmosphere can be great. For example, fog is a condensate occurring around 100% relative humidity, while Summer rain downpours range from 90% to 98% relative humidity. Trees can lose water even during rain storms because at 98% relative humidity, the air is 100 times drier than the inside of a leaf. Trees are always losing water. Figure 6.

The soil, soil/root interactions, vascular system, and leaf all provide resistance to water movement. Increased resistance to water movement makes water less available at the leaf. Water movement resistance is based upon the surfaces and structures which water must move through. The engine which powers water movement in trees is the dryness of air and associated rate of evaporation through stomates. Anything that effects atmospheric demand for water, and stomate control of water loss rates, would affect water movement in a tree.

Taking A Break

The consequences of water movement in trees produce two interesting results: siestas and night refilling. During bright, sunny, hot days when the sun is high enough from the horizon to cause stomates to open, transpiration increases water loss until it out-runs the root's ability to keep-up. As water column tensions increase, a point is reached near mid-day when trees close many stomates on many leaves for several hours. Water column tension continues to pull in water from soil and as tension values decline (water availability increases), stomates begin to reopen.

Many trees take siestas in the middle of the day to minimize water loss and improve resource efficiency. From about 12 noon til 2 pm stomates may be closed and no food produced. Figure 7. As root water uptake catches up with leaf losses, stomates open up in the afternoon and remain open until the sun is about five degree above the horizon before setting. In a well watered and drained soil, stomates may not close at all. In a flooded soil, or soil with little water, stomates may remain closed for a greater part of the day. Under severe water stress, stomates may not open at all for days. In this case, trees must depend upon stored food for survival.

Night Moves

As the sun nears the horizon and night approaches, stomates close in trees. Because of the tension (stored energy) in water columns generated in the day, even after stomates close and the sun sets, water continues to be pulled into a tree, reducing the water deficit (column tension). Water uptake continues through the night. Figure 8. Even though there is little evaporation at night because stomates are closed and the relative humidity is high, water is still moving from soil and up into a tree. Night uptake by roots can amount to 20-40% of tree water needs if water is available. Just before sunrise a tree has pulled in the most water it can and is the most hydrated it will be all day. Because water is being pulled into roots from soil, and all the other plants in the area also are pulling water from soil, tensiometers in soil can measure a site's transpirational pull.

Stomates

Trees act as conduits through which soil water passes into the atmosphere. Instead of water evaporating at the soil surface powered by sunlight energy, a tree provides elevated surfaces for water evaporation and energy impact. All movement of water in a tree is governed by evaporation from tree surfaces. A tree maintains one point of biological control of water movement called stomates. Stomates are tiny valve-like openings dotting the underside of leaf surfaces. A dissecting microscope is needed to see most stomates. In temperate trees (C3 Ps), working stomates are on the leaf blade underside or running along the bottom of indentations on needles. Some tree leaves may have stomates on the upper side of the blade, but these are usually residual and do not function. Figure 9 is an idealized cross-sectional diagram of a broadleaf stomate.

By definition, a stomate is an opening in a leaf epidermis opened and closed by pressure differences in surrounding guard cells. Generically, stomates include the opening and the valve system components taken all together. Some stomates are protected with clumps of trichomes (tree hairs), some are surrounded with deposits of wax, and some are imbedded in pits or fissures deep into the leaf surface. These leaf openings are required in order for a tree to capture carbon-dioxide from air to make food, but unfortunately, an open stomate which allows carbon-dioxide to enter also allows water to escape. Each tree has millions of stomates, which when open, are continually evaporating water and pulling water through a tree.

Water Guards

Two flaccid guard cells lay side-by-side covering an opening to the inside of a leaf. When these guard cells sense sunlight with their photosynthetic units, they begin to be pumped-up with water. Guard cells and surrounding cells convert stored starch and other large materials into sugars and many smaller sized materials. Guard cells free potassium ions which attract large water shells. Because guard cells are tethered to each other only at the ends, they absorb water and lengthen creating a gap between, unveiling an unprotected entrance to inside a leaf.

Carbon-dioxide moves into leaves through stomates and dissolves onto the water-saturated cell walls for use in food making. Water from saturated leaf cell walls evaporate quickly and escape through stomates. The only place in a tree with control of water loss, food resource gathering, and the tree's transpiration stream is guard cells and the leaf entrance they cover. Over-all water loss is passively dependent upon, but strongly tied to, temperature and associated vapor pressure deficits. The physiological health of guard cells, including supplies of sugars, starch, potassium, and water, all influence opening and closing of stomates.

Spreading Out Evaporation

Little can be done to reduce the rate of evapotranspiration from a tree and the surrounding site. Water loss is controlled primarily by the amount of energy present to evaporate water and by soil water availability. Figure 10 demonstrates how transpirational loss of water from soil increases with climbing temperatures.

The efficiency of water use can be improved by increasing the vertical and horizontal extent of shade (tree crowns) on a site and by use of low density and organic mulches. Shade and mulch assure little direct sunlight reaches the soil surface and evapotranspiration is kept to a minimum. Under these conditions, the largest possible fraction of energy can be used in photosynthesis and the most food produced per unit of water evaporated.

Figure 11 is a diagram of a tree with a multi-layered crown surrounded with an organic mulch bed. This tree form is efficient at conserving site water because sunlight energy is spread over a vertically spread, relative large but widely distributed crown surface area which has some self-shading. The low density organic mulch assures little energy directly impacts the soil surface. A multi-height, multi-tree planting configuration could reach the same water use efficiency.

Conclusions

Water is dragged through a tree by molecular electrostatic charges (water stickiness) and by the dryness of the atmosphere. The biological control point for a tree is in the leaves. where valves can be pumped open in order to collect carbon-dioxide (CO2) and then allowed to close . As CO2 enters through leaf valves (stomates), water escapes, dragging other water molecules in behind. Trees are always losing water, and so, are always at the mercy of shifting water contents across the entire organism and site.

Citation:

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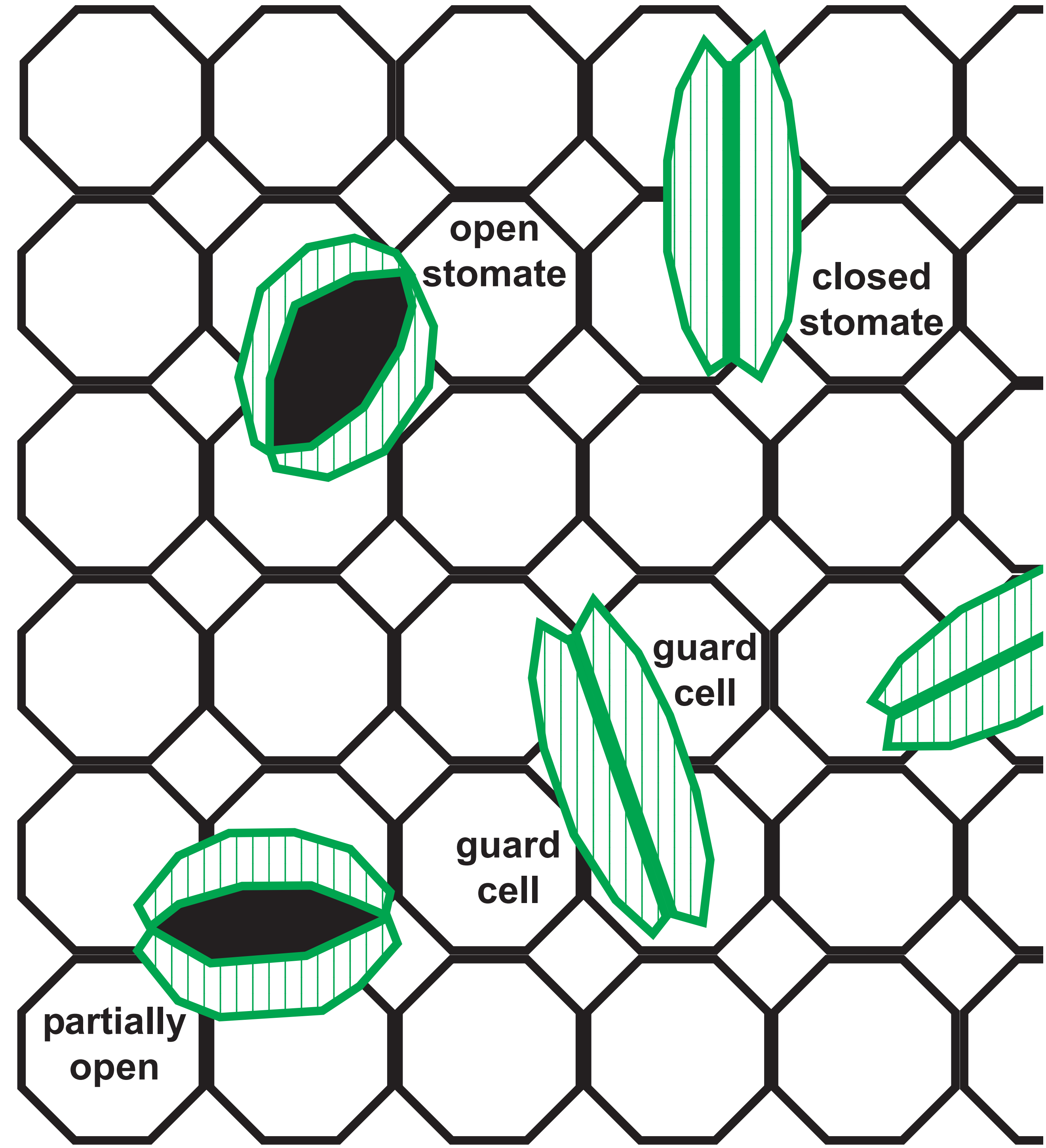

Figure 1: Idealized diagram showing open and closed stomates on underside of a tree leaf blade. The geometric pattern background represents leaf epidermis cells covered by a waxy cuticle.

units of measure	bar	atmosphere	pds-force/in^2	megapascal
1 bar	1	0.99	14.5	0.1
1 atmosphere	1.01	1	14.7	0.1
1 pds-force/in^2	0.07	0.07	1	0.007
1 megapascal	10	9.9	145.0	1

Figure 2: Different units for measuring water potential in trees from the scientific literature, both old and new. Here the older pressure unit measure called "bars" will be used. Read across a single line not down a column. (values have been rounded to fit figure)

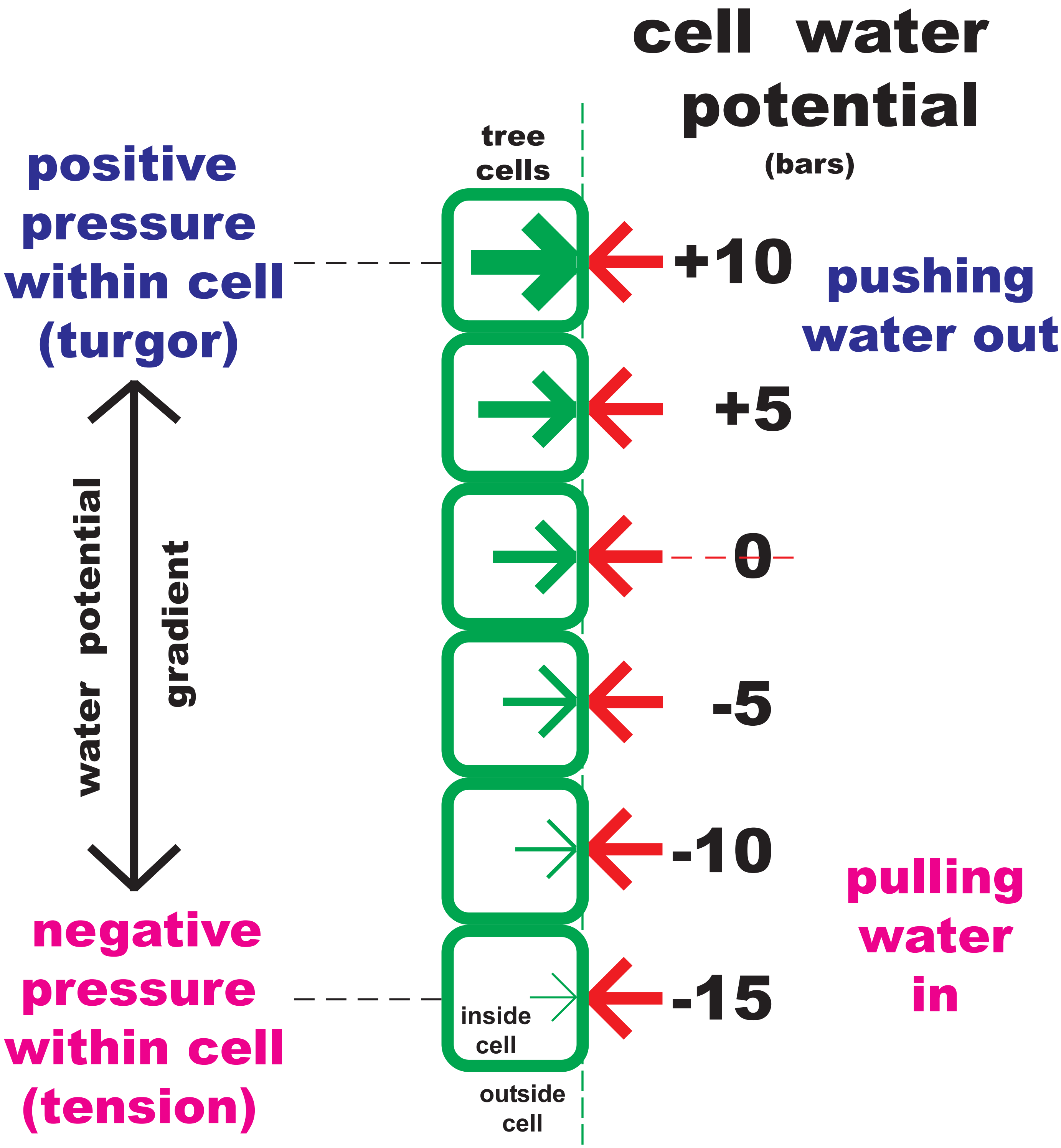

Figure 3: Simplified view of water potential gradient from pressure (positive water potential) to tension (negative water potential) within tree cells.

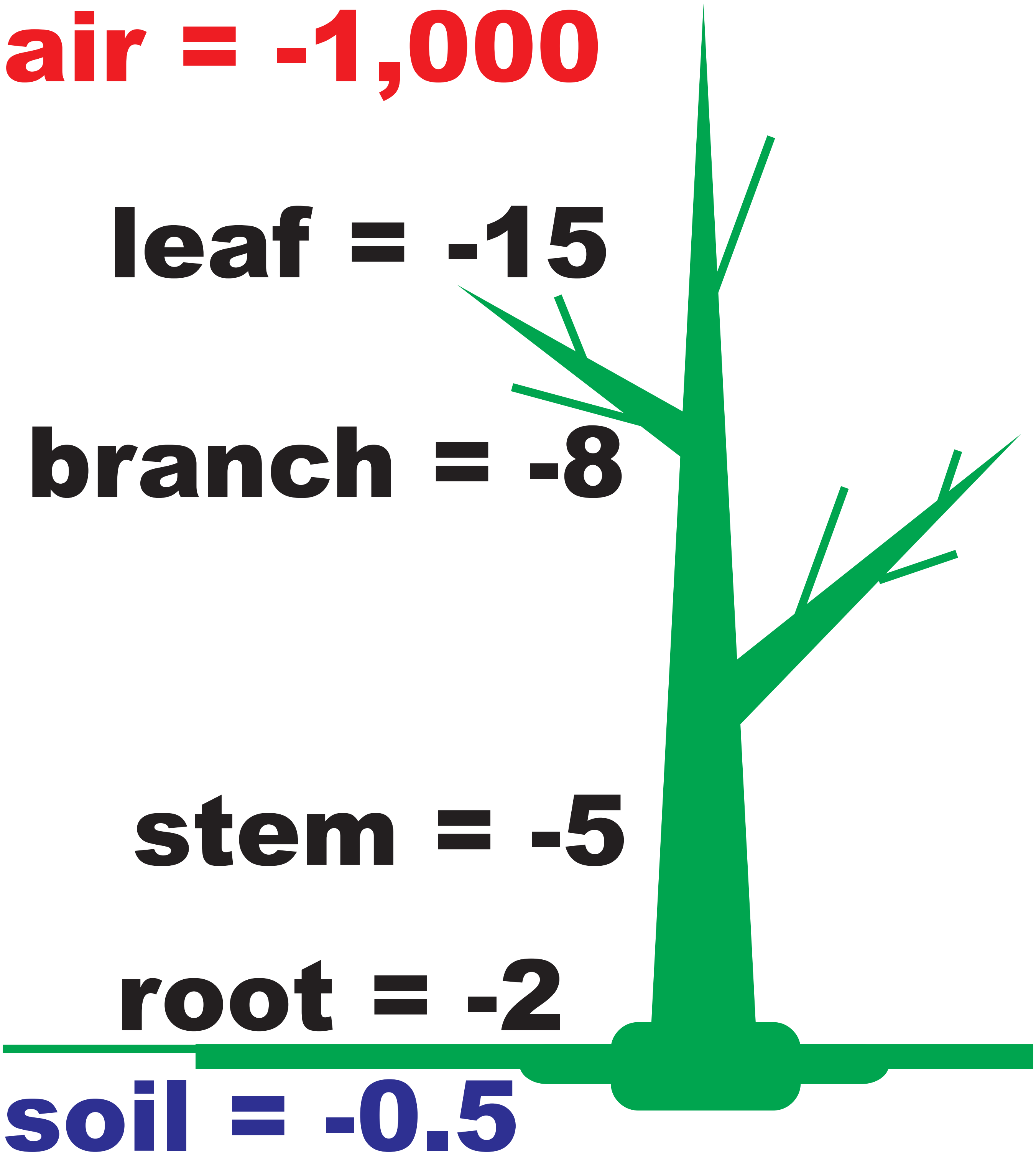

Figure 4: Example water potentials in bars from atmosphere to soil through a tree. Water moves (is pulled by tension) from more positive water potential regions (soil) to more negative water potential regions (leaf).

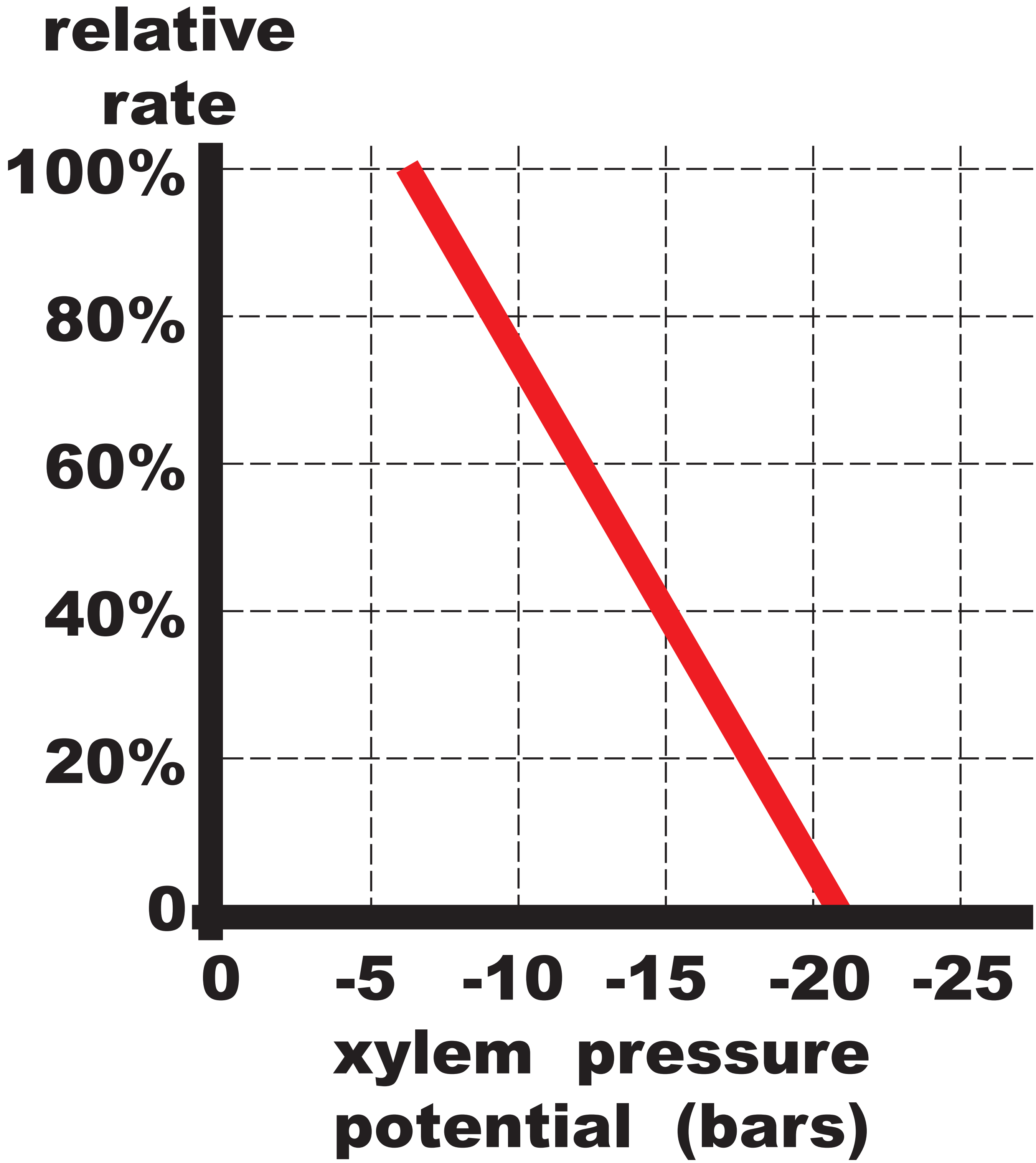

Figure 5: Relative rates of transpiration, net photosynthesis, & stomatal conductance compared with xylem pressure potential. (from Teskey, et. al. 1986)

relative humidity (%)	air temperature (F°)				
	50°	60°	70°	80°	90°
100	0	0	0	0	0
99	-13	-13	-14	-14	-14
98	-26	-27	-27	-28	-28
95	-67	-68	-70	-71	-72
90	-138	-140	-143	-145	-148
70	-466	-475	-483	-492	-500
50	-905	-922	-939	-956	-971
30	-1,572	-1,602	-1,631	-1,660	-1.687
10	-3,006	-3,064	-3,119	-3,175	-3,226

Figure 6: Estimated water potential (bars) of air for various relative humidity values (percent) and temperatures (F°).

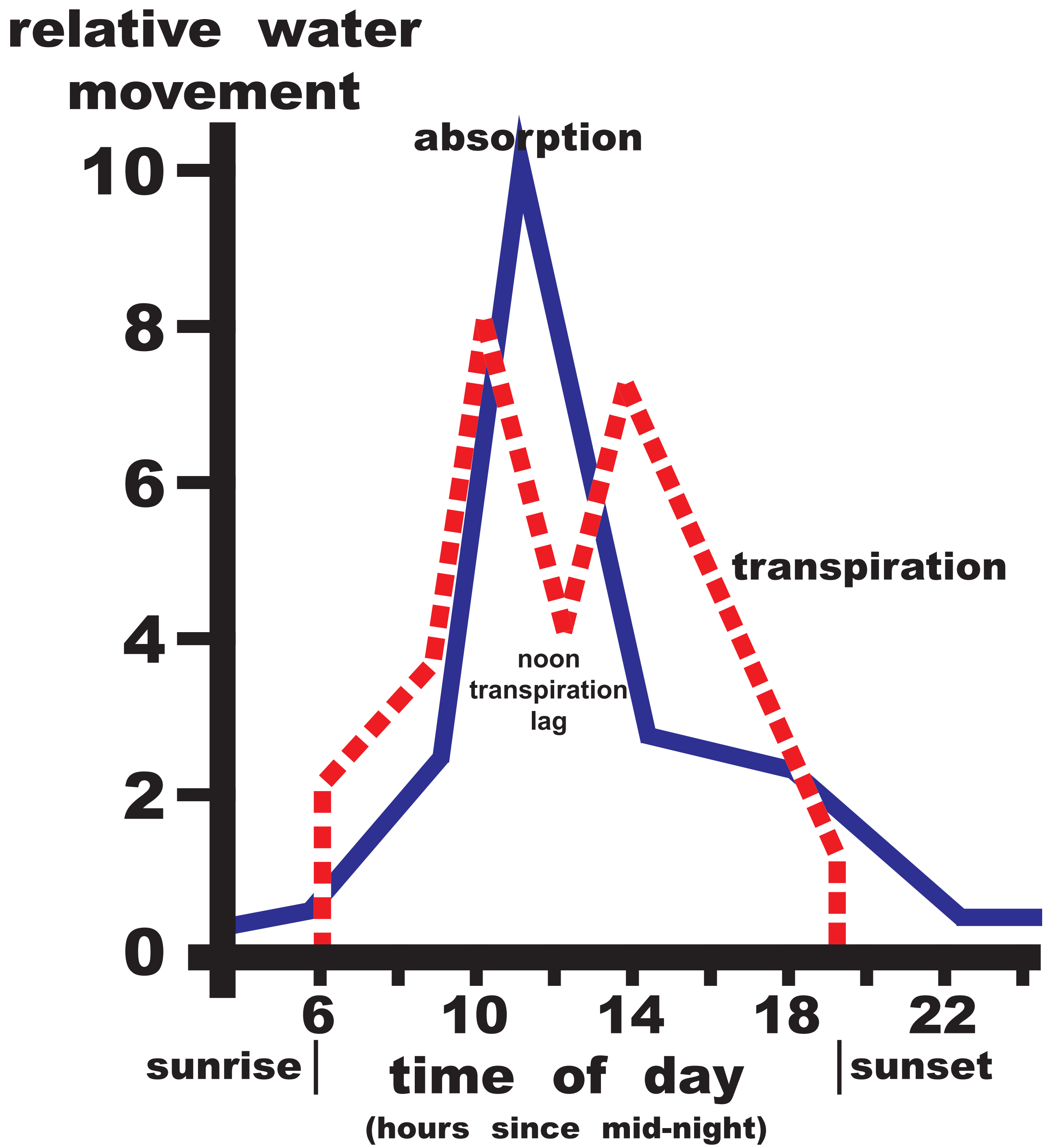

Figure 7: Root absorption and leaf transpiration within a tree and relative amount of water being moved by each process. Note transpiration in leaves begins just after sunrise, is slowed at mid-day, and stops just before sunset. Root absorption continues through the night.

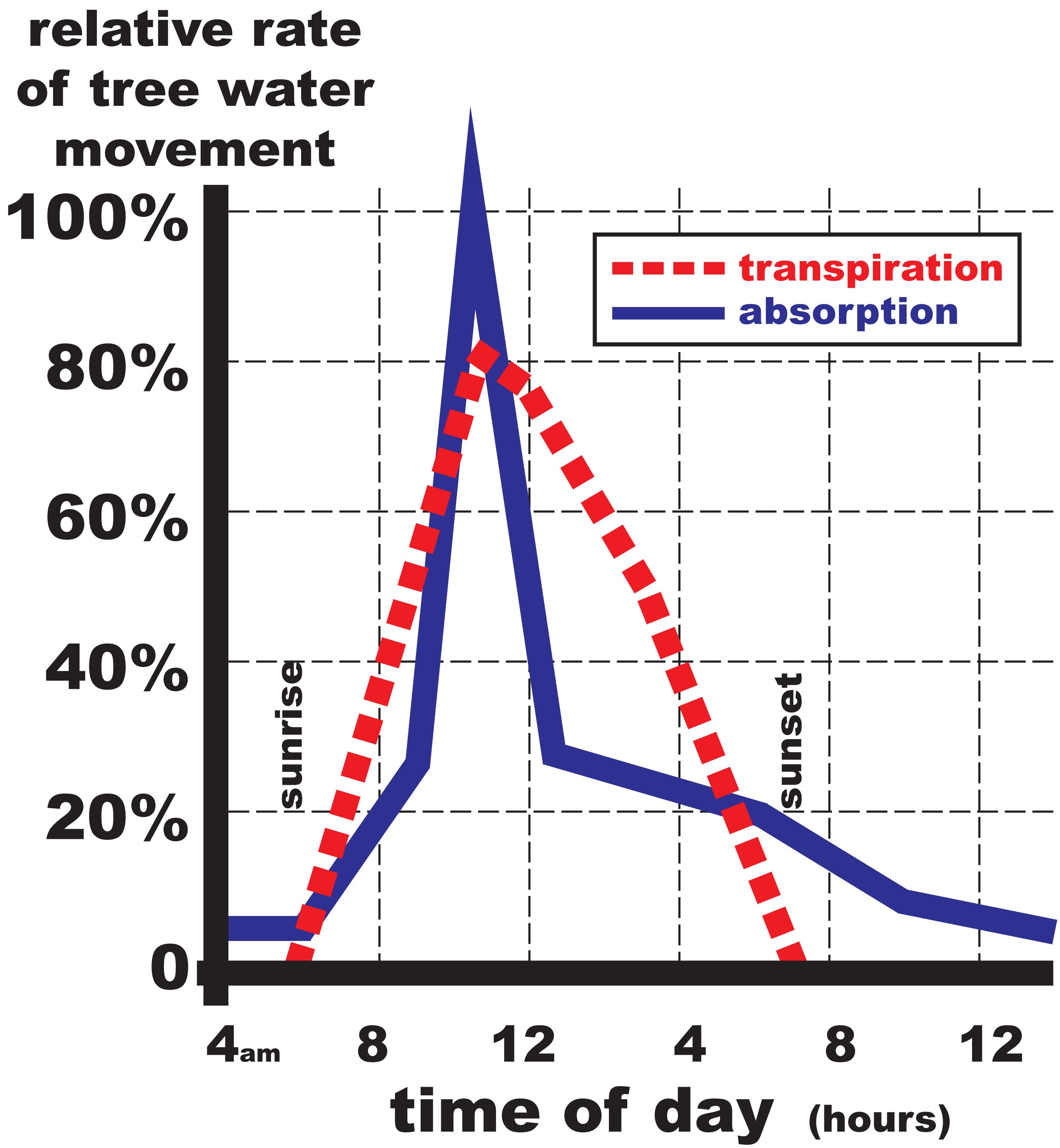

Figure 8: Example of the relative rate of water movement due to transpiration and root absorption within a tree over a growing season day under field capacity soil water conditions and no noon transpiration lag.
(derived from Waring & Schlesinger, 1985)

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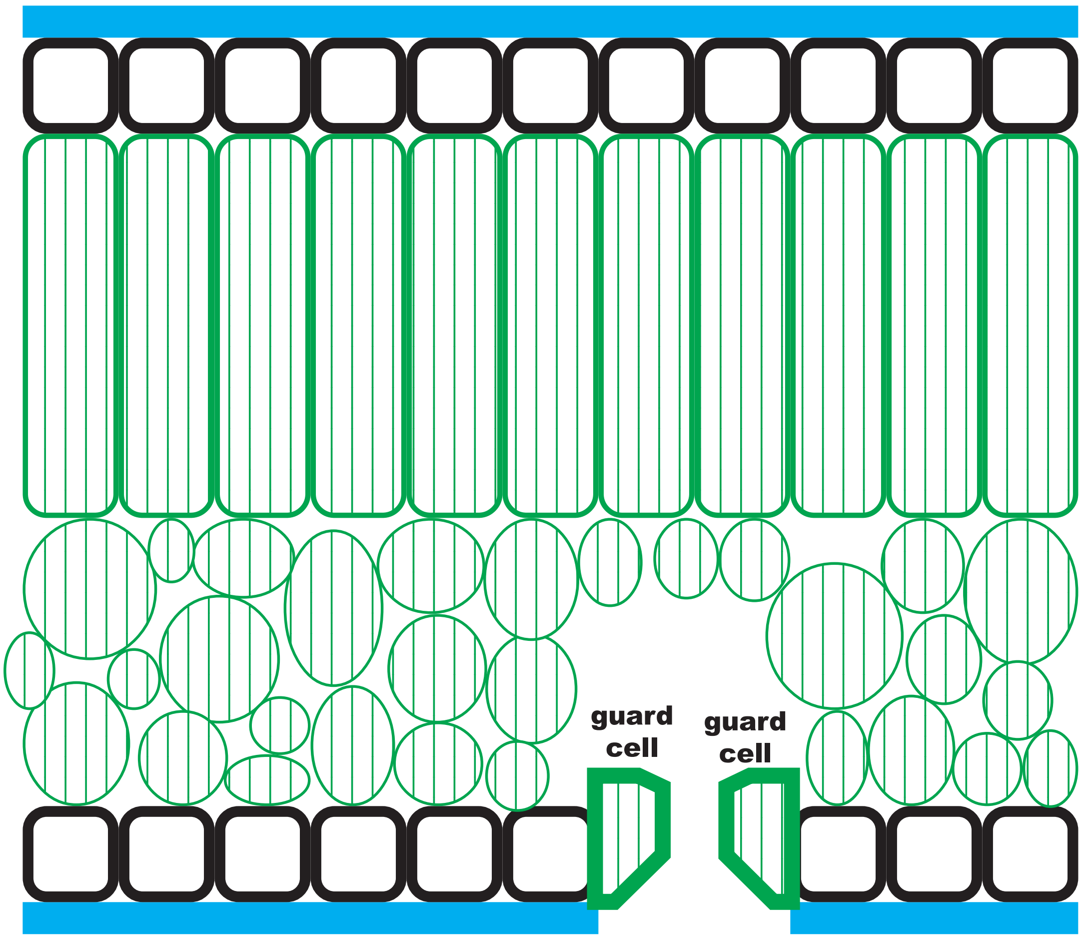

Figure 9: An idealized cross-sectional diagram of a tree leaf blade showing different non-vascular cell layers and a stomate. Cells with shading have chlorophyll. The top and bottom leaf surface is covered with a wax cuticle.

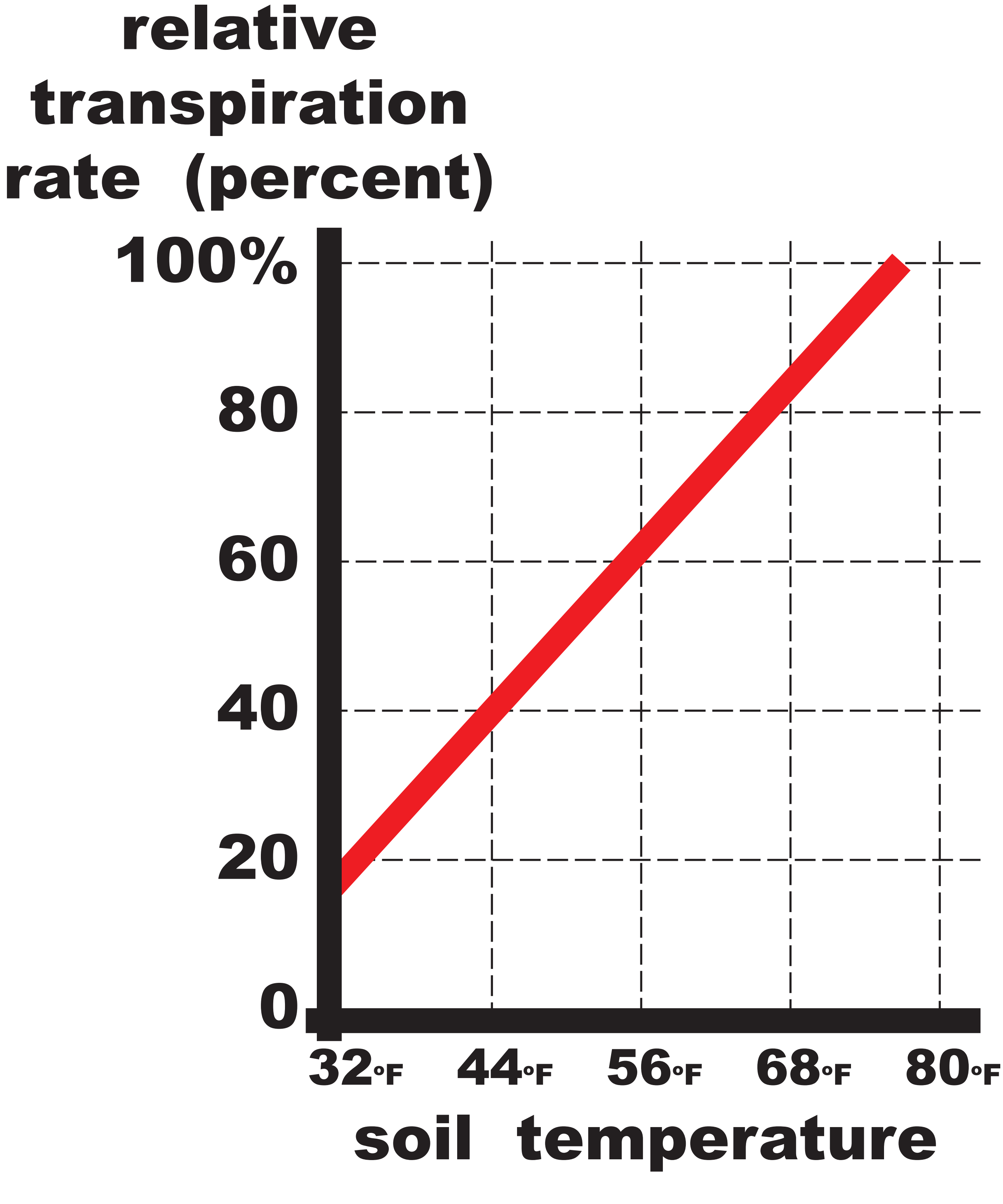

Figure 10: Example impact of soil temperature on transpiration in pines. (derived from Kramer, 1942)

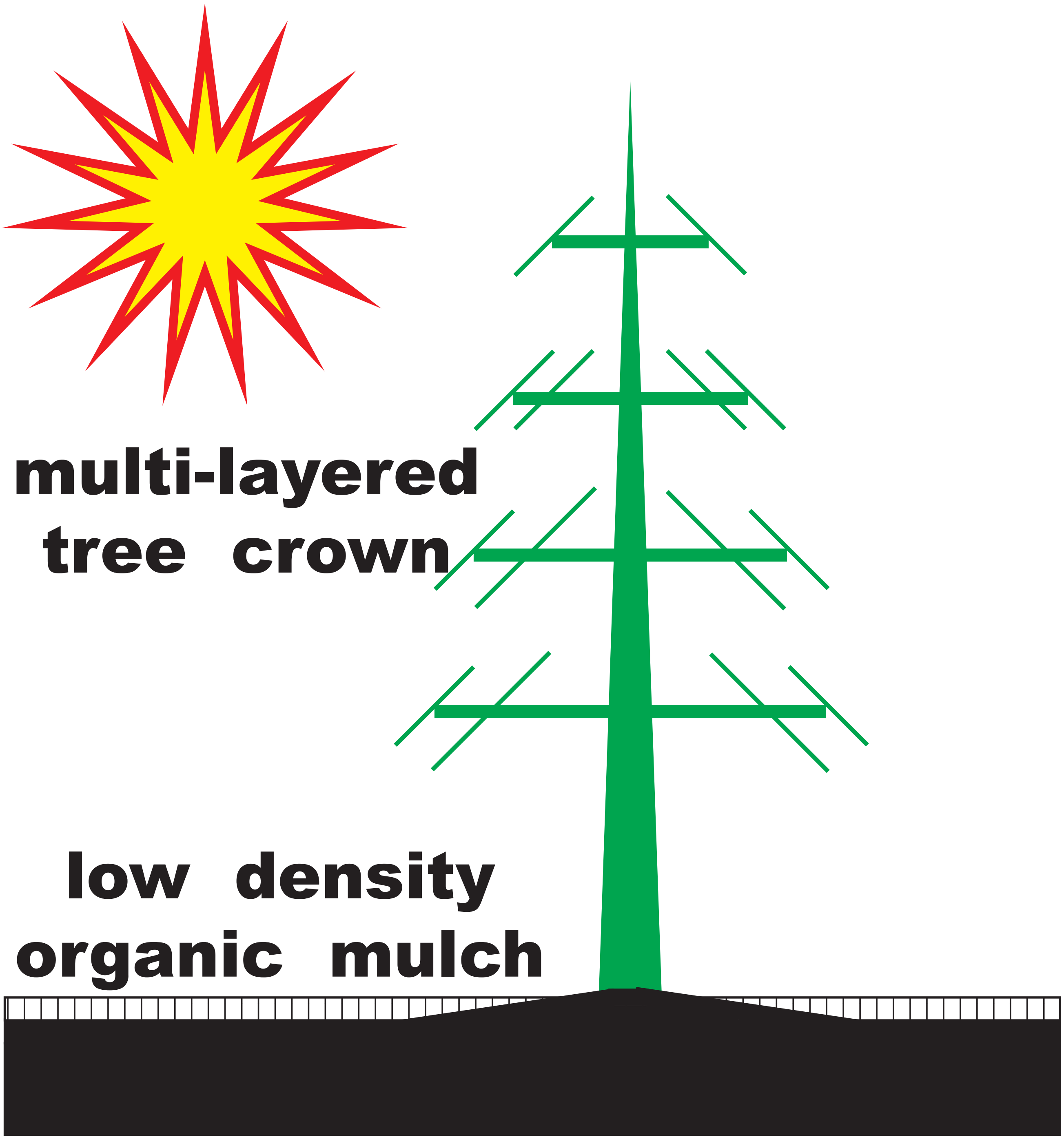

Figure 11: Diagram of tree with multi-layered crown and organic mulch bed. This tree form is efficient at conserving water because sunlight energy is spread over a vertically spread, relatively large, widely distributed crown surface area. Low density organic mulch assures little energy directly impacts soil surface.