Falling Tree Leaves: Leaf Abscission

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Introduction

Trees loose their leaves by design. When leaves become inefficient and unable to produce food and growth regulators, a process of shutting-down and sealing-off begins. Trees shed many parts besides leaves, including fruit, flowers, bud scales, trichomes, twigs, and bark. Leaf abscision is the best example of the process of tissue shedding in trees.

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 actively 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 excessive 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 noticeable. The wound is usually smooth with vascular tissue 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.

Senescence

Abscission is the last step in a planned senescence process within tree leaves. Senescence is an ordered series of events which allow trees to conserve resources, prepare for a dormant 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 period in above-ground portions of a tree.

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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.

Frosts and heavy freezes at night, or below freezing air temperatures, quickly damage living tissues in leaves and petioles (leaf stems). Once killed, the resources leaf cells possess are unavailable to the tree. 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 are shed from 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 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 an established barrier and boundary, if needed.

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. All cell wall changes are caused by enzymes and other materials deposited in the 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. 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)

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 of the same types as found elsewhere in the tree. Abscission zone cells tend to be smaller, more densely packed, with no intercellular spaces, less lignin, and have 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.

Passive & Active

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

The abscission process does require 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 bridges lead to wall weakening. As cells walls weaken, parenchyma cells osmotically expand, generating tremendous shear pressure on surrounding cell wall connections. Water is needed to generate shear force.

Control Mechanism

Auxin is a primary growth regulator produced in the leaf and slowly transported toward the 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 of living tissues by pests, cell wall changes are initiated.

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

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 through out the winter. Understory trees may hold leaves because of juvenility or because they are protected from climatic events which could knock off the leaves. Some trees may abscise all their leaves except on new late-season sprouts.

Conclusions

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 to seal-off and shed old tissues. Abscission of tissues help trees survive another year.

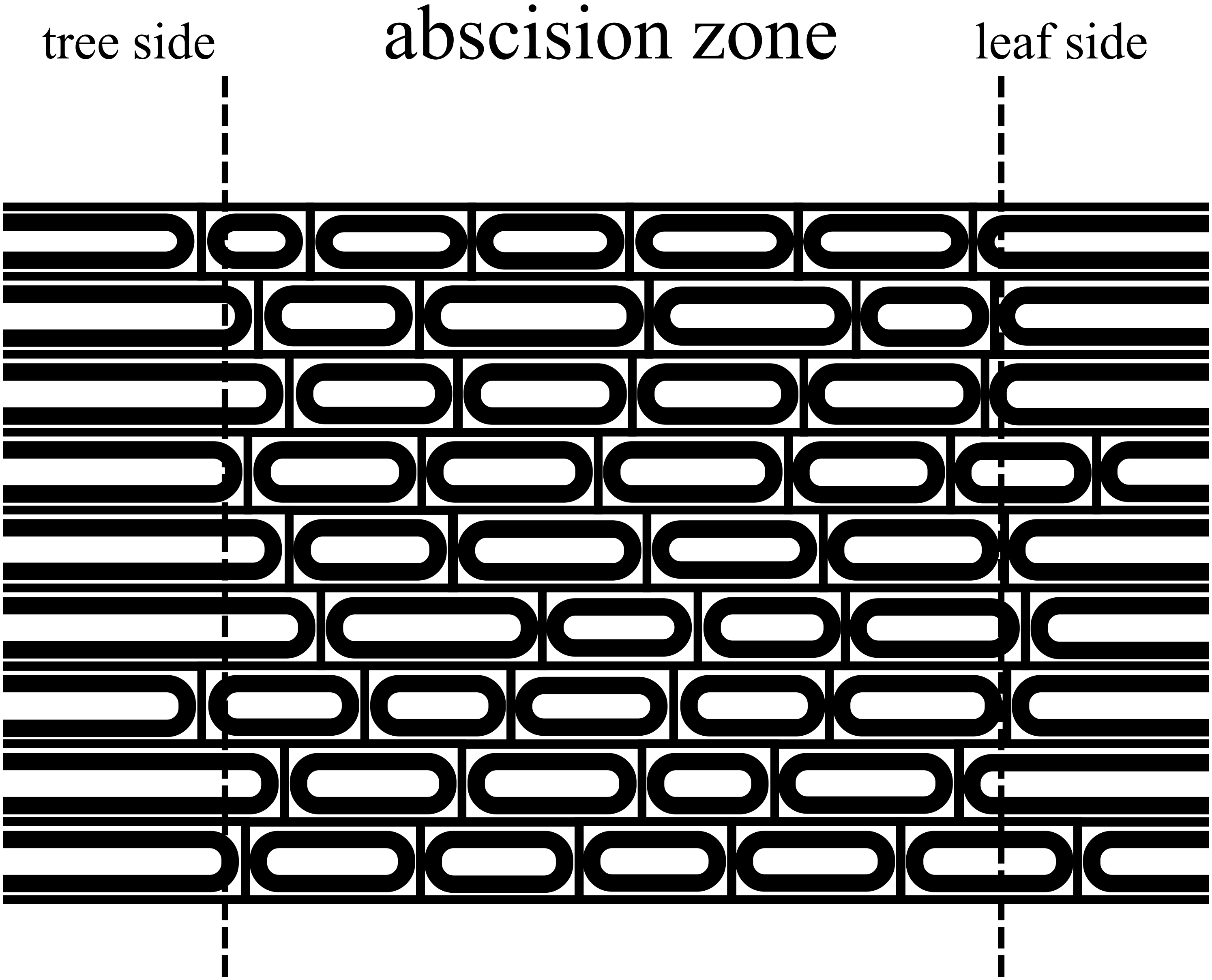

Figure 1: Two-dimensional diagram showing cells in a leaf base abscision zone.

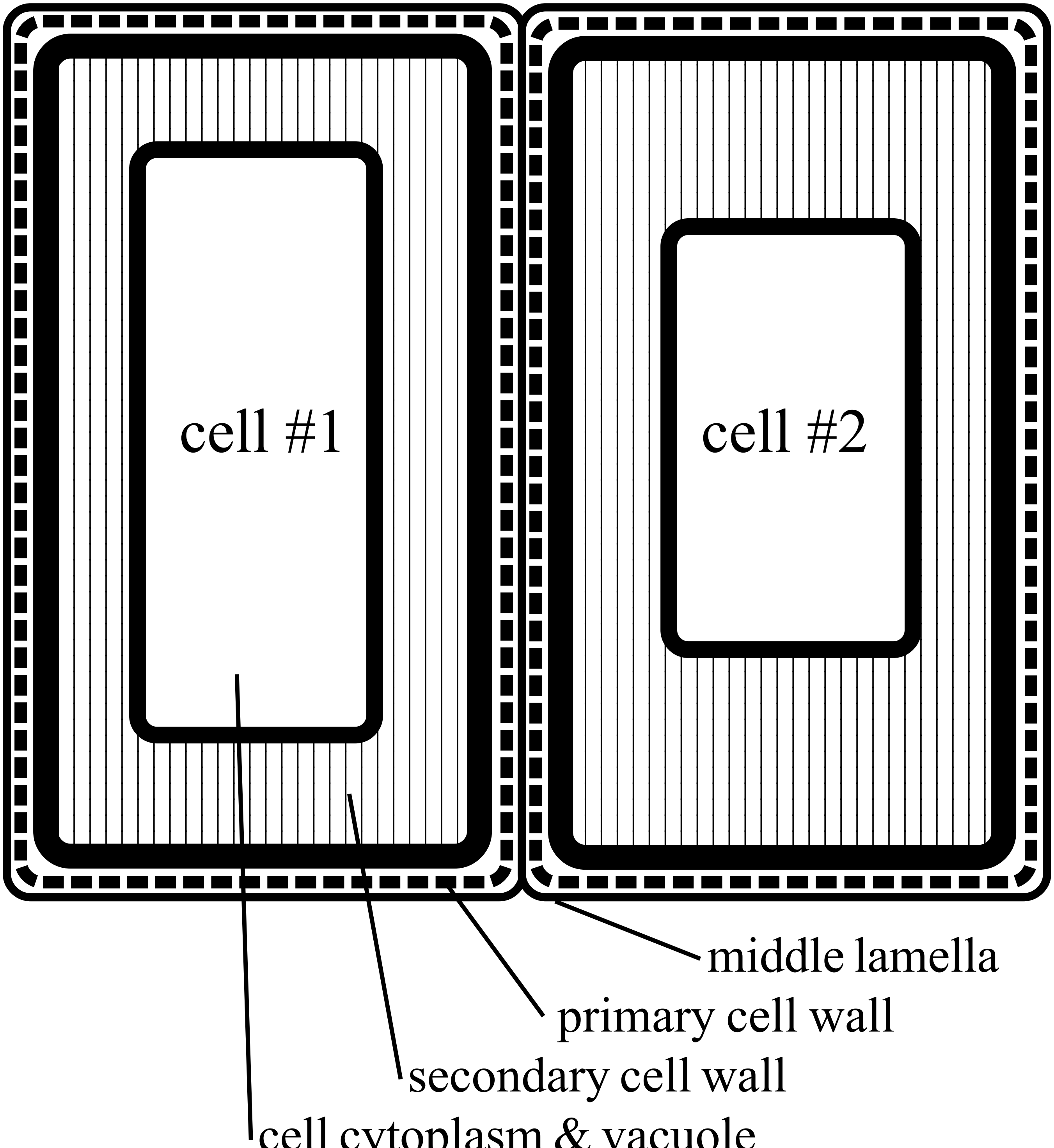

Figure 2: Two-dimensional diagram showing wall components of adjoining cells.

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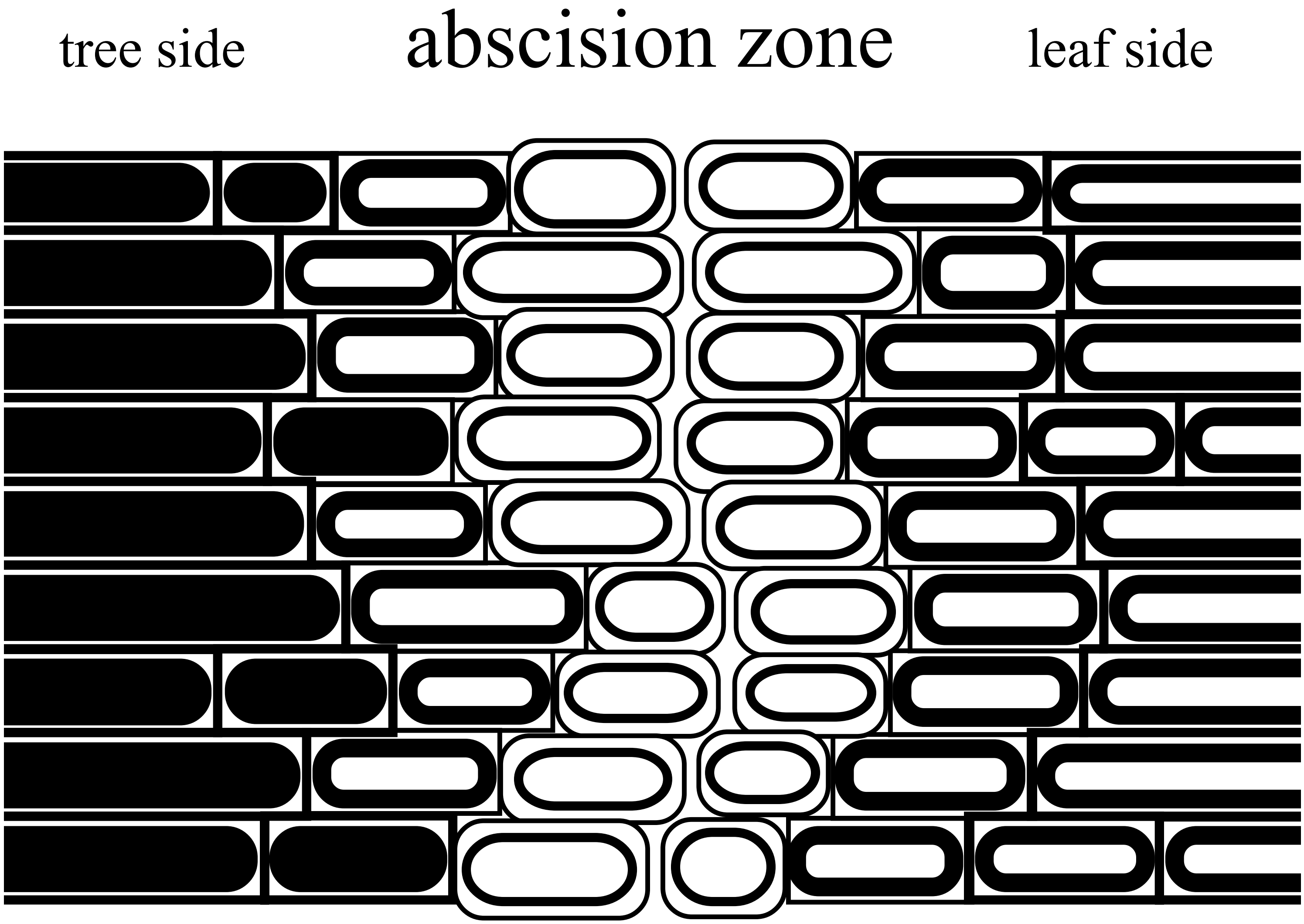

Figure 3: Two-dimensional diagram showing cells in a leaf base abscision zone with a fracture line between cells.

Note tree protection zone, wall degradation areas, and cell expansion zone all disrupting cell-to-cell connections.

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