Environmental Tolerance Series

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Trees & Cold Temperatures

by Dr. Kim D. Coder, Professor of Tree Biology & Health Care

Trees are found all over the globe in a variety of climates. One of the most limiting climatic constraint on tree growth is the lowest sustained temperature which a tree must endure. In addition to low temperatures, climate can damage trees by not allowing time reacting to temperature changes. Temperatures too low and changing too fast or too slow disrupts tree reactions. The tree growth line seen on high mountain sides are usually associated with low temperatures, wind stress, and water availability problems. Trees are not usually found in areas or at altitudes where sustained temperatures in the dormant season fall below -40°F (-40°C). Trees adjust to cold temperatures or die.

The Cold Earth

Most of Earth's land surface can have temperatures below 50°F (10°C). More than 55% of Earth's land can have temperatures below 32°F (0°C), and more than 40% of the land can have temperatures below a minus 15°F (-10°C). Most land is a cool, occasionally freezing, place for trees to live. Seasonal cold comes in climatic waves which are relatively predictable -- Winter will arrive. Unexpected cold temperatures can occur as climatic patterns are chaotically disturbed. Cold also occurs due to topographic position of the tree or its openness to the sky. Trees are damaged by cold temperatures.

Clearly trees have some way of dealing with cool and cold weather. Tree reactions to cold are more than suspending activities through dormancy. Trees have active mechanisms, genetically controlled, to carefully adjust and tune their tolerance of cold temperatures to minimize damage and energy expended. These cold tolerance mechanisms are reviewed here to help tree health care professionals and tree owners to better understand cold damage.

Defining Cold

Cold damage in trees arises from three complex events: 1) rate of temperature change; 2) lowest temperature reached in chilling, but not freezing; and, 3) lowest temperature reached in freezing. Freezing (frost) begins when liquid water starts to change states into solid ice crystals. Trees must react effectively to

changes in temperature to sustain life. Reactions to cool and cold temperatures are termed "cold tolerance" and are derived from several types of processes inside a tree.

Cold tolerance in a tree is derived from preparations to resist chilling impacts and preparations to resist freezing impacts. Chilling resistance is established by strong sensor and regulator communications within a tree setting up reallocation of resources and changing processes to prepare for the physical limitations of cooling temperatures. Freezing resistance is developed from two mechanisms: avoiding freezing and tolerating freezing.

Avoid & Tolerate

Trees are prepared to avoid freezing through their bark insulation which surrounds a massive wet mass of tissue in the stem. The heat transfer across the boundary between cold air and warm moist wood inside a trunk can be slow. Trees also avoid freezing through self shading of one layer of foliage by another. The canopy effect of the top layer of leaves on the space below helps lessen the depth under a tree crown to which radiative frosts penetrate. The canopy acts as an elevated mulch layer shielding everything below. Trees also avoid freezing by delaying ice formation. By breaking large materials into smaller components, water hydration shells become more highly subdivided and tightly held, reducing ice crystal formation. The more dissolved materials in living cells, the lower temperature any liquid water present can reach (to a point).

A second means for trees developing freezing resistance is through mechanisms which allow tolerance of dehydration. Tolerance of protoplasm within living cells to dehydration and associated ice crystal formation in cell walls is termed "hardened." Trees become hardened against freezing genetically and climatically across an annual cycle. Shoot hardening develops as temperatures fall and days become shorter (temperature and light dependent). Roots develop what hardening they attain as temperatures fall (temperature dependent). Hardening occurs in two stages: an initial stage where sugars accumulate and cells dehydrate; and, a second stage where membrane and processes changes in living cells are readied to facilitate water movement out of the cell. The chill short days of Fall pushes tree hardening. Figure 1.

Just Enough?

Cold temperatures initiate and move hardening processes along. The colder the temperature, the deeper into cold tolerance a tree moves. Over time, the ability to reach and sustain a level of cold tolerance, becomes more difficult. As warm days are interspersed with cold days, cold tolerance processes are disrupted and hardening is lessened. At the beginning of Winter trees develop strong cold tolerance. As late Winter approaches, freeze hardening disappears rapidly with every warm day. As early Spring arrives and dormancy is repealed, no cold tolerance remains.

Cold tolerance is an expensive survival process. Trees are prepared to resist cold temperature effects, but can only prepare for average temperature conditions for its particular gene set. Extremes of temperature, and rapid fluctuations in temperatures can destroy freeze hardening in the middle of Winter, leaving a tree open to cold damage. A tree will be hardened to withstand freezing only as much as needed. For example, a tree will not internally prepare for -31°F (-35°C) temperatures if days are hovering around the freezing mark. Only as much cold tolerance as needed, determined by the genetic system, will be developed.

Big Three Failures

The primary damage from cold is determined by three events within a tree: the first event is when a tree, because of sensor errors or genetic background, does not harden enough; second is a tree not hardening rapidly enough in Fall to resist the quick onslaught of Winter; and, third is a tree dehardening too rapidly in late Winter. In addition, trees stressed by pests or abiotic problems may not develop effective cold tolerance.

As light resources and temperatures change from typical growing season levels, sensors and processes in a tree begin to signal change. Figure 2. New processes are initiated and old processes are changed to meet new survival contingencies identified by tree genetic materials. Some trees do not have any capability to successfully react to cold. Other trees have only limited means of preparing to withstand cold temperatures.

Tropical and sub-tropical trees are not equipped to respond to cold temperatures. As progressively colder temperature thresholds are reached and passed, tropical trees begin to show physiological stress symptoms. The first temperature threshold is chilling below 65°F (18°C). As this temperature is reached, the living processes in a tropical tree begin to malfunction. Figure 3. Protein synthesis, photosynthesis processes, and membrane sustainability decline. More sulphur containing proteins, sometimes called stress proteins are produced. Potassium leakage from membranes and membrane-resident processing systems are disrupted.

Changing of the Fats

One of the classic concepts used to describe membrane problems in trees under chilling uses vegetable and animal fats as models. Primary tree membranes are all double lipid layers, or can be thought of as fat films or bubbles. For example, when butter comes out of the refrigerator it is fairly hard and difficult to spread. As butter warms it becomes easier to work over bread. As butter becomes too warm it starts to melt and is difficult to control. Margarines are easier to work with immediately out of the refrigerator, compared with butter, and may not melt as easily. Different fats behave differently depending upon their components. Fats and oils with fewer saturated fat constituents remain softer and more flexible when chilled compared with fat having higher saturated contents.

Tree membranes under cold conditions can be modified with the addition of more unsaturated fats to keep membranes functioning. Trees can change their membranes for better performance under increasing cold temperatures. Some trees can successfully modify membranes to handle cold conditions while other trees (primarily tropicals) cannot modify their membranes for dealing with slightly cooler weather. Most membrane changes are reversible, but damage to other processing systems may not be easily nor quickly recoverable even if temperatures rise.

How Low

Thresholds for tree tissue reacting to chilling are reached at 65°F (18°C), 50°F (10°C), and 40°F (4°C). Most tropical trees will be killed by 40°F tissue temperatures. These trees have no means to respond effectively to chilling below 50°F (10°C), and the physiological dysfunction culminates as 40°F (4°C) is approached. Temperate zone trees continue to modify their membranes as temperatures continue to fall. Membranes in temperate trees remain pliable and functional at cold temperatures. At 50°F (10°C), temperate trees allocate more carbohydrates and lipids to storage. As 32°F (0°C) is approached, special lipid and protein components are manufactured.

Different tree species differ in the depth of low temperatures each can survive. For example, live oak (Quercus virginiana) can survive down to about 20°F (-7°C); magnolia (Magnolia grandiflora) down to 5°F (-15°C); sweetgum (Liquidambar styraciflua) down to -15°F (-26°C); American elm (Ulmus americana) down to -40°F (-40°C); and, black willow (Salix nigra) down to -100°F (-73°C). These are tests made under ideal conditions with stock from the coldest parts of a species' range. Climatic races exist in trees. Moving a warm derived individual to a cold area, even though within the native species range for that species can cause damage or death. Trees are genetically programmed to handle average cold conditions of their local range.

Chill Down

Chilling down to 40°F (4°C) for short periods does not usually represent a terminal stress for most temperate trees. Tree stem tissue, composed of high moisture content wood, represents a huge heat reservoir or thermal mass. Rapid fluctuations in temperature above 40°F (4°C) to below 95°F (35°C) is stressful and requires physiological energy to make adjustments, but does not usually lead to death. Unfortunately, the thermal mass of the trunk and root-associated soil are not present at the crown edge where small twigs, vegetative and flower buds, and succulent growing shoots are present. Tips of the most upright and tallest twigs are most susceptible to wild variations in temperatures including cold winds and frosts.

As chilling continues and approaches 32°F (0°C) (the freezing point of pure water), new physical and biological problems begin to intensify. Freezing temperatures begin a series of changes in tree tissues. Water which freezes outside living cells release small amounts of heat as it freezes. This small amount of heat can slow ice from forming inside cells. A number of trees which handle chilling temperatures well, do not adjust effectively to freezing unless there is adequate physiological preparation time. Preparation time is essential to adjust to freezing temperatures.

Iced

Freezing means there is formation of ice crystals. The sharp, expansive ice crystals can form quickly and draw water molecules onto the ice surface, expanding the crystal's reach and extent. Ice crystal formation inside a tree cell membrane will puncture and crush cell structures and membranes. Ice inside a living cell leads directly to cell death. Ice crystals outside the cell membrane in a cell cavity or in cell walls are survivable. External ice crystals draw water molecules from living cells. As living cells loose water, they can shrink severely (as much as 2/3 previous size). This dehydration and shrinkage of living cells mean a loss of contact with surrounding cells and cell walls, and if all living connections are lost -- death from isolation.

As freezing commences in tree tissues, photosynthesis quickly declines and fails. Membranes are being unsaturated as fast as possible to allow permeability, but the pace is slowed by the low temperatures. It is essential water moves freely across membranes to prevent internal ice crystal formation. Energy production processes in cells and food (carbohydrate) allocation processes grind to a halt. Living tissue is being desiccated by freeze drying. Salts, organic acids, waste materials, and intermediate reaction compounds accumulate and become more concentrated. It is critical cold temperatures do not generate ice crystals inside living tissues.

Ice Daggers

Ice crystals stab and puncture living cells. Tree tissues which are fully hydrated are susceptible to ice crystal formation and rapid crystal growth. Hydrated tissue can be frozen with little damage if frozen quickly to prevent large ice crystal formation. On the other side, warming must be quick to prevent melting of small ice crystals and their sublimation onto large crystals. Natural warming is usually too slow to prevent large ice crystals from forming. Many times it is the slow warming and the changing ice dynamics inside tree tissues which kill cells. Dehydrated tissues (like a dry seed) can be kept for long periods in cold or freezing temperatures because there is little water to freeze into crystals.

Fast freezing prevents large, damaging crystals from forming. Slow freezing allows water to move in a vapor state onto ice crystal surfaces, potentially forming large ice crystals. Because of the thermal mass of wood tissue (due to water held in cell walls and living tissue), rapid temperature change is unusual. As freezing temperatures are approached, membrane changes which facilitate water movement outward can only occur at a slow biological rate. Cooling at less than ~3.5°F (~2°C) change per hour is needed to continually modify membranes in living cells. These interlaced biological and physical processes suggest slow cooling, fast freezing, and rapid warming are best to protect living cell integrity. Clearly these temperature change events do not occur in nature and so tissues are damaged.

Thresholds of Change

The defensive process in a tree to prevent cold damage changes with temperature. The first set of changes are to membranes and cell walls. Membrane are made more unsaturated and cells walls have more pectins and proteins temporarily applied. As 32°F (0°C) is reached, living cells are converting large starch particles into smaller sugars, and increasing the number of dissolved materials in cell protoplasm. Increasing solutes acts as a short term anti-freeze and is effective down to 30°F to 22°F (-1°C to -5°C). With solutes increasing, and ice crystals beginning to form outside cells, water from cells are pulled out onto the surface of ice crystals. It is critical there is enough volume of apoplast to support ice crystal expansion or the crystals will puncture and crush living cell membranes.

As temperatures drop further, any water present is in shells surrounding dissolved materials. These extensive liquid hydration shells inside living cells are supercooling. As cell temperatures reach 10°F (-12°C) much of the water in cells have already moved out to cell wall ice crystals. This dehydration process is critical to survival. Cell membranes must allow easy water escape and tolerate cell wall ice. Pectins and proteins in the cell walls fill gaps and minimize ice crystal size. Between -5°F (-20°C) and -36°F (-38°C) water reaches the limits of supercooling and begins to freeze. At -40°F (-40°C) cells have been "freeze dried" and all water remaining in hydration shells surrounding cell molecules are crystallized in place. Table 1.

Cell Changes

As trees are challenged with cold temperatures, cold tolerance genes turn-on. In Fall, growth regulation processes hasten senescence under light frosts, but are hindered by cell death from heavy frosts. Cold temperatures at any time trees have enough time to react initiate production of new proteins. These new proteins inside cells are designed to minimize ice crystal formation and size, and to buffer living components from dehydration. Cold temperatures initiate many changes inside a tree to better prepare for cold temperature – it takes cold temperatures to cause preparations for cold temperatures to be fully engaged. Unfortunately cold temperature also slows the pace of growth regulator transport, food reallocation, and greatly slow enzymatic functions. Energy production and use processes, water uptake and transport, and essential element processing slow greatly.

Thermal Mass & Exposure

Different tissues in a tree are capable of responding to environmental changes at different rates and to different degrees. Some of these differences are based only upon physical features of a tissue's hydrated mass and exposure to cold temperatures. Other differences seen in tree tissues are due to biological processes of preparation and tolerance. Active roots do not tolerate freezing well primarily due to their large surface area open to moist soil, lack of dormancy, and to smaller intercellular spaces for ice crystal growth. The root collar area is protected from cold damage primarily from its massive size and location in the soil. The root collar area does not develop cold tolerance well when compared to shoots. Stem tissues are protected somewhat from cold by the trunk's large hydrated mass (the trunk is slow to change temperatures). Living cells in the trunk develop strong cold tolerance over time.

As stem tissues are subdivided into progressively smaller branches and twigs, the thermal mass of tissues dramatically decline and exposure to radiative and advective chilling processes dramatically increase. Development of cold tolerance is great, but wide fluctuations in temperature occur, including surface ice crystal formation in frosts. Well hydrated, succulent, new small tissues, like new leaves, are highly susceptible to freezing. A number of tree flowers and the phloem which supports their development are highly susceptible (18°F (10°C) more sensitive than twigs) to brief freezing temperatures. More active tissues are more easily damaged than inactive or dormant tissues by cold. On the other hand, given time to react to temperature changes, dominant buds may be more tolerant of cold than lateral buds.

Physical Forces

Freezing can kill living cells. Freezing also exerts a variety of mechanical forces in tree tissues. The cambium area with developing xylem, ray, and phloem cells is susceptible to cold damage. The cambium is protected somewhat by insulating bark and by the thermal mass of the stem beneath, but is prone to damage. Cambial area damage can include wood faults called frost rings where newly developed xylem has been damaged or killed. Freezing of woody tissues causes greater tangential stress than in other directions. Any tissue growing over and sealing small injuries can be pulled apart along the cell fiber length to form a potentially elongating fault called a "frost" crack or rib.

Within large dead xylem cells transporting water, there is no active resistance measures to freezing. Free water in xylem freezes to ice as temperatures pass 32°F (0°C). With trunk mass and bark coverage, freezing of free water in xylem elements requires cold temperatures for an extended period. Xylem elements in small twigs and leading to flowers, leaves and buds, are quickly frozen. Freezing causes any dissolved air in water to be pushed out of the ice and collects in small bubbles. If temperature of wood and ice reach below 28°F (-2°C), only a small volumes of the air bubbles can be redissolved upon thawing. Small bubbles coalesce to form large, xylem blocking embolisms upon thawing. Embolisms in water conducting tissues reduce water flow by more than 98%.

Management Symptoms

Most management activities have some impact on the cold tolerance of a tree by modifying reactions in how temperature change is sensed or in how genetic systems prepare cells. For example, acidic or oxidative air pollutants damage tree surfaces and interfere with freeze hardening. Management activities to minimize cold damage in trees are mostly up-scaled versions of small plant protection – cover and wrap. More intensive management for cold protection is heating surrounding soils or air, circulating air, or removal of ice nucleating bacteria. Reduction in ice nucleating particles or bacteria on tree surfaces can slightly lower ice formation thresholds but account for only 1/3 of freezing problems.

A great deal of tree damage from cold temperatures arise from different tree parts having different temperatures. For example, if the roots are in frozen soil and the top is in cool, not frozen temperatures, the top will be damaged by excessive water loss (Winter drying or burn). Localized warming, such as the Southern sunny side of a thin barked tree, can produce as much as a 25°F (-4°C) temperature difference around a stem. Localized freezing and thawing causes drying and death to patches of tissues, called sunscald. Night to day temperature differentials around the freezing mark can be damaging as ice crystal form, grow, and contract.

Management Solutions

If cold temperatures are a key stress for a tree and on a site, several solutions to cold tolerance can minimize growth constraints. The first solution is site selection. Sites open to radiative frosts, strong advected air flow from cold areas, or areas of cold air drainage should be identified. It is not the general temperature climate to attack in management, but small variations caused by site which offer some small relief to cold tolerance processes. A second solution to cold tolerance concerns is tree selection. Tree cold tolerance is a genetics regulated reaction. Cold tolerance is a highly selected processes over time and many tree generations. Pick trees adapted to the temperature climate. Tree gene sets from more than 100 miles North or South of your location may have increased pests and stress problems due to poor responses to cold temperatures.

Conclusions

Cold tolerance in trees revolves around good sensing and genetic expectations of cold temperatures, coupled with effective responses to cold temperature impacts. In trees, ice crystal formation and dehydration must be dealt with for successfully surviving cold temperatures.

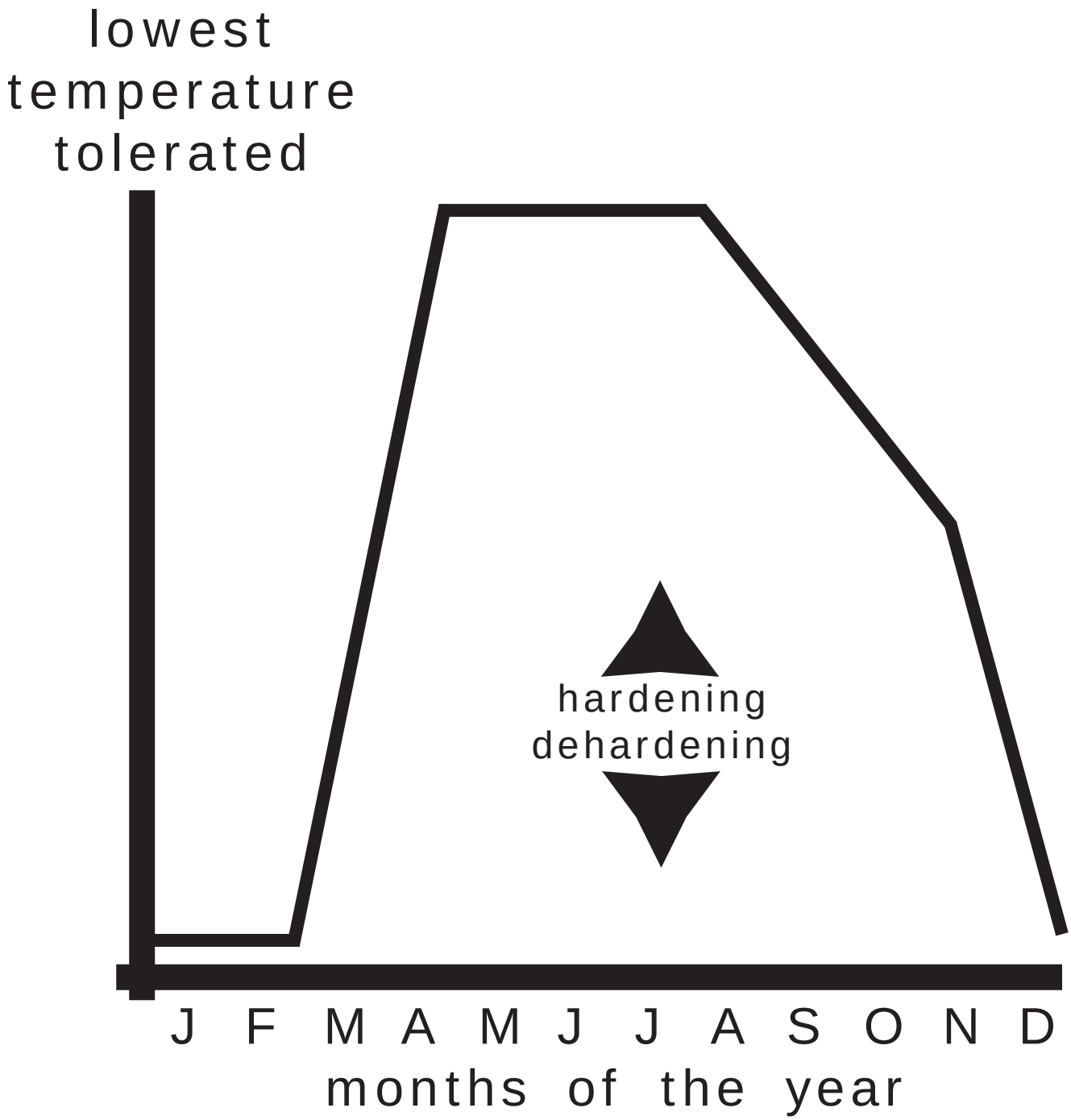

Figure 1: General hardening / dehardening cycle in trees over one year.

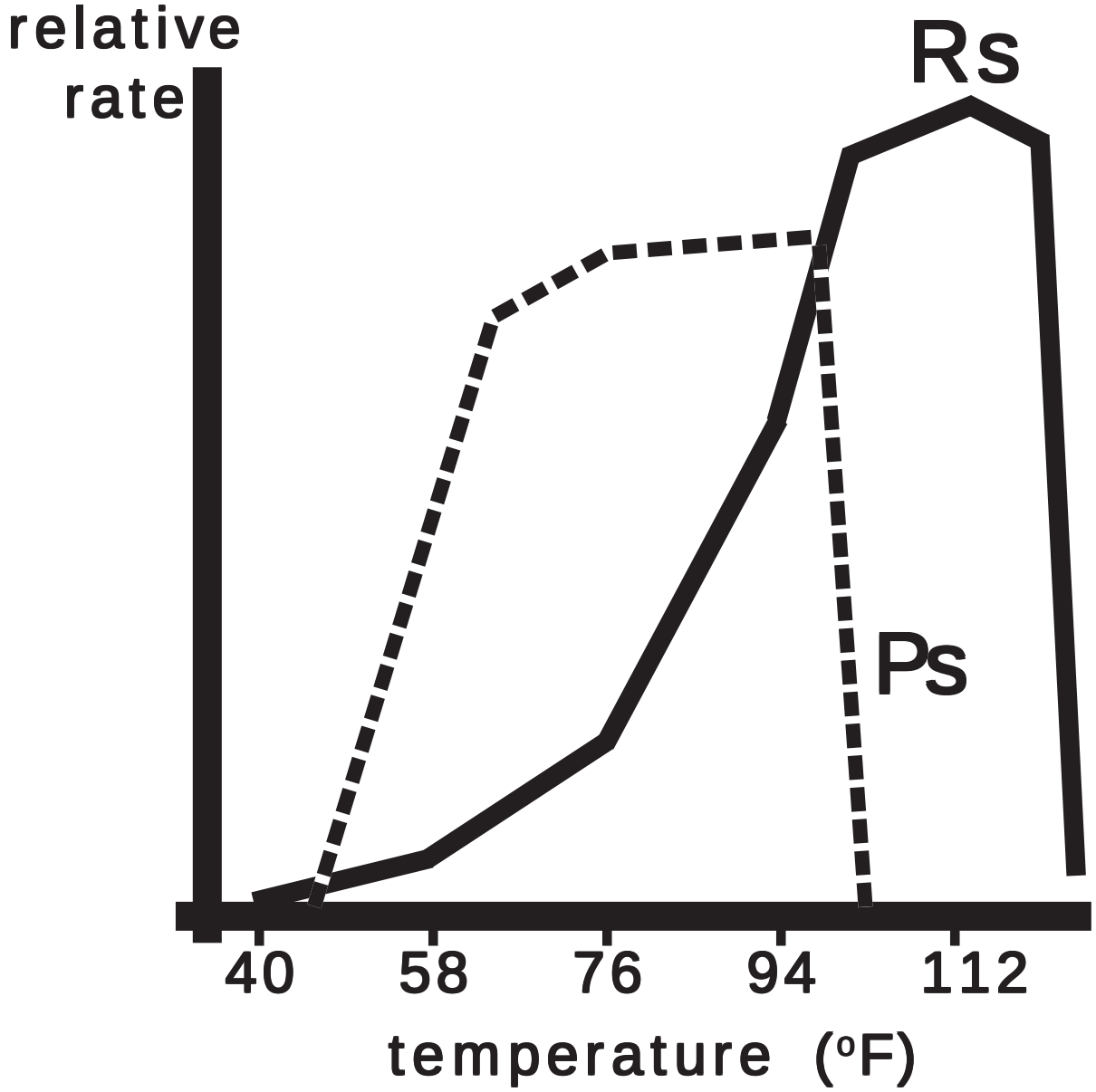

Figure 2: Relative rates of photosynthesis (Ps) and respiration (Rs) in a tree. Note respiration declines exponentially with decreasing temperatures and photosynthesis quickly falls as 60°F (15°C) is passed.

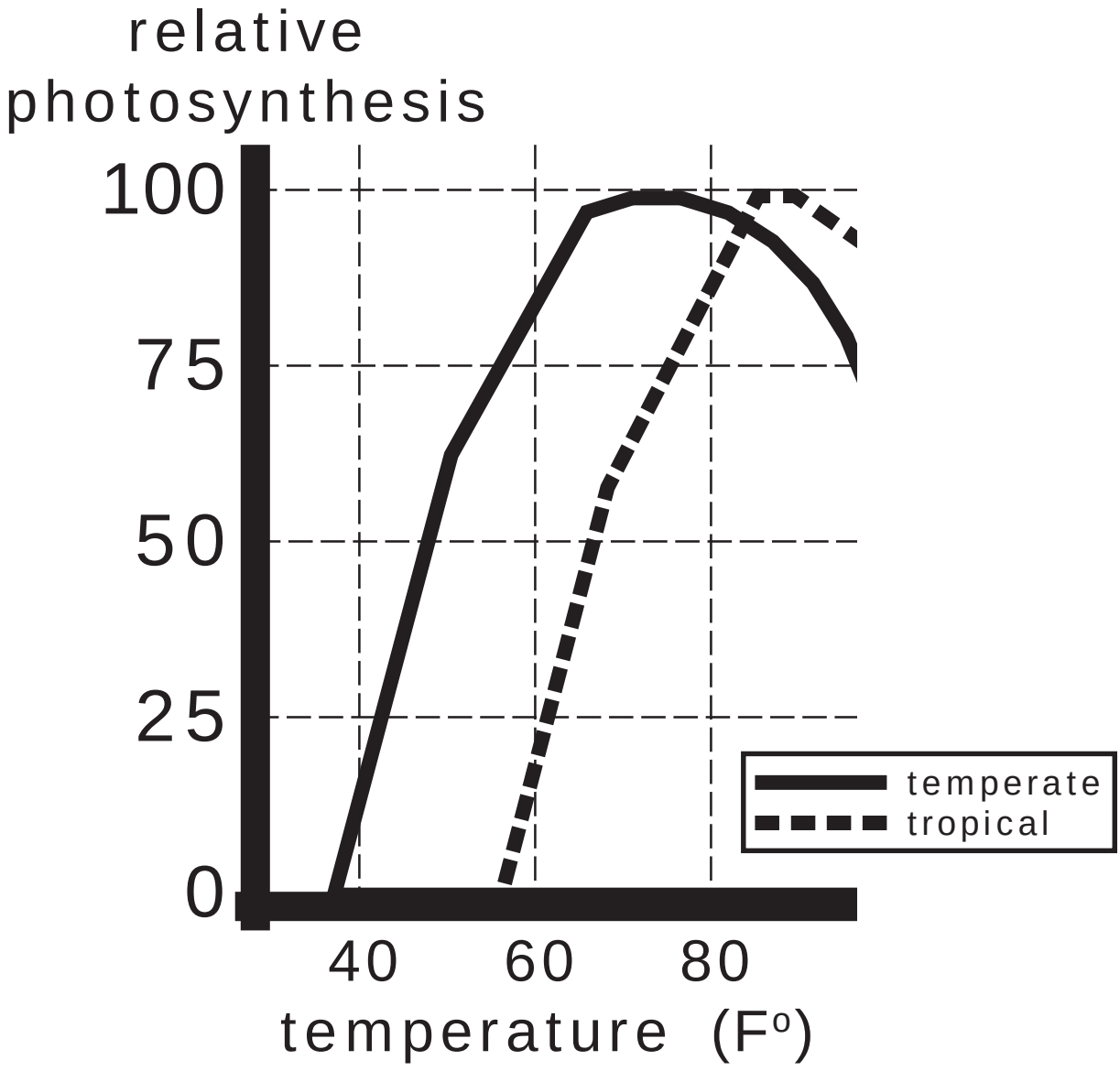

Figure 3: Impact on photosynthesis of temperature for temperate and tropical tree species.

Table 1: General tree reactions to different temperatures below 42°F (+5°C).

stage	temperature	reaction in trees
Preparation	+5°C to -1°C (42°F to 30°F)	-- Cell membrane changes and deposition of materials in cell walls to minimize ice crystal formation and size.
Antifreeze	-2°C to -5°C (29°F to 21°F)	-- Ice crystal formation slowed by more small dissolved particles in cell (increase in solutes).
Dehydration	-6°C to -15°C (22°F to 4°F)	-- Cells continue to dehydrate and large crystal formation is minimized in cells walls.
Supercool	-16°C to -30°C (3°F to -22°F)	-- Remaining water continues to supercool and is held in small hydration shells around dissolved particles.
Freeze Dried	-31°C to -40°C (-23°F to -40°F)	-- Complete dehydration of cells and crystallization of any water remaining.