



Tree Growth Regulation & Control Process

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NOTE: This publication is a synthesis of the tree growth regulation and correlation literature. General processes and systems presented here represent educational models which professionals can use to better appreciate and understand basic tree functions. These models do not represent actual physiological mechanisms, but simple theoretical means of explaining tree reactions within the environment.

A critical feature of tree growth regulation involves functionally balancing the top of the tree with the bottom. Concepts of shoot / root ratios and how a tree can maintain a resource balance between apparently competing needs have been proposed and tested for accuracy. Of all the working models examined, one form has proven over the last two decades to serve in simply describing regulatory partitioning between shoot and root in trees. This model is called a “Thornley” model, although many derivations and more refined systems exist.

The result of this model is to serve as a means for understanding tree functions in a holistic sense and predicting resource allocation patterns between shoot and root. Generically, shoot size and function is equated with root size and function. The purpose of a shoot is to utilize soil gathered resources to capture and ship carbon to a root. The purpose of a root is to utilize carbon to capture and ship soil resources to a shoot. Using only a few basic attributes of shoot and root can estimate the scale and intensity of shoot / root interactions. Figure 1

Estimating Balance

To calculate the proportional change patterns seen in trees, or their “functional balance,” only four components are required under this model: sapwood shoot mass, sapwood root mass, photosynthesis rate, and nitrogen uptake rate. Figure 2 Trees will attempt to balance shoot mass and photosynthetic rates against root mass and nitrogen uptake. A tree will adjust the mass of roots or shoots to correct any deficiency in photosynthesis rates or nitrogen uptake. Carbohydrate shortages will initiate more shoots and nitrogen shortages will initiate more roots.

Note the photosynthesis and nitrogen uptake rates are highly susceptible to both external and internal environmental changes. This model will work for other root-absorbed, biologically active materials besides nitrogen (i.e. phosphorus), but because of significant energy expense involved with nitrogen assimilation and its limiting levels in most terrestrial environments, root-absorbed nitrogen works best in this model.

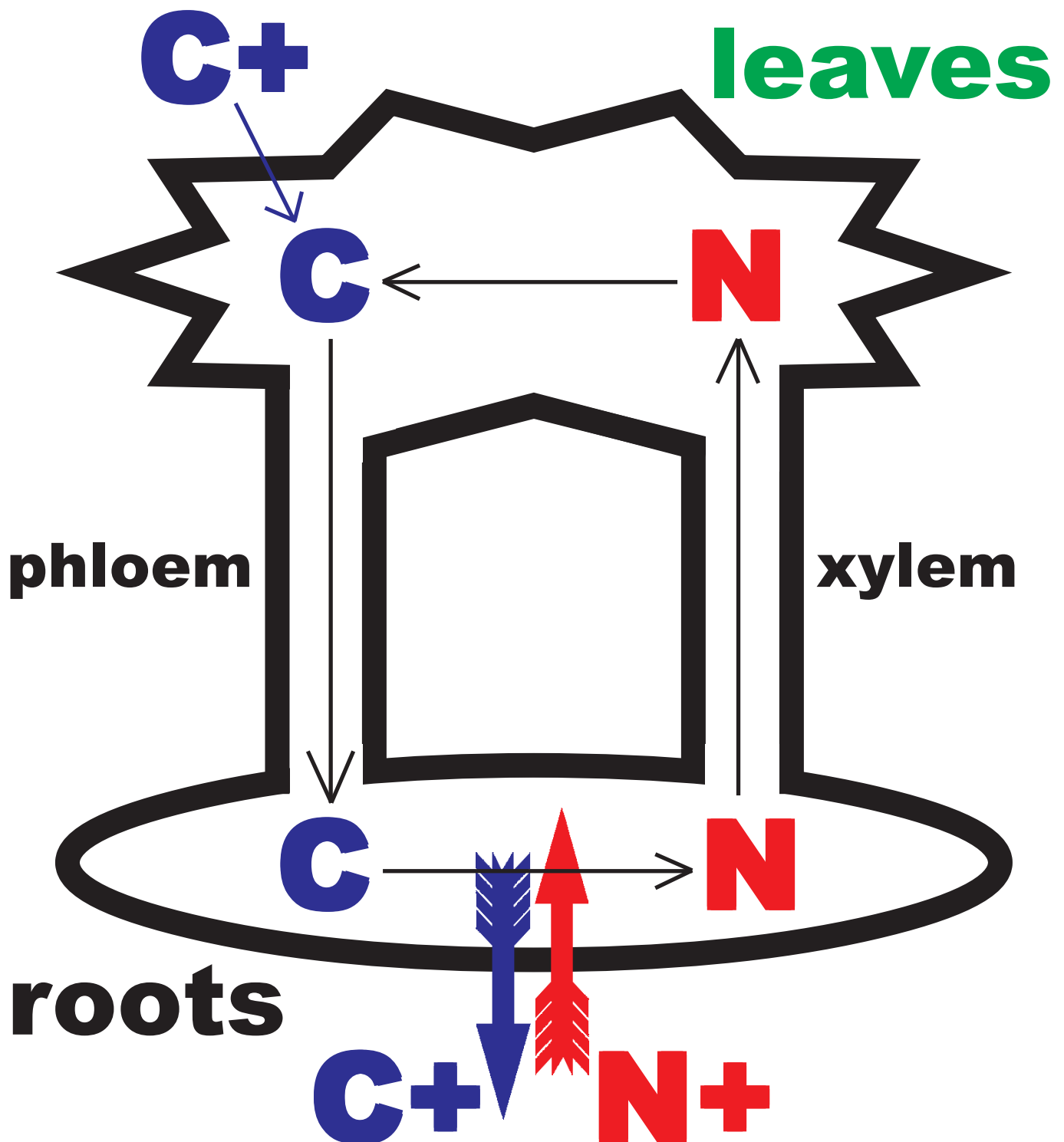


Figure 1: Carbon is captured by leaves and transported to roots for use in gathering nitrogen. Nitrogen is captured by roots and is transported to leaves for use in gathering carbon.

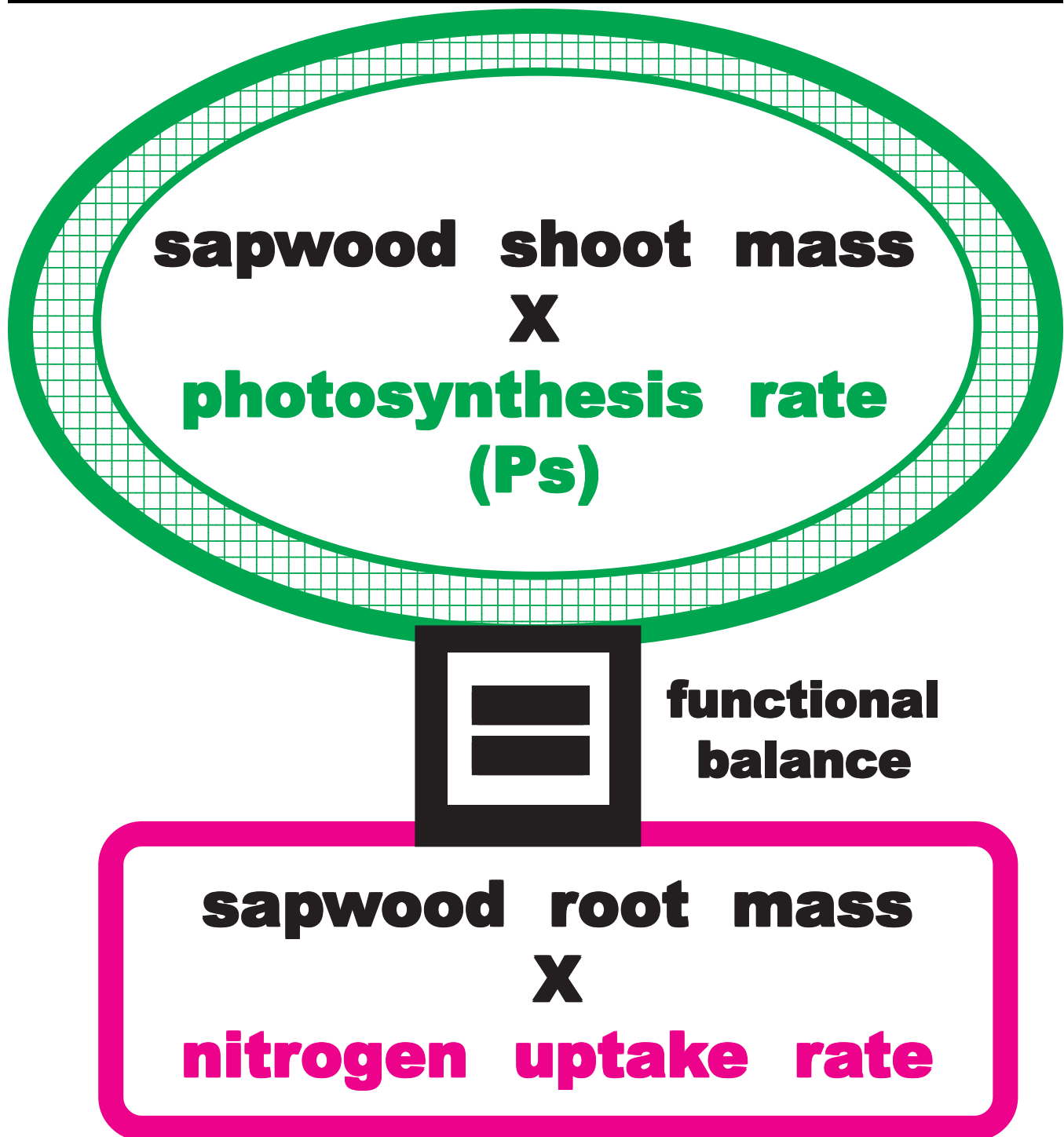


Figure 2: A tree shoot / root balance equation is graphically shown utilizing four components. It is generically called a “Thornley” model after its developer.

Critical Resources

The critical resources shown to be limiting, and shown to represent a functional balance between shoot and root, are: 1) Carbohydrates produced in photosynthesis (CHO); and, 2) Nitrogen absorption (in its three forms — nitrate, ammonium, and urea) from the soil.

Each critical resource's impact on shoot and root balance is dependent upon its absolute amount, its resistance to movement in transport processes, and its transformations and storage within the tree. For carbohydrates there is an addition storage problem with its form — starch or sugar.

Root Example

In shoot / root models a benchmark process and its associated living tissue mass must always be balanced with its “opposite” process and living tissue mass throughout the tree. In this case, as nitrogen absorption declines, what nitrogen remains is concentrated more within roots and used preferentially in roots. This leads to less shoot growth and/or more root growth to keep the model equation an equality. More root growth using carbohydrate from the shoot provides more absorbing root surface area, and potentially more nitrogen uptake.

When nitrogen uptake declines and deficiency becomes a chronic problem, the stockpiling of carbohydrates may occur in a tree. Excess carbohydrate, especially in the sugar transport form, provides a significant pathological risk. This model, and the tree represents, are sensitive to small changes in nitrogen contents and photosynthesis rates. For example, even before growth is noticeably reduced, a tree is reallocating limited nitrogen to the most vital processes. One vital need is in the absorbing roots where more rapid turnover (absorbing root fan death and regrowth) is occurring as nitrogen concentrations fall.

Shoot Example

Moving from the roots to the shoots — a decline in carbohydrate from slowing photosynthesis (as also occurs in green wood pruning) causes carbohydrates to be preferentially held in the shoot. The result is a greater allocation of carbohydrate to shoot production and less to roots. With falling photosynthesis rates, more shoots are initiated, with each allocated more carbohydrate resources to generate more photosynthetic surface. Over time, if carbohydrate levels remain reduced, the smaller allocation of carbohydrate to roots mean less nitrogen uptake. As pathogens, damage, toxins, stress, etc. limit photosynthesis, less root area is generated.

The struggle of a tree to internally balance this model equation leads to some interesting management concerns. With supplemental nitrogen fertilizers and water, relative root growth declines and shoot growth increases. In addition, the added nitrogen causes a decline in starch and an increase in sugars within the tree. Increased sugar contents and additional nitrogen generate improved successful access and attack conditions for a number of pests. If more living (sapwood) shoot tissues are removed by pruning, carbohydrate production is reduced, leading to reduction of root growth and nitrogen uptake. Everything a tree health care manager does which effects the balance equation components will have serious and long-lasting effects on the whole tree.

Mycorrhizae

The natural state of tree root systems is infected with mycorrhizal fungi. The result is a larger absorbing root system with less start-up and maintenance costs for a tree. Mycorrhizal fungi generate (mimic) tree growth control signals and become part of growth control pathways. The structural result of the combination of tree root and fungi, termed mycorrhizae, can confer many advantages to a tree. One example is infected absorbing roots seem to be better protected from surrounding damaging soil microbial populations.

The symbiotic relationship can help minimize energy loss to the environment, allowing for more time to elapse before root energy loss in a single root fan area initiates compartmentalization. This slowing in the root turnover rate allows trees to use significantly less total carbohydrate and nitrogen per unit of living mass while having a greatly enlarged absorbing root area, even though a portion of tree resources are being consumed by the fungal symbiont.

Infection Advantages

With the tree / environmental interface expanded by mycorrhizal fungi infection, several energy efficiencies are realized by a tree. The tree receives some of its nitrogen supply already reduced into amino acid form and another respiration path is made available to a tree for uptake of materials. Overall, the carbohydrate cost of infected roots are less than tree roots alone, plus a surface area and respiration advantage is realized when absorbing soil resources.

Mycorrhizae represent major modifications in shoot and root functional balance, yielding more root area at a smaller building and respiration cost. Infection also provides some allelopathic, soil colonization, and anti-pest values to a tree. In root limited area, in stressed tree systems, and where major pruning has occurred, (as long as good aeration is maintained), mycorrhizae can be of great value by biologically and physically buffering environmental impacts on a tree. Mycorrhizae modify the shoot / root functional balance in a positive sense, and under some severe soil limitations, may determine tree survival.

A Question of “Balance”

It is critical to differentiate between the control field necessary to allow growth (internode expansion) and the control field necessary for growing point initiation (node development). Based upon tissue culture and vegetative propagation experiments, the contrasting requirements between node and internode development and expansion demonstrates an always balancing (never balanced) process. Node or growing point initiation helps facilitate growing point elongation -- while internode elongation helps facilitate internode initiation. As node initiation is set-up in the shoot, growth is occurring in the root. Root growth is essential for shoot growth, which in turn, is essential for more root growth.

The reciprocal nature of root and shoot growth (like a pendulum) assures efficient and effective resource use in the whole tree and a functional balance between shoot and root. Philosophically, there can be no true balance except at the end of life. The unbalanced nature of shoot and root generate changes necessary for the continuation of life. Also, because age, damage, size, and sheer chance in the tree system is constantly changing, the unbalanced aspects of shoot and root represents life's struggle against an ecological and biological background of continuous change.

Approaching, Not Arriving

A visualization of this concept could be described as pointing a weapon at a target — not only is the weapon wobbling back and forth across the target, the target itself is moving in a not-quite-predictable way. This process makes the tree system always in flux, never static, and never cast into one stable form. A reactive tree represents the ability of life to adjust and change under the poorest conditions. The unbalanced nature of a tree system is required in order for it to respond to change. There can be no true static shoot / root balance!

Model Summary

Trees exist in a state of internal and external flux. The dynamic interactions of various tree parts are correlated through growth control regulators and resource allocations. From moment to moment, trees are

attempting to solve a series of simultaneous biological equations. The answer for the tree, and for human observers of tree reactions, is a never ending optimization process played out among a chaotic and varied mixture of site, tree, and other organisms. Tree health care managers need to understand how cultural treatments change tree growth regulation patterns and the “functional balance” between top and bottom.

Growth Control

Trees use environmental sensors and internal feedback mechanisms to modify genetically designed reactions. The numerical magnitude, separation distances, and surface area of meristematic tissues clearly present a command and control problem for a tree. Any portion of a tree could, without holistic control, appropriate resources to its advantage and the tree’s disadvantage. Only through the severe stress of pesticides, pathogens, and physiological dysfunction does this actually occur. The tree maintains a correlated growth process where resources are allocated to maximize the chances for gene set success — always at the whole tree level.

One of the clearest needs for growth control in a tree is the correlation between shoot and root. Both shoot and root must effectively operate and share resources to ensure tree success. Trees utilize a chemical growth regulation system. This chemical regulation system does have electrical components, but is predominantly a chemical based message system.

Regulation Chemicals

The single growth regulation system in a tree has two different conceptual representations — one at the single cell level (growth control field) and one at the whole tree level (growth control path). Figure 3. Within the tapestry of living cells, tissue types, and organs in a tree there are a myriad of health “states” and demand / supply “circuits” or pathways. These states and circuits are established and maintained within a tree by cells using predominantly three major growth regulators: auxin (primarily a shoot signal); cytokinins (primarily a root signal); and, abscisic acid (a dormancy and subordination signal). Figure 4

Auxin — Auxin flows only in one direction through living cells in an energy requiring process. From the moment of the first cellular division, top and bottom — shoot and root — are established. Auxin pathways are formed along the most direct vertical connection between the top and bottom of a tree through living cells. Auxin moves downward / rootward with gravity slowly only through living cells. An auxin signal is stopped by cuts and other types of girdles of tree tissues. If tissues are moved into new positions, auxins pathways begin changing direction to flow away from generating shoot tips in the most direct line to the tree base. Auxin is destroyed by root tip enzymes (requiring oxygen) in order to prevent signal buildup or recycling. Small amounts of auxin are generated by all living tissues.

The auxin flow pathways in a tree vary in strength by the number, vitality, and dominance of the generating shoot tips. The most dominant, active, terminal growing points (within buds) usually generate the strongest signal. This signal varies across a growing season, day-to-night, and with the health of a growing point or bud. Waves of auxin flow out from the bud areas, creating a unidirectional signal (a morphogenic wave) to all cells below. Auxin is essential for root growth.

Cytokinins — Cytokinins, (not kinins as in animals) are nitrogen containing compounds produced in root tip areas and dumped into the transpiration stream. Cytokinins lead to destruction of dormancy control chemicals, and are essential for shoot growth. Cytokinins represent a signal on the health of roots, and general quality and

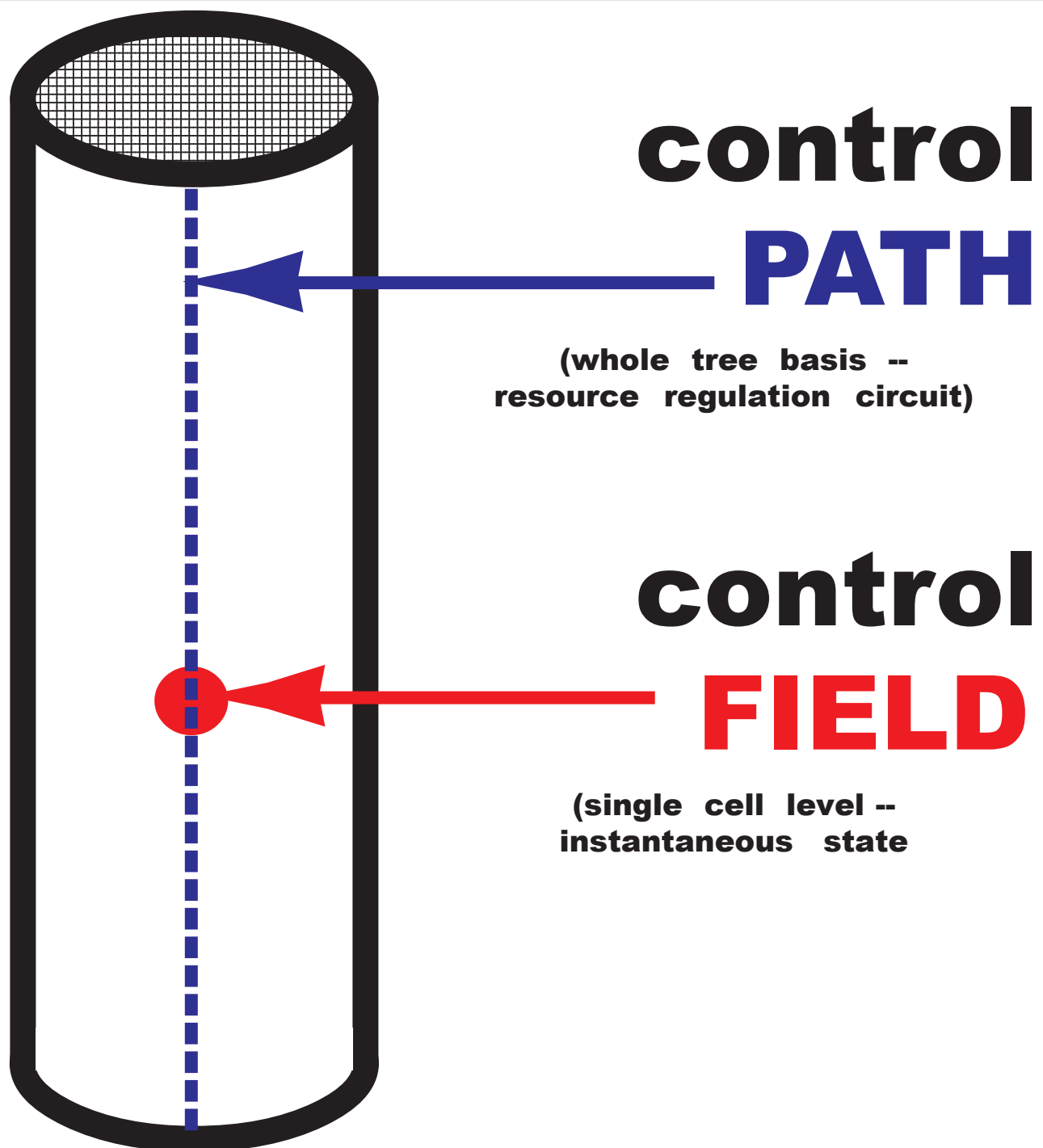


Figure 3: Functional description of tree growth regulation system represented by each individual cell reading at any moment along a resource command & control “circuit” carrying communications between tree shoots and roots.

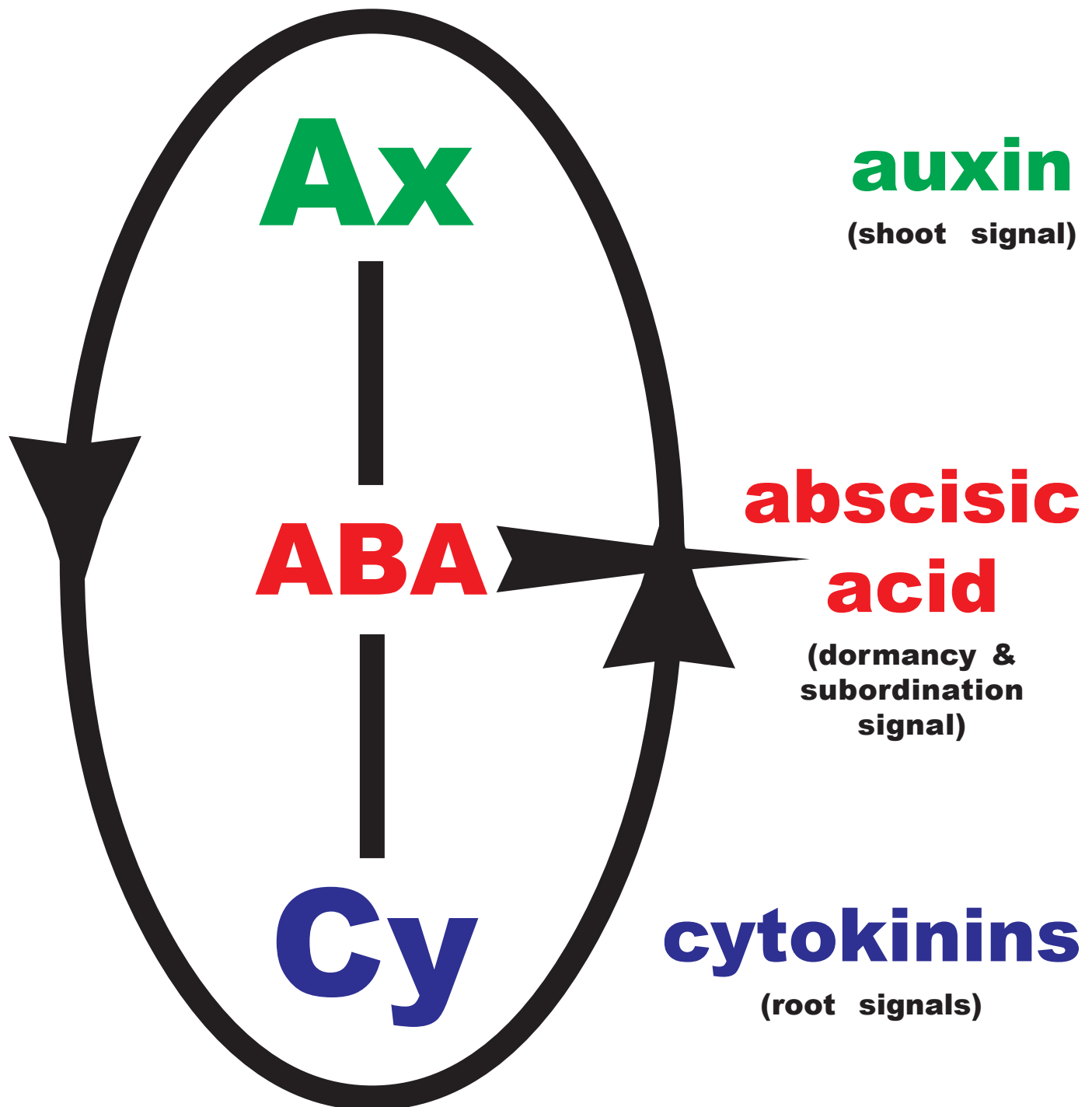


Figure 4: A tree generates chemical signals which are translated by living cells into specific genetic responses to resource levels.

quantity of root-absorbed materials. Cytokinins are transported preferentially to areas where the auxin pathway is strongest. The shoot destroys the cytokinin signal to prevent buildup or recycling of the signal.

Absciscic Acid (ABA) — Absciscic acid is a material that is broken down quickly in the presence of cytokinins. ABA is generated in photosynthesizing cells and can be accumulated over a growing season. When ABA reaches a specific level, as defined in a tree's genetic material, growing points and leaves begin the senescence process and enter dormancy. Cytokinins added to dormant buds initiates ABA destruction and releases the bud to grow. ABA accumulates out of the way of the main auxin pathways because of cytokinins. ABA in tissues like a lateral bud, determine whether they will remain dormant and dominated by other buds generating a strong auxin signal. This is the mechanisms of how a terminal bud dominates and subordinates other buds.

Control Field

Every living cell is a part of, and an amplifier for, the growth regulation signals generated in a tree. Every living cell in a tree is part of a correlation circuit used to control resource supply and demand. At any one point in a tree, each cell is reading the combined, integrated growth regulation message. This combination message generates not three individual responses, one for each growth regulation compound, but a single, genetically identified response to the integrated message. The combined message represents a chemical "control field," similar to an electric / magnetic field. The control field type and strength assures a tree responds as one organism even when various meristems and storage tissues are tens of meters apart.

The control field strength represents one moment in time along a supply / demand circuit set-up by living cells further above and further below the signal-reading cell. The control field is composed of combined signals from auxin, cytokinins, and ABA. Because ABA and cytokinins are so closely and inversely correlated, a ratio of auxin and cytokinins alone can be used to approximate control field strength in any one location. Auxin / cytokinin ratios and their functional results will be discussed later.

At any given point, a meristematic cell reading the control field would respond by generating growth (internode), growing point initiation (node), material storage changes, dormancy timing changes, no change in operations at all, or an amplification of, or decay in, the local control field. Reading of the control field by a cell is influenced by the cell's health, juvenility of the tissue, and environmental features such as oxygen content and temperature. Local application of control field signals is spread by using other signal carrying materials, such as gibberellic acids (GAx) for secondary control of development and growth.

Growth Control Path

From a whole tree perspective, the growth control paths (circuits) determine where gathered resources are transported, used, and stored. A growth control path is set predominantly by auxin moving in one-direction (away from the generating shoot tip), through living cells, seeking the most direct path between tree top and bottom. Along this chemically charged path, cytokinins are delivered to facilitate growth. ABA builds-up in areas away from the dominant pathways, and slows growth or initiates dormancy. The main growth control pathway's strength is controlled by the dominance (health and growth) of the main shoot's growing point on each tree, branch, or twig.

On one twig, a terminal bud may be the only dominant growing point. This dominant growing point generates a strong auxin pathway, which in turn, demands plenty of cytokinins delivered to the growing point. This in turn, allows the bud to generate an even stronger auxin signal. Under limited resource availability, the dominant growing point becomes stronger and subordinates all other growing points below.

Once the growth control signal (auxin wave) leaves the local twig, it becomes just one of many growth regulator flows in a river of pathways from other twigs on the same branch. The stronger, more dominant twigs have stronger growth control pathways and garner more cytokinins, which allow them to become even more dominant. Figure 5.

Woven Paths

Within a stem is the combined growth control paths of all growing points above. The demand / supply pathways are set through this process. Only the most successful growing points generate a strong enough growth control pathway to receive the cytokinins needed for more growth. The rest of the growing points are slowed or controlled.

While a tree is still young and has 100% sapwood, the growth control pathways involve the whole cylinder of living cells. With development of heartwood (internal shedding — development of non-living core) pathways can become more and more concentrated around the last few, most exterior sapwood increments and can develop a heavier flow along one side of the tree. These pathways may spiral around the living cylinders of tree branches and stem, but represent a dominant pathway between one area of the crown and one area of the roots. The tendency toward enduring 1:1 shoot/root connections (or sidedness) is most pronounced in ring-porous hardwoods and gymnosperms.

Pathway Types

There are four types of growth control pathways in a tree: primary, active, marginal, and dormant. Figure 6.

Primary (1°): A primary pathway is developed behind a single or multiple terminal growing point(s) or bud(s) controlling a tree. These transport pathways correlate supply and demand throughout a tree, directing a majority of tree food to be transported along their dominant path or axis, and allocating a majority of soil-gathered resources be transported along this path.

Active: An active pathway is associated with productive twigs and branches generating major amounts of food for the rest of a tree. Significant amounts of food along these pathways are stored in adjacent living ray cells.

Marginal: Marginal pathways may have been active at one time but because of shading, damage, or position effects, are barely generating a positive auxin and food outflow along the pathway.

Dormant: Dormant paths still contain signal but not enough to demand a break in control. Loss of signal along what was once a pathway defines growing point death.

Communicating Change

As trees age and become physically larger, and supply and demand patterns become more complex and convoluted, the growth control paths continue to change. Large tree changes include greater physical distance over which signals must be sent (height and reach increases) and more intricate pathways develop because of

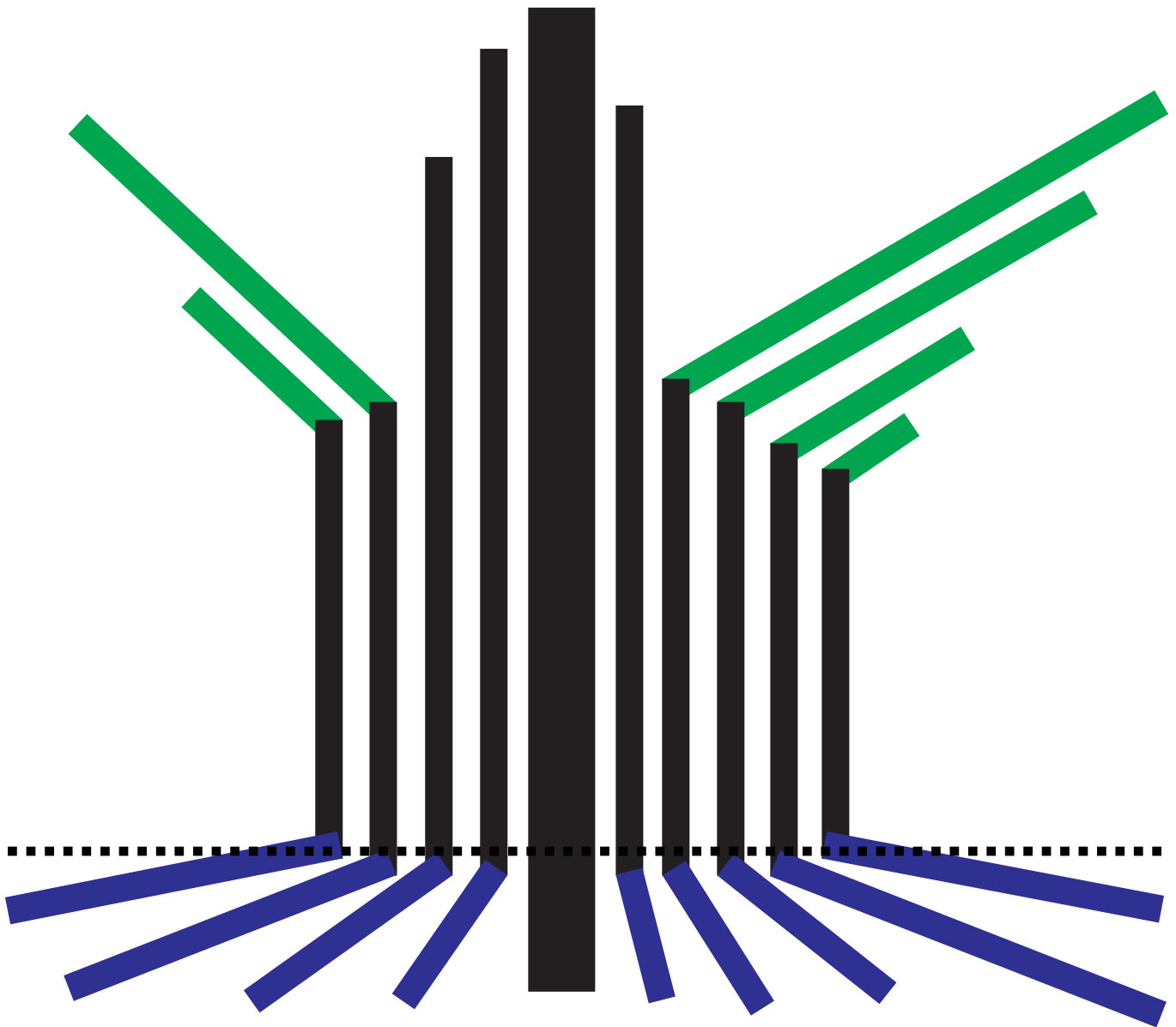


Figure 5: Simplified representation of growth control pathways (supply / demand “circuits”) within a tree.

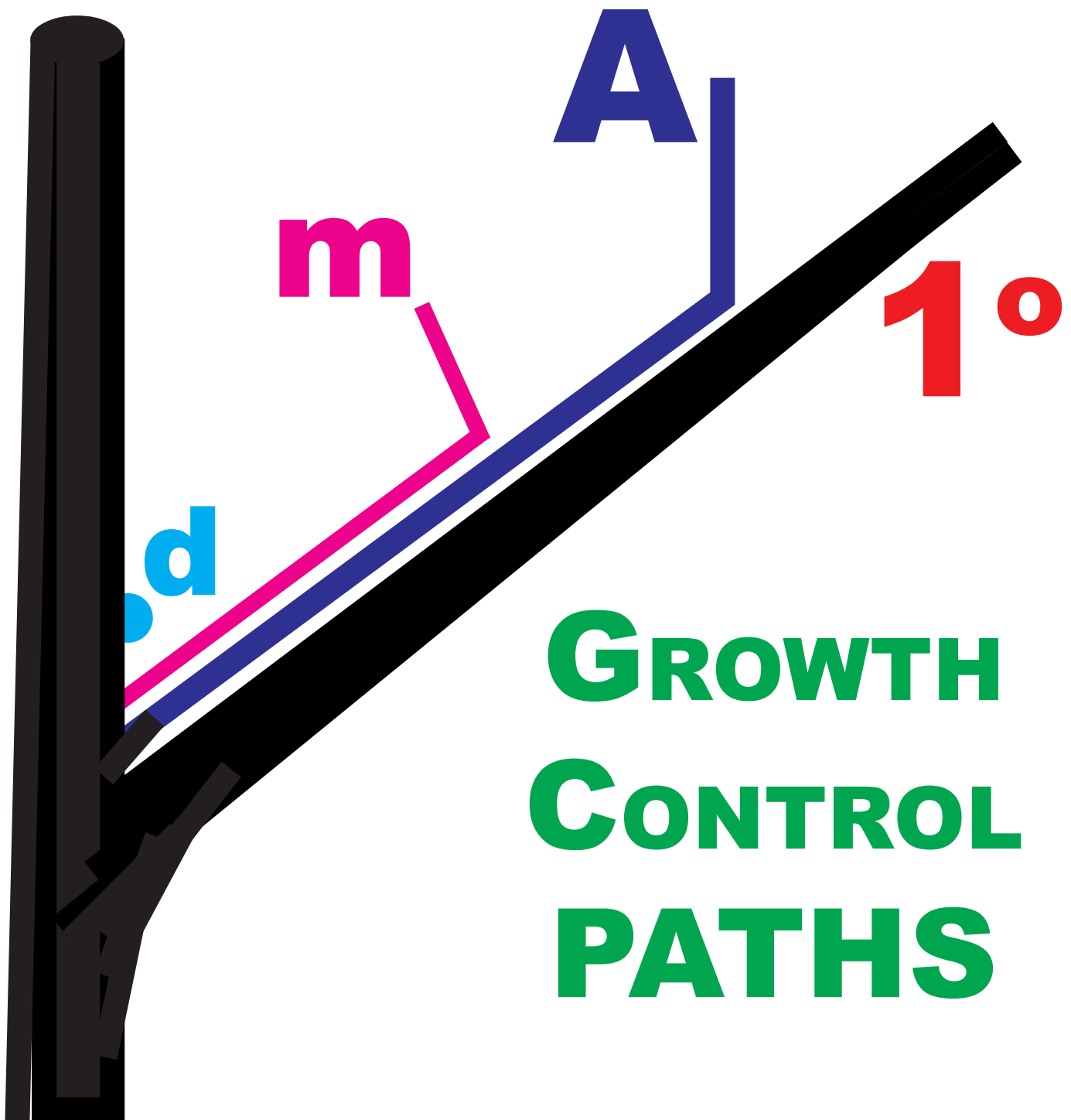


Figure 6: Types of growth control pathways: primary (1°), active (A), marginal (m), & dormant (d).

shedding and compartmentalization processes. The result is a longer transport time inside a tree between full signal cycle peaks. The result is a slower effective response time to changes within large mature and over-mature trees. Figure 7

The growth control pathways are designated by position, type and strength of the integrated effects of growth regulators. Unfortunately, having circuits with the proper control field and connections does not mean any action will occur. As in an electrical model, having wiring with open switches does not mean work will be completed unless electricity (electron flow) is available. For trees, in order for the system to function, there must be the proper available resources to transport and utilize.

Without resources being absorbed by the roots and without food being made by the leaves, maintaining the dominant growth control pathway in a tree is meaningless. Both essential resources and a growth control system are needed to allow a tree to survive and thrive. In other words, circuits paths may be open but may contain no materials for growth, generating no response.

Field Strengths

The control field in a tree changes weekly. Currently, only the most coarse estimations can be generated from whole tree control field levels, and then only as they shift major events in the tree during the growing season. More technical insights and better research tools are needed to identify more specific signal responses inside a tree. Of the general control field levels, the following can be identified from whole tree growth models starting before bud-break, and ending in the middle of the Winter or dormant period: Figure 8

- A) **Low field strength** (low auxin / cytokinins ratio) — root growth & shoot initiation, also initializes the tree for Spring start-up.
- B) **High field strength** (high auxin / cytokinins ratio) — shoot growth & root initiation, new pathway connections fashioned, & springwood produced.
- C) **Moderate field strength** (intermediate auxin / cytokinins ratio) — stem growth, adjustment to root & shoot balance made, & summerwood produced.
- D) **Low field strength** (low auxin / cytokinins ratio) — root growth & shoot initiation.
- E) **Very low field strength** (minimal auxin / cytokinins ratio) — Winter or dormant period activity suspension.

Response Summary

Trees must actively sense and respond to changes in internal and external environments. To correlate growth processes across a large expanse of area with mixtures of living and dead cells, trees use growth regulators to carry messages. Trees use growth regulation signals to maintain an effective and efficient use of internal and external resources to meet biological goals set by its genetic materials.

Growing A Tree

Tree growth and development are dependent upon a few basic mechanisms. These mechanisms are responsible for a tree making holistic adjustments to a changing external environment. These basic mechanisms

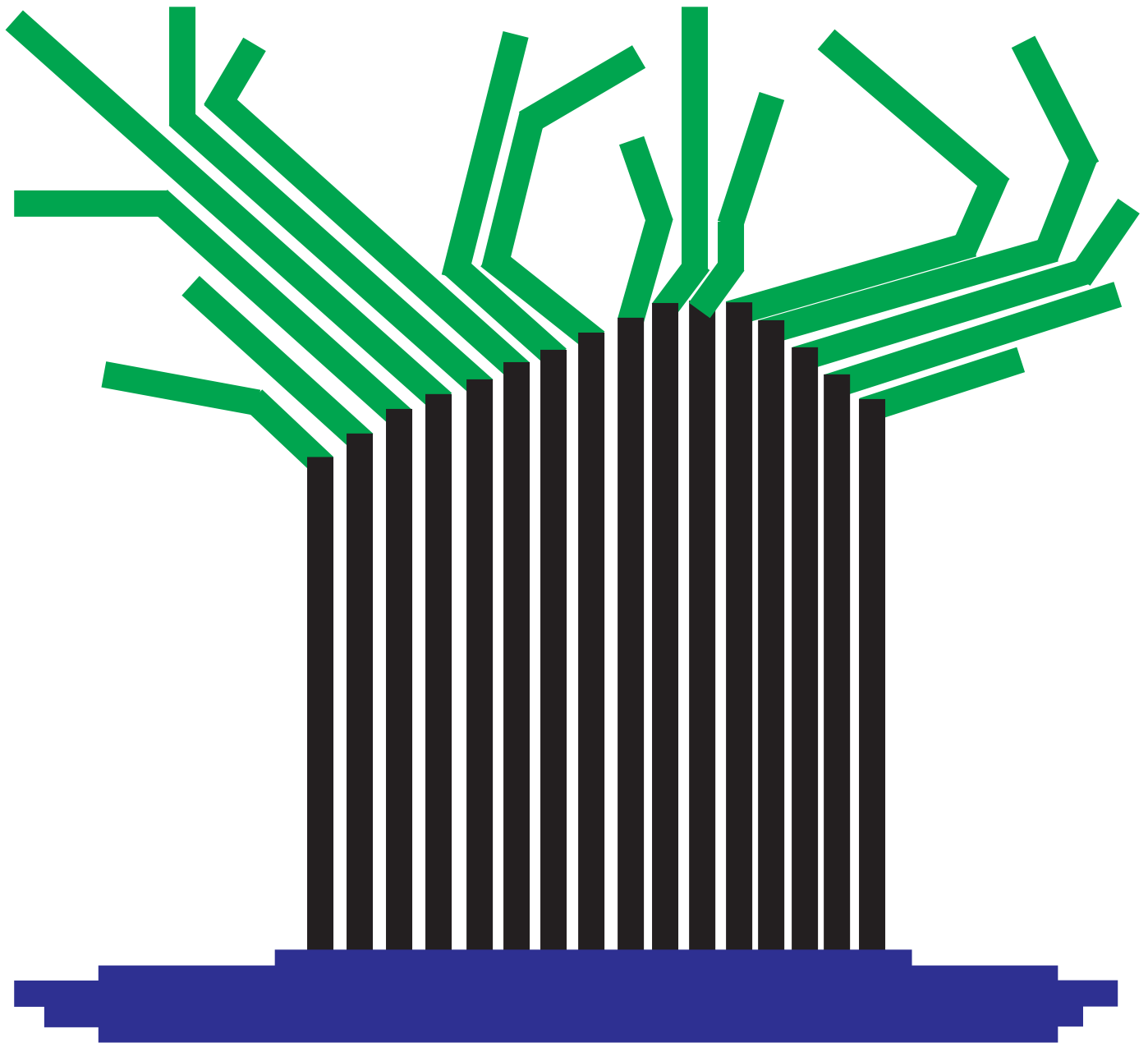


Figure 7: The resource allocation patterns in a tree represent the inter-connectedness of, and communications between, tree parts which are chemically maintained links.

Supply / demand and health problems can change or sever past and current connections.

**AUXIN /
CYTOKININS
RATIO**

**Growth
Control
FIELDS**

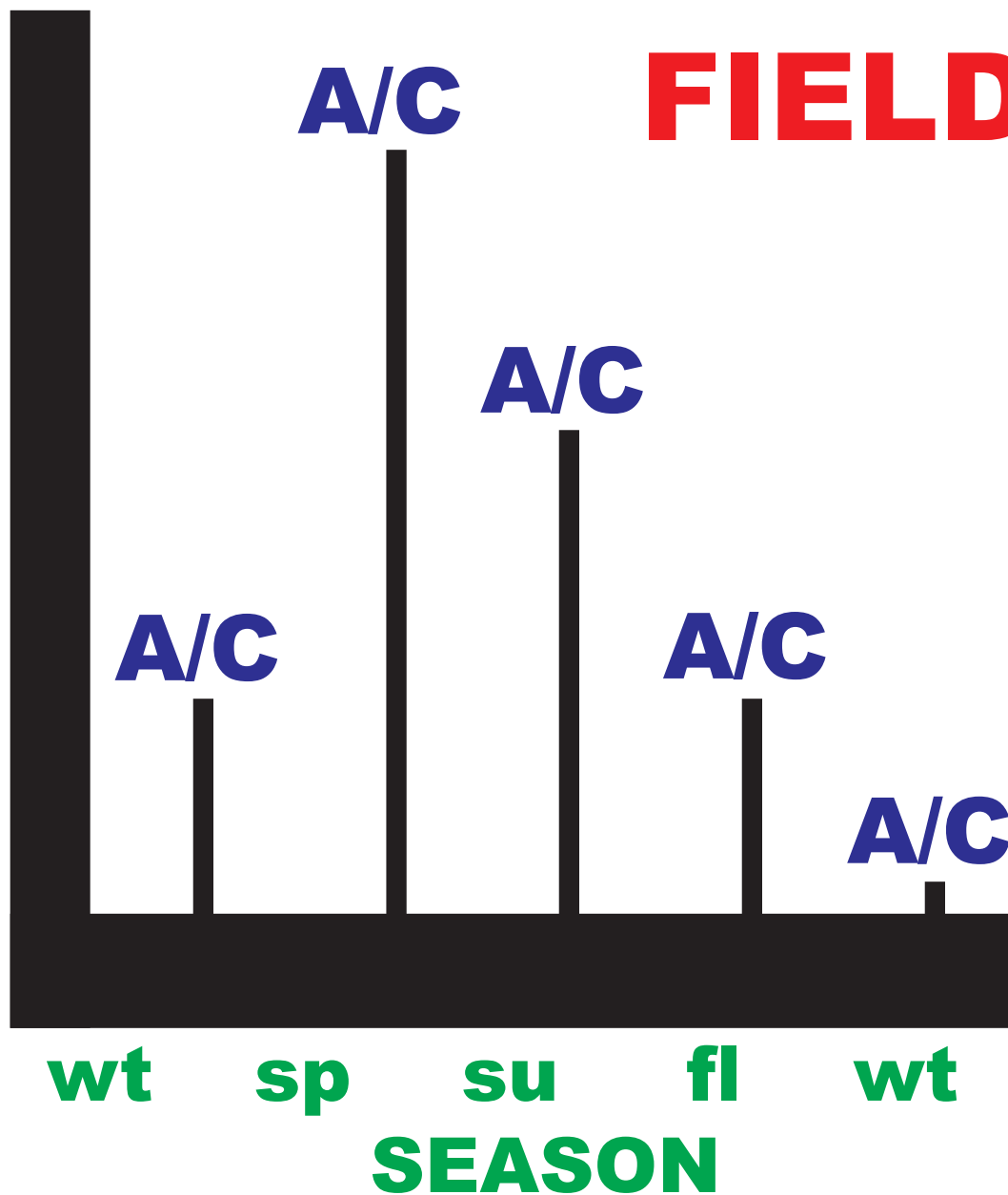


Figure 8: Changes in growth control field strengths over the growing season.

(wt = Winter; sp = Spring; su = Summer; fl = Fall)

also allow for correlation of processes internally. One means of understanding tree reactivity to external and internal changes can be partially visualized in shoot/root interactions. Once the basic mechanisms of how whole trees react to change are delineated, additional impacts such as pruning, fertilization, drought, etc. can be better understood.

Trees are complex organisms with highly evolved sense and response systems. Because a tree as a whole is too complex to comprehend at a functional level, simplified models are used to understand tree reactions to change. Reviewed here, in a very basic manner, will be how trees control their own growth and how this growth control changes internal resource allocation patterns.

Basic Tree Model

In the most simple way of visualizing tree reactions, a tree is split into three reactive components: leaves and buds, connecting tissue, and absorbing roots. By keeping track of how each of these components interact with each other, a tree health care manager can develop specific expectations from management inputs and better understand tree reactions. Each of these three primary components have specific functions, react to changes, and are tied to their respective meristem and associated sensor system. Figure 9

Leaves & Buds — Leaf tissue and growing points are tied to shoot tip meristems, must deploy resources to collect light and carbon-dioxide efficiently, and must draw required resources from storage and from absorbing roots. Leaves are net photosynthesizers.

Absorbing Roots — Absorbing roots are tied to root tip meristems, must use resources to effectively collect and control soil resource space (water, essential elements, nutrients), and must draw required resources from storage and from leaves. The absorbing roots are respiring organs.

Connective Tissues — All current (and accumulated past) biologically and physically active tissues between leaves and absorbing roots are tied to the cambial zone meristem and the periderm generating phellogen (bark cambium). The connective tissue provides for storage volume, conversion processing of sugar and starch, material transport system protection, and structural support. Connective tissues draw required resources from leaves and absorbing roots. The connective tissues are net respiring areas.

Growth Sensors

All three primary components of a tree listed above use integrated sensors to determine the state of external and internal environments, as well as estimating rates of change. There are dedicated biological sensors generating signals which illicit responses from meristems and modify growth control messages to the rest of a tree.

Primary sensor locations are: active buds, outer chlorophyll containing cells (secondary cortex) of twigs and stem, proto-chlorophyll containing cells of roots, active root tips, and leaves. In order of importance, sensors track: electron flow into the oxidative environment, light (season, quality, and quantity), oxygen status,

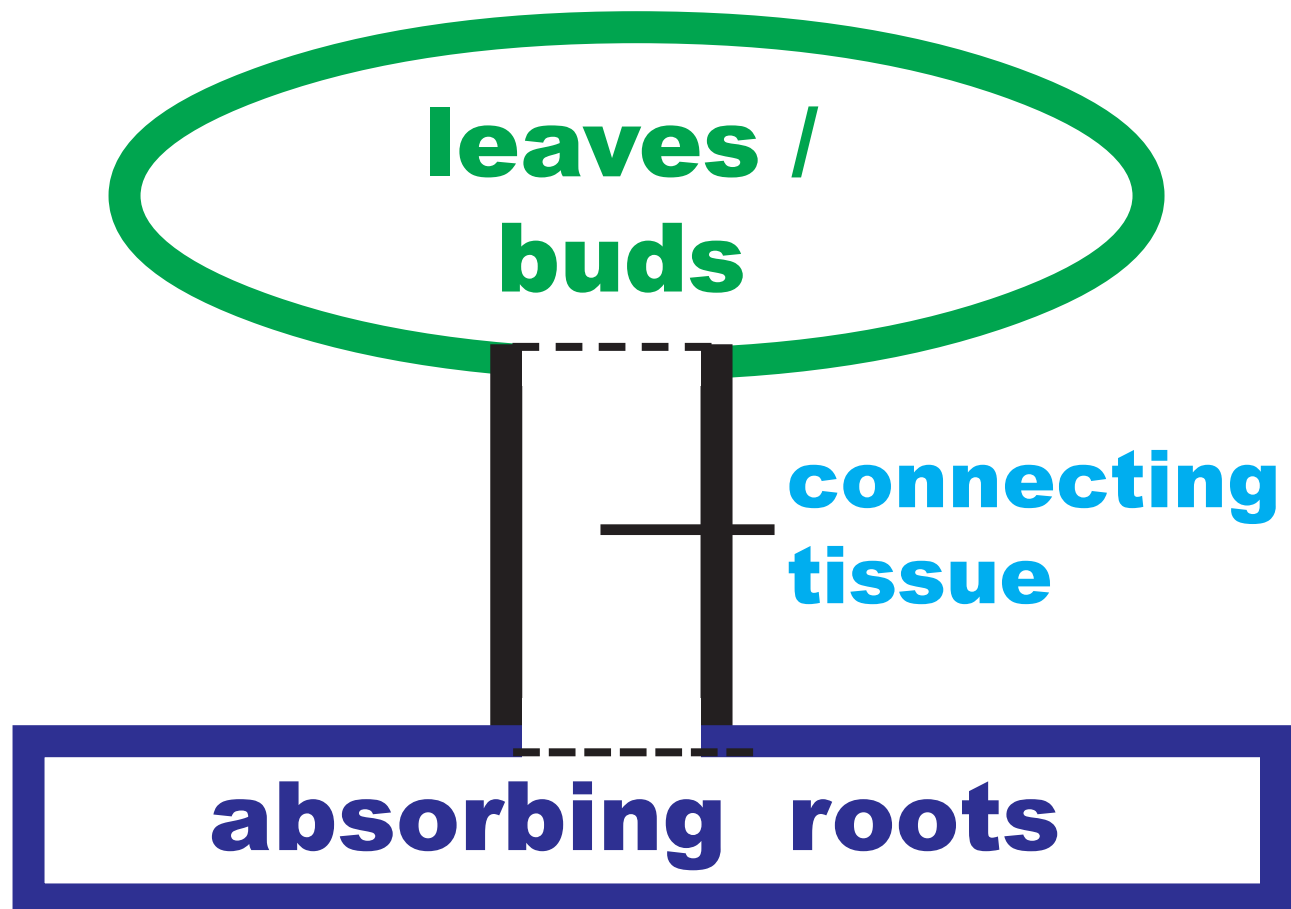


Figure 9: Tree control systems have three main anatomical components: leaves & buds, connecting tissues, and absorbing roots. Each of these components have their own sensors for registering change in the environment, and their own signals to dispatch throughout a tree.

temperature, water status, essential element status, carbohydrate (food) status, and position and mechanics (leading to trophic, nastic, and reaction wood responses). Trees respond to sensor messages by generating growth regulator changes which modify a tree's control field, growth control pathways, and resource levels.

Electron Flow Control

A tree system is designed to efficiently use energy collected in the photosynthetic process.

Photosynthesis is an electron (energy) concentrating process utilizing chemical bonds of carbon compounds and concentration of protons (H^+). Carbon compounds provide a means for transporting and storing concentrated electrons (energy). In this way, benign and movable carbon compounds carrying light-derived energy can be transported to the farthest and darkest reaches of the roots. By breaking chemical bonds between carbons, energy can be generated. The process of allowing electrons to slowly and systematically leak back to the oxidative environment while performing cellular work (i.e. respiration), allows tree life to be sustained.

Across cell membranes in a tree is a small but measurable concentration gradient of electrons from inside to outside. Inside cells, a high levels of electrons are maintained by photosynthesis which acts as an electron concentration pump. Trees are extremely sensitive to electron loss through damage, pest attack, or environmental changes. Rapid increases in electron flow to the environment are sensed instantaneously. A tree's reaction to slow any significant and unexpected electron loss is called compartmentalization.

A tree's growth regulation system maintains electron flows to optimize tree life and minimize electron theft by the environment (atmosphere, pests, stresses, etc.). Tree systems sense and regulate electron flow changes, and the production and use of electron-dense materials (food).

Food Storage

Storage materials in a tree are concentrated electron (energy) sources. Carbohydrates can only be stored and retrieved within a living cell. Storage of critical resources require efficient control systems to assure materials can be removed from storage, transported and used where needed. Carbohydrate storage in a tree is in living parenchyma cells, primarily ray cells. Only cells in the last few annual increments are utilized as easy access in any storage system.

A major source for new growth is the locally available carbohydrate immediately behind an expanding growing point. Once the growing point is expanded and self-sufficient in food production, this old storage center of last season is not restocked because now the needs of a branch will have moved to be nearer its tip, and the location of the next growing season's critical needs.

Branch Autonomy

Food is made locally, stored locally and used locally in trees. Each twig and branch is almost completely autonomous in suppling its own food. There is little sharing, and no welfare provided for marginal or net food-loss areas. Those twigs or branches that cannot generate enough food for themselves and some extra to ship away will be seen as electron loss areas and be compartmentalized off from the living tree. Branch autonomy is the principal reason proper branch and twig pruning can work without massive physiological damage to a tree.

A growing point expands using carbohydrate stored just behind the buds and in the outer annual increments. Figure 10 With full expansion of shoot and leaves, the first priority in the shoot is deposition of carbohydrate behind the new buds. Shoot storage is always filled with carbohydrate from the tip downward. As new light resource areas are expanded into, these spacial gains are consolidated with storage of

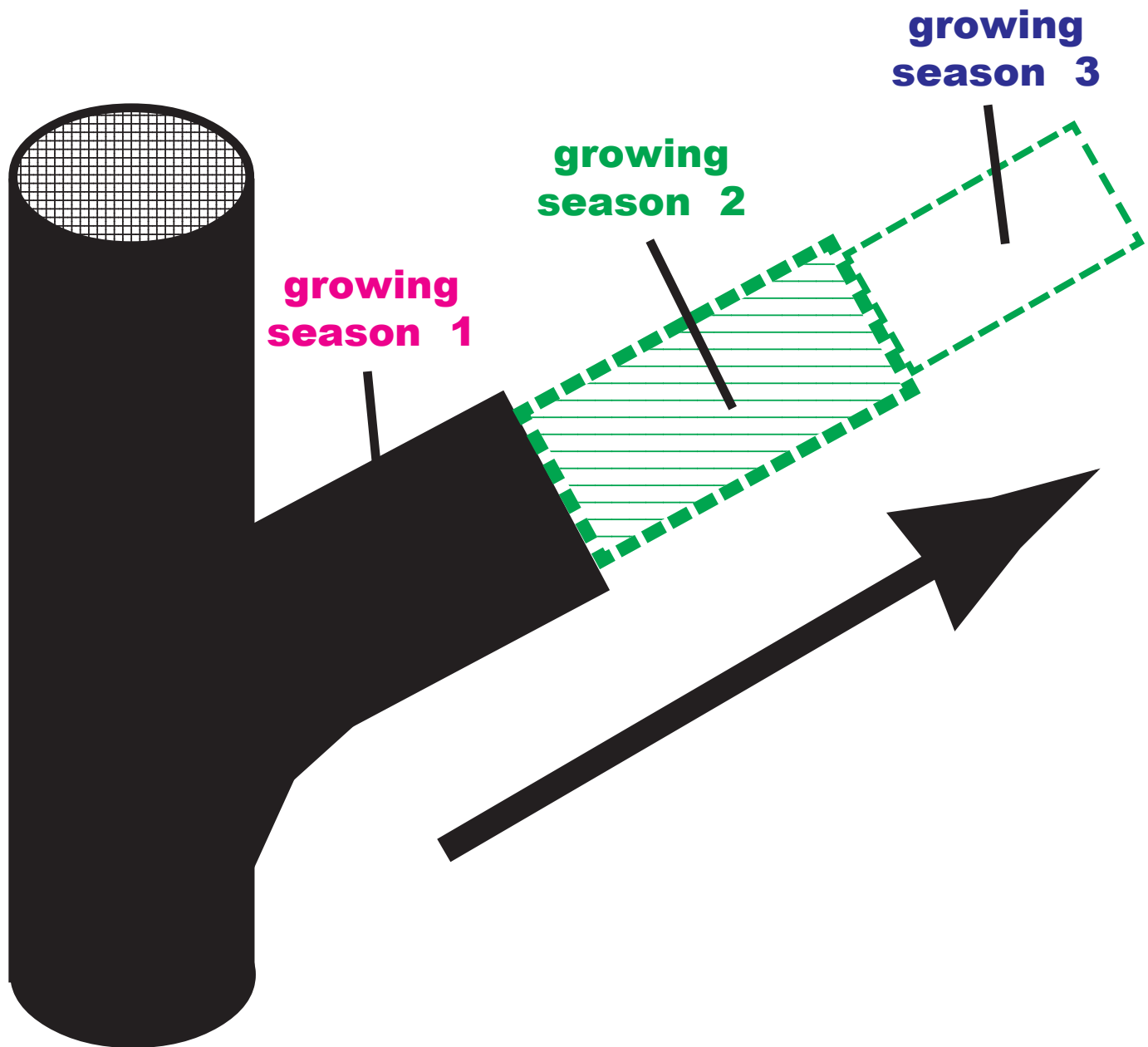


Figure 10: Trees consolidate control of resource space through episodic elongation of twigs followed by periods of filling-in behind each expanded segment with food, in preparation for the next elongation period. Carbohydrates are positioned to power taking & controlling resource space.

carbohydrate at the site of the next expansion. Electron dense materials are positioned where they are needed in order to hold space and support growth.

Growth Segments and Sheaths

Trees are modular or segmented organisms. Figure 11. An autonomous twig expands to the limits of its resources. If expansion has yielded potential for further resources, healthy twigs will further expand into the area when growth is again allowed. Connections between twigs and branches, and branches and stems, contain boundary setting zones. These boundary zones can seal-off any branch not generating net carbohydrates, or can act as a barrier to the environment if a branch is removed by storm or pruning. Mechanically and biologically, trees are composed of modular growth units which allow a tree to fall apart (or be taken apart) in these same modular units.

Each growing period, a tree expands its biological size. A tree forms a new functional sheath of tissues over last growing season's xylem from stem tip to root tip. Unfortunately, this continued expansion of living mass can not be sustained. A tree keeps only the most efficient and effective modular units. Other tree parts that may not be carrying their own weight, plus some extra for the rest of the tree (connection tissue and roots), will be shed. Trees shed materials to the outside which die and eventually falls off / pulls away from the tree. Trees also shed materials to the inside. The internally shed area inside a tree is called heartwood. The model that describes this process is termed a "skin / core" system. Figure 12

Conclusion

Trees are complex reacting organisms which grow in dynamic, rapidly changing environments. Tree biology must provide for defense, reproduction, growth, and control of resources. Understanding simple models of tree growth can prepare tree health care managers for anticipating internal and external changes, and any symptoms generated.

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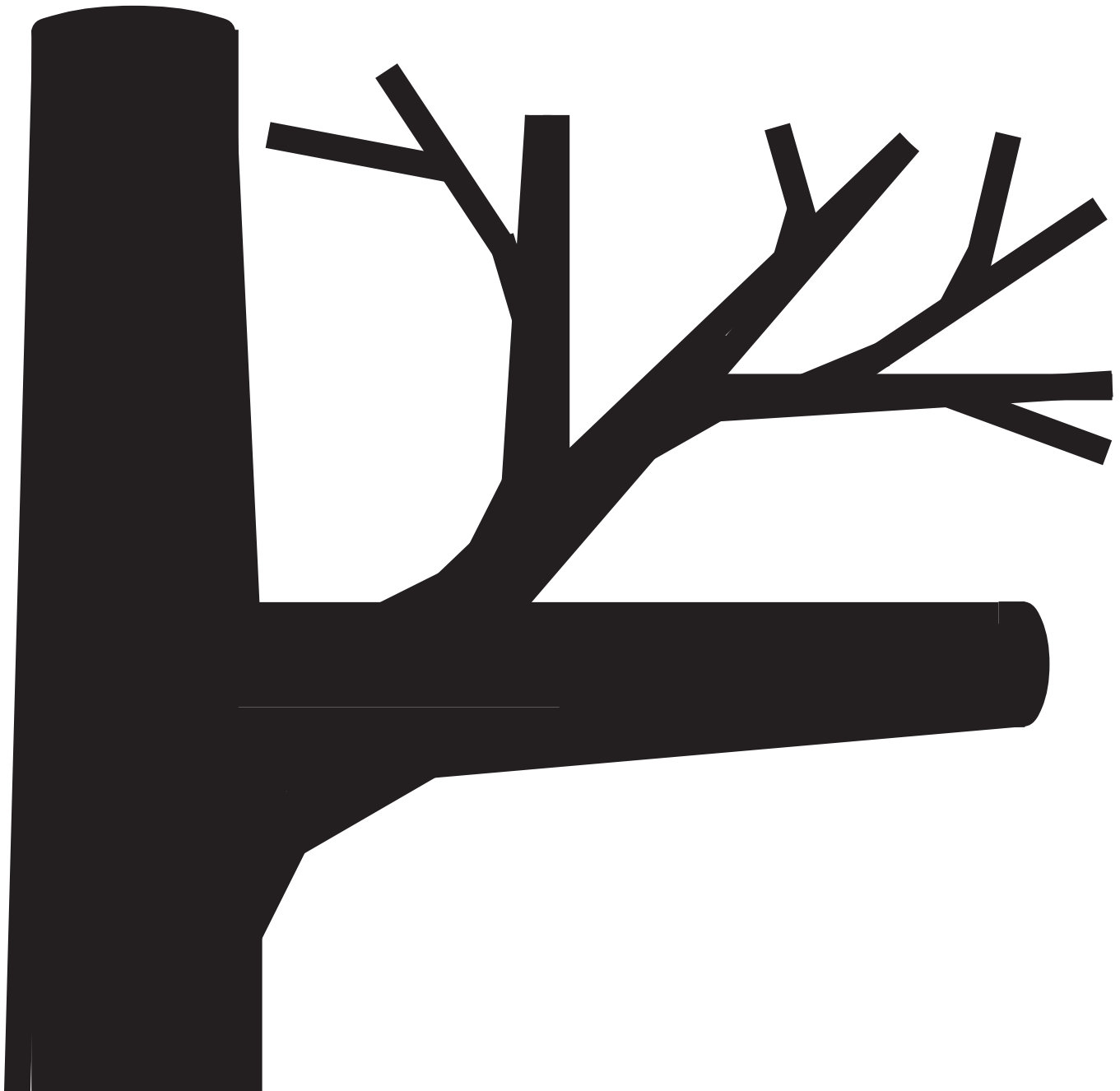


Figure 11: Tree are modular and segmented in their assembly through elongation and diameter growth. Growth segments occupy space, secure and control resources, and remain disposable through compartmentalization at each boundary zone in each node.



Figure 12: Tree growth is a living skin growing over a dead core. Senescing tissues are shed to the outside into the environment, or shed to the inside as heartwood.