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Leaf Senescence & Abscission

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Spring flower colors are raised in fall to crown the trees. Many of the pigments are the same but the colored containers have changed from dainty petals to coarse, broad leaves. It is living leaves that reveal in their decline and fall last summer's results and next spring's promise. The living process in a tree generating autumn colors is called senescence.

Designer Colors

Senescence is the pre-planned and orderly dismantling of light gathering structures and machinery inside a leaf. Part of senescence is the development of a structurally weak zone at the base of a leaf stock or petiole. Live cells are needed in the leaf to unmask, manufacture, and maintain the tree pigments we appreciate as autumn colors. Fall coloration is a result of this positive life process in a tree. Freezing temperatures kill leaves and stop the senescence process with only decay remaining.

Endings & Beginnings

Senescence is a planned decommissioning process established with leaf formation. Inside the leaf, as photosynthesis began to generate food from carbon-dioxide, light, water and a few soil elements, a growth regulation timer was started that would end in Winter dormancy. The fullness of Summer production helps establish dormancy patterns as dormancy processes establish allocations for the next growing season.

In senescence, a tree recalls valuable resources on-loan to the leaves, and then enter a resting life stage. The roots continue at a slower pace to colonize and control space, and gather resources, waiting for better conditions. Frosts and freezing temperatures kill living cells in tree leaves. Dead cells cannot conserve and transport materials back into the tree, and so do not produce colored pigments as a by-product. Temperature-killed leaves, which have not started to senesce, are a sign that many tree resources were unable to be recalled and now lie outside the tree in falling leaves.

Green Is Life

To appreciate new and unmasked colors of fall, consider the color of tree life -- green. The green color comes from a large, hard-to-maintain and expensive to build molecule with a magnesium atom in its center called chlorophyll. Chlorophyll is the most precious of molecules. The tree conserves, protects, and maintains chlorophyll. With failing light, food, elements or energy, loss of the chlorophyll pigment is a first visible sign of problems. Yellowing or chlorosis in trees is a symptom of many different pests and environmental impacts because chlorophyll manufacture and maintenance is so sensitive to damage.

Trees do not manufacture chlorophyll until well illuminated. In healthy but unlighted tissues, a good supply of colorless chlorophyll components (requiring iron (Fe) to make) are kept in storage. Until there is light to capture, chlorophyll is not produced. After leaf tissues are exposed to light, the pale yellowish tissue colors are cloaked by the green of chlorophyll. Chlorophyll is clearly visible and concentrated in leaves. Chlorophylls are also found in most near-surface tissues in a tree exposed to light. The inner bark of twigs (cortex), light-exposed roots, and inner portions of buds all possess chlorophyll.

Last Effort

In fall, with changing resource availabilities (like light quantity and quality), chlorophyll production and maintenance begins to decline. The preliminary steps needed to make chlorophyll are slowed and stopped by low temperatures, regulation signals generated from the tree's light sensors, and a build-up of photosynthesis by-products. At the same time, longer dark periods, cool temperatures and bright sunlight, help initiate chlorophyll demolition. Drought conditions can accentuate chlorophyll loss. The green curtains in the leaf begins to withdraw.

Leaf starch or stored food, begins to be rapidly broken apart and shipped out of the leaf. What chlorophyll remains, continues to generate energy gradients used to power remaining living cells. The products being shipped from leaves are having a more difficult time escaping through the developing abscision zone in the leaf-stem base. More sugars and mobile elements are unbound in the transport and production cells. These conditions lead to chlorophyll loss when leaf energy concentrations are still relatively high.

Revealed Colors

Chlorophyll veils slowly drop away and reveal a great pallet of colors, some brand new to this autumn and some having lain hidden all season. One of the tough pigments that share chlorophyll's cellular containers, are the red, orange and yellow carotenoids. These pigments were made to shield and protect chlorophylls, but now can be clearly seen. Some color pigments are newly made using materials that cannot quickly leave the leaf. Rich sugar contents, slight drought stress, and developing element deficiencies in living cells help initiate anthocyanins, blue to red colored pigments used to protect light sensitive processes in leaves.

The artistic pallet of tree colors is diverse. Carotenoids are like bright oil paints. The always variable anthocyanins are like watercolors, blending across a tree covered landscape. Behind all these colors remain the deep browns of tannins (the color of tea) and the basic light browns of tree tissues. The number of different color combinations is almost infinite. See Appendix 1 for color expressed by species. In some forests, all the colors contrast with evergreen trees. The colors in deciduous leaves eventually fade to brown, the color of the earth.

Failing Connections

A weak zone at the leaf base is initiated when normal growth control messages and supply of food materials moving out of the leaf are reduced. Shorter days, longer cool nights, and changing light quality help throw internal genetic switches which change growth regulators and food allocation patterns. The tree begins to build a physical and chemical seal across several layers of living cells near the leaf stem base. On the leaf side of the seal, cell walls are weakened and become thinner. Across this basal zone of change, the living connections between food transport cells (phloem) become more tenuous.

Water connection (xylem) cells continue to supply water to replace evaporative losses in the leaf. These water supply cells are part of strong but dead connective strands within the leaf stem. As the leaf blows in the wind and is loaded by rain, the leaf stem starts to tear at its weakest point, the leaf-stem-base. As leaf-stem-base cells weaken, internal pressure causes them to swell more than surrounding cells. This mechanical strain causes one living cell to shear away from its neighbors. This zone of separation, or abscission zone, is a design feature of many mature tree leaves.

Falling Leaves

A point is reached when all living cell connections are broken at the leaf-stem-base and only the dead water connections hold the leaf onto the tree. Only a little bit of force is needed to snap these connections and the leaf will fall to the ground. A single fall wind storm can sweep the colors from the trees. The wound left on the tree (a leaf scar), sometimes highly characteristic of a given species, is the outward face of a constructed barrier wall established to keep the environment outside.

Breaking Away

Trees shed many parts besides leaves, including fruit, flowers, bud scales, trichomes, twigs, and bark. The mechanism of tissue shedding has two components – active and passive. The active part is development of an abscission zone. Tree tissues, like leaves, are actively prepared for removal through biological and mechanical means. The passive part of tissue shedding is development of structurally weak areas along which force can be concentrated and tissues torn away by the environment. In other words, some tissues have cells which are forcibly broken apart, while other tissues have built-in weak zones which allow these tissues to be ripped away.

Shedding

Trees are shedding organisms. Trees shed inefficient or dead tissues internally as heartwood. Trees also shed tissues to the outside as root turnover, leaf and twig abscission, bark shedding, and through general compartmentalization. Shedding allows trees to maintain the most effective and efficient tissues to assure survival. If internal allocation problems or external environmental damage occurs, trees can eliminate unmaintainable living mass through shedding.

Leaf fall at the beginning of the dormant season in deciduous trees is one of the most visible of all shedding processes. By carefully examining fallen leaves and the leaf scars from where each fell, several things are apparent. The wound is usually smooth with vascular tissue ends clearly visible. The wound looks as though the leaf snapped-off in one catastrophic moment. Actually, leaf abscission is the culmination of many events and actions by the tree and within the environment.

End of Senescence

Abscission is the last step in a planned senescence process within tree leaves. Senescence is a series of events which allow trees to conserve resources, prepare for a resting period, and shed inefficient tissues. Senescence is not a disruptive series of unrelated events cued by worsening climatic factors. Senescence is a highly ordered and carefully controlled set of steps initiated in preparation for a resting stage in above-ground portions of a tree.

Near the end of the senescence process, designed fracture or failure lines develop at the base of tissues to be shed, like leaves. These prearranged fracture lines allow leaves to tear away without exposing the tree to additional damage. Leaf abscission is part of a process which allows the tree to seal-off tissues which will soon be killed or consumed by the environment. Trees use a senescence sequence to systematically remove valuable resources from leaves before they die. Once the resources are recaptured by the tree, dead and dying leaf tissues can then be shed. Frosts and heavy freezes at night, or sustained below-freezing air temperatures, quickly damage living cells in leaf blades and petioles. Once killed, all the resources leaf cells possess are unavailable for reabsorption into the tree.

Abscission Zones

Abscission zones occur at the base of leaf petioles and at the base of leaflets. Figure 1. Abscission zones are designed to allow for leaf shedding. Leaves are shed through a number of biological actions which weaken cell walls and initiate cells tearing away from one another. Abscission zones are composed of three critical portions: A) a cell wall degradation area; B) a shear force generation area; and, C) a tree protection zone. All three abscission zone portions are required for successful leaf shedding and effective tree survival. Most abscission zones are pre-positioned to facilitate shedding. Abscission zones may not be needed or used, but they are set-up to act as a potential barrier and boundary.

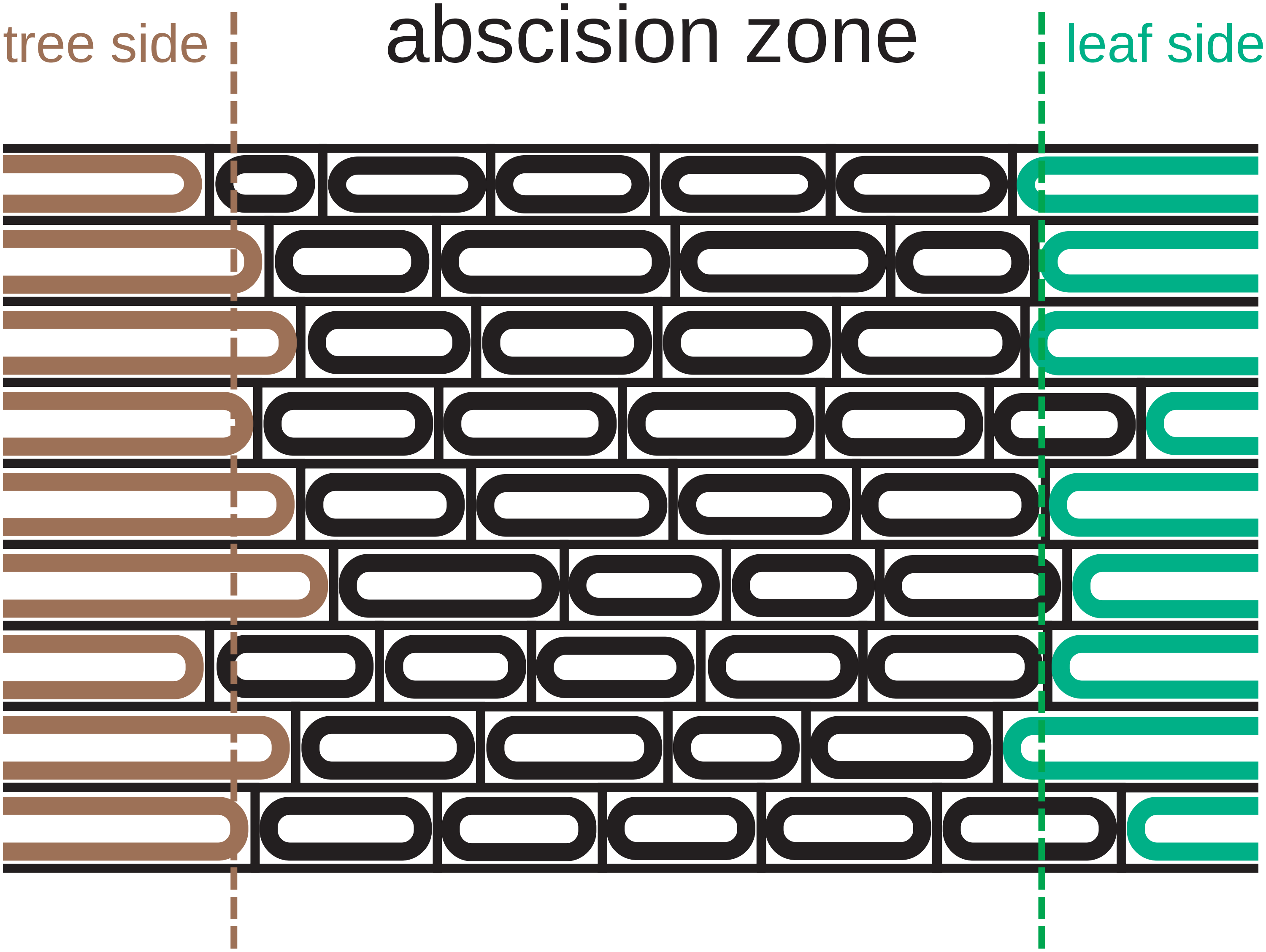

Figure 1: Two-dimensional diagram showing shorter cells in a leaf base abscision zone.

Wall Weakening

The abscission process begins with growth regulator signals initiating cellular changes. Abscission zone cells secrete pectinase and cellulase (wall degradation enzymes). These enzymes degrade the strength of the middle lamella and primary wall between cells. Figure 2. The middle lamella, the "glue" which holds cells together, begins to dissolve in the abscision zone.

At the same time, surrounding primary walls begin to swell from changes in chemical components. Calcium bridges across cell wall materials are removed. Cell wall changes are caused by enzymes and other materials deposited in cell walls produced by surrounding living cells. The cells in the abscission zone are dense with cytoplasm and organelles. Each cell is actively respiring and using energy to produce abscission materials. These cells remain alive and active until abscission.

More Wall Changes

As cell wall interconnections are weakened, water pressure within thin walled cells (turgor pressure in parenchyma) cause these cells to expand. As cells expand, they generate shear forces by pushing and pulling on surrounding weakened walls. Mechanically, fracture lines begin to develop between cell walls. In addition to internal forces, gravity and wind tugging on leaves help fracture lines grow.

As cell walls pull apart from one another, this open wound is being closed by deposition of blocking materials and protective compounds on the tree side. A strong protective boundary zone is prepared to defend remaining tree tissues from the environment and pests. Tyloses, suberin, lignin and other protective boundary-setting materials are developed and deposited on the tree side of the abscission zone. Figure 3.

Passive & Active

In the abscission zone, xylem elements and epidermis cell walls are either not degraded or are slow to weaken. These cells usually must be torn, stretched, or broken physically after connections between surrounding cells have been already fractured. Many types of circumstances like gravity, wind, precipitation and animal actions can break apart any remaining connected tissues and allow leaf fall.

The abscission process does require cell respiration and turgor pressure control. Breakdown of select carbohydrates, loss of small but key carbohydrate and protein wall components, increase of pectinase and cellulase enzymes, and removal of calcium wall connectors lead to wall weakening. As cells walls weaken further, parenchyma cells continue to osmotically expand, generating tremendous shear pressure on surrounding cell wall connections. Water is needed to generate this shear force. Rainfall or irrigation after an extended droughty period may lead to immediate leaf fall.

Control Mechanism

Auxin is a primary growth regulator produced in the leaf and slowly transported toward the leaf stem base through living cells. As long as auxin is effectively being transported across the abscission zone, abscission zone cells remain unreactive. As auxin production begins to wane in fall and auxin transport rates begin to decline due to less auxin availability, damage to living cells transporting auxin, and/or accelerating infection or wounding of living tissues by pests, cell wall changes are initiated.

Cell wall changes increasingly inhibit auxin transport, increase auxin concentrations on the leaf side, and accelerate ethylene production. Small amounts of ethylene hasten abscission zone development. ABA (abscisic acid), responsible (in part) for dormancy on-set in the leaf, stimulates ethylene production and inhibits auxin transport further.

In The Zone

Abscission zones in trees can be between 5-40 cells wide. Within this abscission zone only 1-3 cells will disconnect from each other. Cells in the abscission zone are the same types as found elsewhere in the tree. But, abscission zone cells tend to be smaller, more densely packed, with no intercellular spaces, less lignin, and have

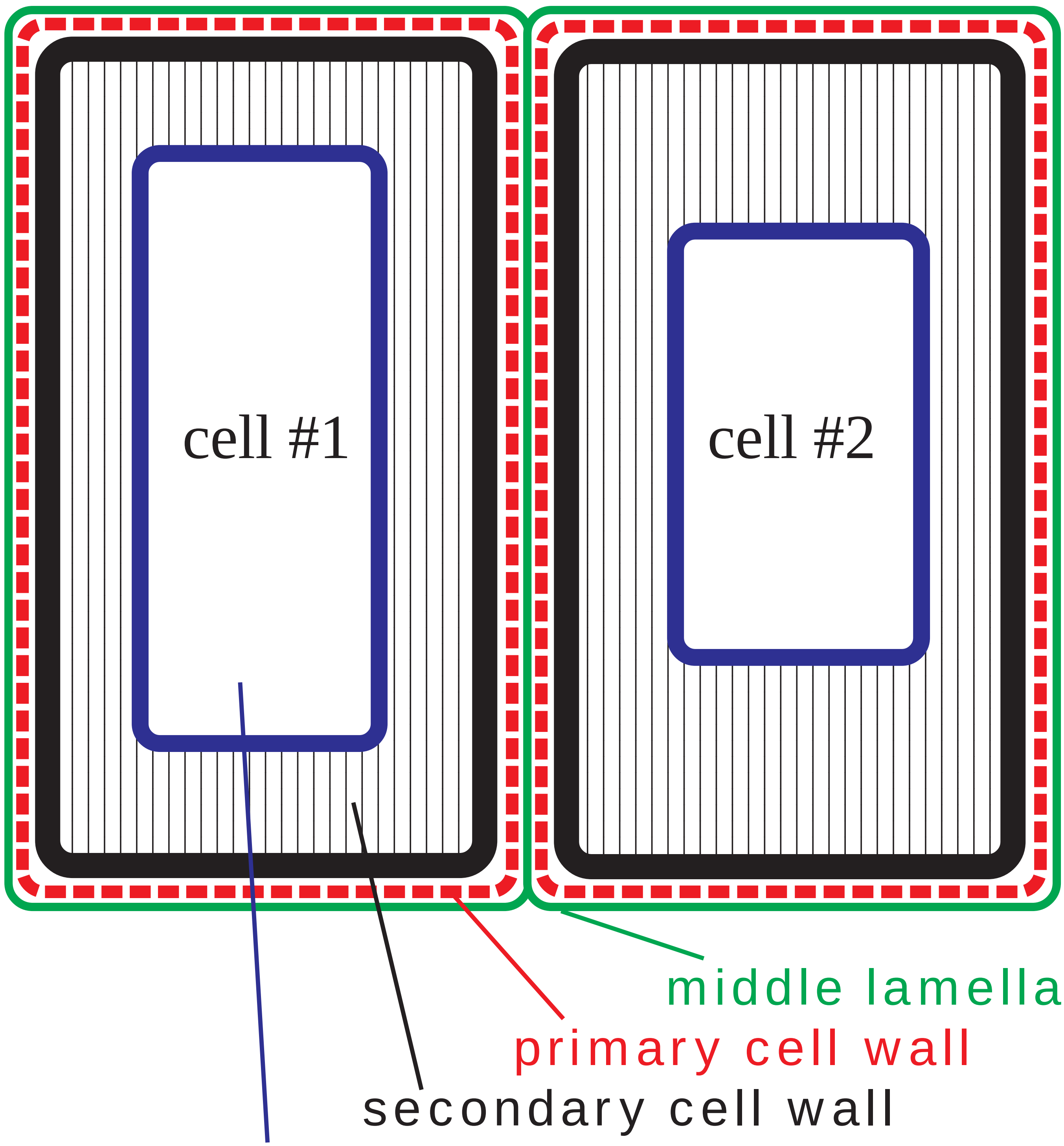

Figure 2: Two-dimensional diagram showing wall components of adjoining cells.

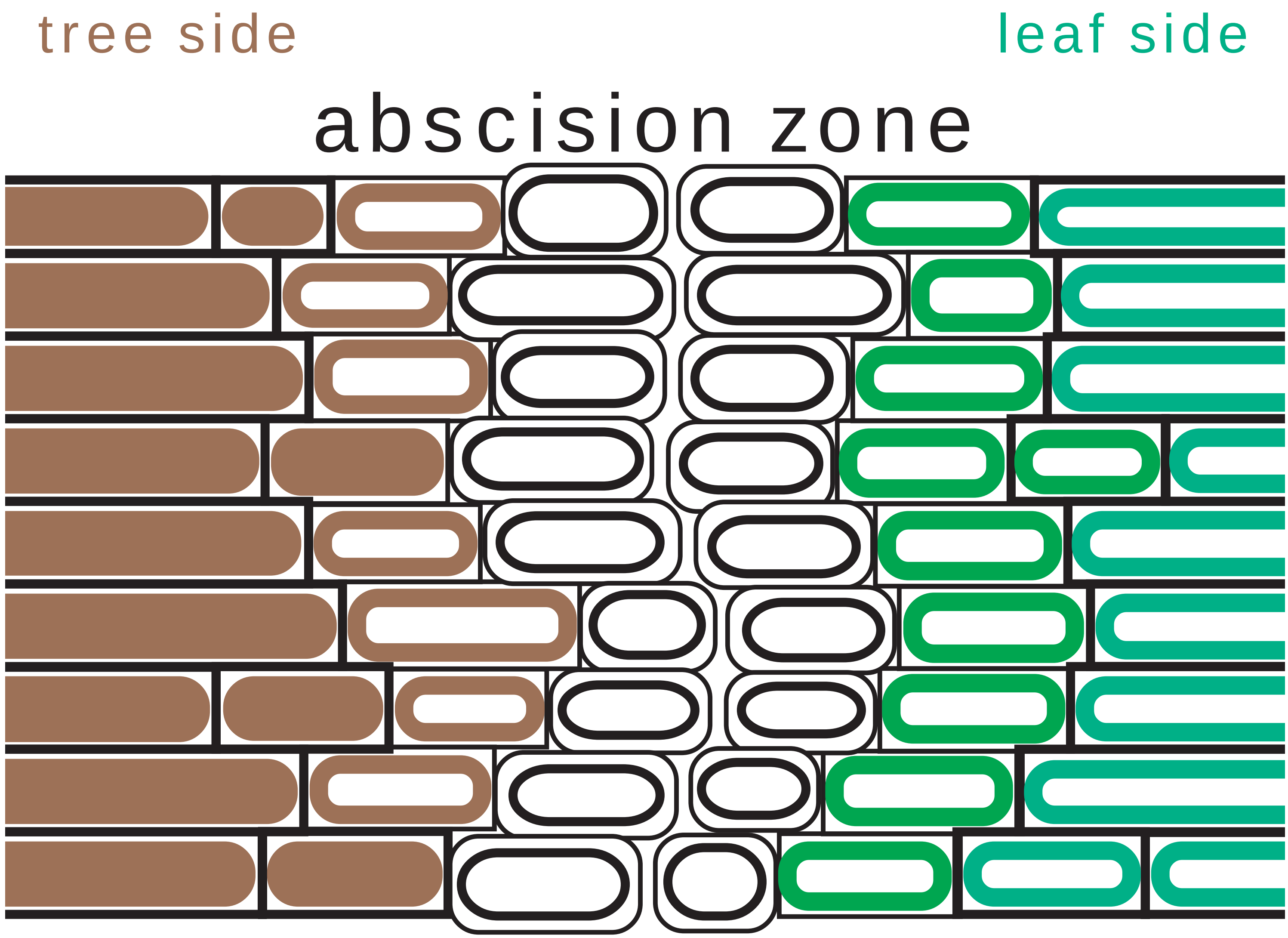

Figure 3: Two-dimensional diagram showing cells in a leaf base abscision zone with a fracture line between cells. Note tree protection zone on the tree side, wall degradation areas, and cell expansion zone all disrupting cell-to-cell connections.

remained in a cell division phase longer than surrounding cells. Additional cell divisions in this zone prepares these cells for later abscission processes. Starch is stored in the abscission zone cells to assist in generating turgor pressure and enzymes for wall degradation.

In most abscision zones there is a single fault line which develops and is accentuated by additional wall degradations. Cells adjacent to fault line cells will have weakened walls also, allowing any fractures to propagate along several paths for short distances. Rarely, several full fault lines occur leaving the abscission wound ragged-looking. Fault lines follow the path of the middle lamella between cells.

Tree Responses

Deciduous trees do not loose all their leaves at once or just in the Fall. The larger and stronger any connecting xylem elements through the abscission zone, the longer leaves may be held on the tree. Some species do not fully set an abscission layer until early Winter. In other species, shear forces are not concentrated in the abscission zone until the beginning of the Spring growth period. Juvenile trees may not establish effective abscission zones at all and hold dead leaves throughout the Winter. Understory trees may hold leaves because of juvenility or because they are protected from climatic events which could knock off leaves. Some trees may abscise all their leaves except on new late-season sprouts.

The End?

Leaves are discarded by their trees to assure valuable resources are conserved, and in order to protect the tree. Leaves are designed to be disposable and pass through a senescence process which ends with abscission. Leaf abscission is both an active and passive process designed to seal-off and shed old tissues. Abscission of tissues help trees survive another year.