Crown Pruning Effects on Roots*

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Introduction

Tree growth and development are dependent upon a few basic mechanisms. These mechanisms are responsible for the tree making holistic adjustments to a changing external environment. These basic mechanisms 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 (not individual parts) react to change are delineated, additional impacts such as pruning can be better understood.

Trees are complex organisms with highly evolved sense and respond systems. Because the tree as a whole is too complex to comprehend at a functional level, we must use simplified models to understand tree reactions to change. We will review in a very basic manner how trees control their own growth and how this growth control changes internal resource allocation patterns. Then we will examine how pruning of living tissues in the crown of the tree can directly and indirectly influence the roots.

Basic Tree Model

In the most simple way of visualizing tree reactions, the tree is split into three reactive components: leaves, connecting tissue, and absorbing roots. By keeping tract of how each of these components interact with each other, we can overlay our management inputs and understand tree reactions. Each of these three components have specific functions and can react to changes. Each of these three primary components are tied to their respective meristem and associated sensor system.

Leaves -- Leaf tissue is tied to the shoot tip meristems, must deploy resources to collect light and carbon-dioxide efficiently, and must draw required resource from storage and from the absorbing roots. Leaves are net photosynthesizers (Ps).

Absorbing Roots -- Absorbing roots are tied to the 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 the leaves. The absorbing roots are respiring (Rs) organs.

Connective Tissues -- All the biologically and physically active tissues between the leaves and the absorbing roots are tied to the cambial zone meristem and the bark cambium. The connective tissue provides for storage volume, conversion processing of sugar and starch, transport and structural support. The connective tissue draws required resources from leaves and absorbing roots. The connective tissues are net respirating areas (Rs).

Growth Sensors

All three 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 illicite responses from meristems and modify growth control messages to the rest of a tree. Primary sensor locations are: active buds, outer chlorophyl containing cells (cortical-like cells) of twigs and stem, proto-chlorophyl 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), position and mechanics (leading to trophic, nastic, and reaction wood responses), temperature, oxygen status, water status, essential element status, and carbohydrate (food) status. Tree respond to the sensor messages by making growth regulator changes which modify the 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 the chemical bonds of carbon compounds. These carbon compounds provide the 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 is released. The process of allowing electrons to slowly and systematically leak back to the oxidative environment (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 the cells, a high levels of electrons are maintained by photosynthesis which acts as an electron 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 trees reaction in order to slow electron loss is called compartmentalization. The tree's growth regulation system maintains electron flows that will facilitate 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 Space

Storage materials in a tree are concentrated electron (energy) sources. Carbohydrate can only be stored and retrieved within a living cell. Storage of critical resources requires efficient control systems to assure materials can be removed from storage, transported and used where needed. Carbohydrate storage in the tree is in parenchyma cells, primarily ray cells. Only cells in the last few annual rings are utilized. Easy access is an important part of storage systems. The major source for new growth is the locally available carbohydrate immediately behind the 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 the branch will be near its tip.

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 can not generate enough food for themselves and some extra to ship away will be seen as electron loss areas and be compartmentalized off. Branch autonomy is the principal reason proper branch and twig pruning can work without massive damage to the tree.

A growing point expands using carbohydrate stored just behind the buds and in the outer annual rings. With full expansion of the 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 area is expanded into, these gains are consolidated with storage of 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 Regulation

Trees use environmental sensors and internal feedback mechanisms to modify genetically designed reactions. The numerical magnitude and the surface area of the meristematic tissues clearly presents a command and control problem for the tree. Any portion of the 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.

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 evel (growth control path). Within the tapestry of living cells, tissue types, and organs in a tree there are a myriad of demand and supply "circuits" or pathways. These circuits of demand and supply are established and maintained by three major growth regulators: auxin (primarily a shoot signal), cytokinins (primarily a root signal), and abscissic acid (a dormancy and sub-ordination signal).

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 the most direct vertical connection between the top and bottom of a tree through living cells. Auxin moves downward slowly through living cells. The 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 downward in the most direct line to the tree base. Auxin is destroyed by root tip enzymes (requiring oxygen) to prevent signal build-up 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 tip. The terminal buds usually generate the strongest signal. This signal varies across the season, day-to-night, and with the health of the bud. Waves of auxin flow out from the buds, creating a unidirectional signal to all cells below. Auxin is essential for root growth.

Cytokinins -- Cytokinins, (not kinins as in animals) are a variety of nitrogen containing compounds produced in root tip areas and dumped into the transpiration stream. Cytokinins destroy dormancy and control chemicals, and are essential for shoot growth. Cytokinins represent a signal on the health of the root and the general composition of root adsorbed materials. Cytokinins are transported preferentially to areas where the auxin pathway is strong. The shoot destroys the cytokinin signal to prevent build-up or recycling of the signal.

Abscissic Acid (ABA) -- Abscissic 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 the tree's genetic material, tree buds 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 the cytokinins. ABA in tissues determine whether they will remain dormant and dominated by other buds that generate a strong auxin signal. This is the mechanisms of how a terminal bud dominates and controls subordinate 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 the tree, each cell is reading the combined, integrated growth regulation messages. 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 "control field," similar to an electric / magnetic field. The control field type and strength assures the tree responds as one organism even when shoot and root meristems and storage tissues, could be tens of meters apart.

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

At any given point a meristematic cell reading the control field would respond by generating growth (internode), growing point initiation (node), storage change, dormancy timing changes, no change in operations at all, or an amplification or destruction of the control field. Reading of the control field by a cell is influenced by the cell's health and juvenility of the tissue, and environmental features such as oxygen content and temperature effects. The application of control field signals uses 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 used and stored. The growth control path is dominated by auxin moving in one-direction (downward), through living cells, seeking the most direct path between tree top and bottom. Along that path cytokinins are brought in 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 growing point on the tree, branch, or twig.

On one twig, the terminal bud may be the only dominant growing point. This dominant growing point generates a strong auxin pathway, which in turn, yields 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 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.

In the stem is the combined growth control paths of all the growing points above. The demand and 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 the 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 along one side of the tree. These pathways may spiral 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.

Control Pathway Types

There are four types of growth control pathways in a tree: primary, active, marginal, and dormant. The primary pathways are the single or multiple terminal buds controlling the tree. These pathways correlate supply and demand throughout the tree, generate the majority of the food, and use a majority of the soil-gathered resources. The active pathways are associated with productive twigs and branches generating major amounts of food for the rest of the tree. Significant amounts of food along these pathways are stored if there is excess. Marginal pathways may have been active at one time but because of shading, damage, or position effects, are barely generating a positive food flow along the pathway. Dormant paths still contain signal but not enough to demand a break in control. Loss of signal along what was once a pathway defines death.

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 shedding and compartmentalization processes. The result is a longer resonance time inside the tree between full signal cycles. The result is a slower effective response time to changes within mature and over-mature trees.

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 the wiring and the switches open does not mean work will be completed. 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. Circuits may be open but may contain no materials for growth, generating no response.

Control 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 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:

A) Low field strength (low auxin / cytokinins ratio) -- root growth and shoot initiation, also initializes the tree for Spring start-up.

B) High field strength (high auxin / cytokinins ratio) -- shoot growth and root initiation, also new pathway connections are fashioned, and springwood produced.

C) Moderate field strength (intermediate auxin / cytokinins ratio) -- stem growth, also redirection and adjustment to root and shoot balance, and summerwood produced.

D) Low field strength (low auxin / cytokinins ratio) -- root growth and shoot initiation.

E) Very low field strength (minimal auxin / cytokinins ratio) -- winter or dormant period activity suspension.

Anti-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 growth is essential for shoot growth, which is in turn, 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 death's doorway. The unbalanced nature of shoot and root generate the 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 are presented against a biological background of continuous change. One could say that 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 -- but represents the ability of life to adjust and change under the poorest conditions. The unbalanced nature of a tree system is required in order to respond to change.

Shoot / Root Model

The next step in understanding tree functions in a holistic sense is determining resource allocation patterns between shoot and root. (Thornley model) To approach or calculate the proportional change patterns seen in trees, or their "functional balance," only four components are required: sapwood shoot mass, sapwood root mass, photosynthesis rate, and nitrogen uptake rate. Trees will attempt to balance shoot mass and Ps 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 that the photosynthesis rate and nitrogen uptake rates are very susceptible to both external and internal environmental changes. This model will work for other root-absorbed materials besides nitrogen, but because of the significant energy expense involved with nitrogen assimilation and its generally limiting levels in most terrestrial environments, root-absorbed nitrogen works well in this model.

The critical resources shown to be limiting, and shown to represent a functional balance between shoot and root, are the carbohydrates produced in photosynthesis (CHO) and nitrogen absorption (in its three forms) 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 storage within the tree. For carbohydrates there is an addition storage problem with form -- starch or sugar.

General Model Examples

Remember that in the shoot/root ratio model, an important benchmark process and its associated tissue mass must always be balanced with its opposite process and tissue mass across the tree. For example, as nitrogen absorption declines, what nitrogen remains is concentrated more in the roots and used preferentially. This leads to less shoot growth and more root growth. A side issue is the build-up of carbohydrates in the tree which is of pathological concern. Even before growth is noticeably reduced, the tree is reallocating nitrogen to vital processes. One vital need is in the absorbing roots where more rapid turn-over is occurring as nitrogen concentrations fall.

Moving from the roots to the shoots, a decline in carbohydrate from failing photosynthesis (as in green wood pruning) allows carbohydrates to be preferentially held in the shoot. The result is a greater allocation of carbohydrate to shoot production and less to roots. After a time of internal nitrogen reallocation, the smaller allocation of carbohydrate to roots mean less nitrogen uptake. As pathogens, damage, toxins, stress, etc. limit photosynthesis, less root area is generated.

With supplemental nitrogen fertilizers and water, root growth declines and shoot growth increases. In addition, the added nitrogen causes a decline in starch and an increase in sugars. Increased sugar contents and additional nitrogen generate improved access and attack conditions for a number of pathogens and insects.

Pruning and Control Pathways

Examples The pruning of a marginal branch in a tree creates a wound, severs tissue connections and disrupts the growth control pathway. The remaining control field near the wound releases dormant growing points if there are carbohydrates available. If the branch was marginal and had been barely hanging on for several seasons, then local storage in the rays would have been depleted. What growth control pathway is present, with assocaited poor connections to the remaining tree, could be taken over by an active shoot above this path. This realignment to other growth control pathways will cause little disruption in the tree.

On the other hand, if an active growth control pathway is pruned and disrupted, the local control field at the wound will release dormant growing points, initiate adventitious buds, and demand food supplies. The large growth control pathway will be partially taken over by other active and primary pathways arising from further above the wound. If the active pathway was from a small diameter branch, then the released sprouts should quickly recover the active growth control pathway that ends in the roots.

If the branch was active and large in diameter, as sprouts become self-sufficient, the growth control pathway will be reestablished from the wound downward. There will be some areas taken over by adjacent pathways, and some tissue in the stem and roots may be compartmentalized off. Large branch (heartwood exposure) wounds are periods of weak control for tree defenses and so provide pest attack opportunities. Finally, after several seasons of adjustments, new pathways are efficiently established and new connections made.

Pruning Impacts

Given the mechanisms of how trees adjust shoot and root functional balance, and how the tree correlates control of growth processes, pruning impacts can be surmised.
Functionally, pruning produces a:

1) failure of the tree to generate food.

2) failure of the tree to generate fuel for nitrogen (and other materials like phosphorus) uptake.

3) loss of significant volumes of storage space and initiation of storage connectivity problems. 4) use of significant amounts of stored food reserves in reallocation processes.

5) major disruption and modifications of control fields and pathways (connection between shoot and root), similar to the reallocation or initialization of the system during Spring start-up -- a period of confused control messages, resource allocations, and defenses.

6) control field signals for immediate shoot initiation and release.

7) growth control pathway, in the short run, initially requests the growth of any primary or active pathway roots where carbohydrate is available following these priorities: healthy primary pathways stimulate many roots -- active healthy pathways stimulate few -- marginal and unhealthy pathways stimulate none. Note that under warm temepratures, food supplied in the transport pathway from the pruned branch will be used before the slow moving growth control field changes -- a lack of switch and food syncrony.

8) growth control pathway, over the long run as shoots are rapidly expanding and generating food, requests minimal root growth.

9) new expanding sprouts generate stronger and stronger growth control pathways, disrupting primary and active pathways already functioning.

Conclusions

The summary result is the whole tree is stunted by pruning of living tissues. The stunting effect is developed by (regardless of control field effects on a few released sprouts): less shoots, less roots, less carbohydrate supply, less storage, and less nitrogen uptake.

Root impacts are proportional to the amount and strength of the growth control path destroyed. Topping or primary pathway disruption leads to tremendous root problems. Large amounts of active pathway pruning will constrain root growth. Marginal growth control path disruption probably has little effect on roots.

Pruning should concentrate only on active and marginal pathways because the primary paths will be maintained (sometimes strengthened). Timing of pruning for minimizing root impacts would be dormant season and mid-summer, if pests can be minimized. Overall in roots under significant crown pruning, root growth slows and can decline, while health may be compromised.

Suggested Literature On Shoot / Root Interactions

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