Control of Shoot / Root Balance in Trees

by Dr. Kim D. Coder, University of Georgia January 1998

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 describing regulatory partitioning between shoot and root.

The type of model proven to be most effective is called a "Thornley" model, although many derivations and more refined systems exist. The result is a means of 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 the shoot is to utilize soil gathered resources to capture and ship carbon to the root. The purpose of the root is to utilize carbon to capture and ship soil resources to the shoot. Using only a few basic feature of shoot and root can let us estimate the scale and intensity of shoot / root interactions. (Figure 3A)

Estimating Balance

To 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. (Figure 3B) 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 highly susceptible to both external and internal environmental changes.

Note that 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.

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 storage within the tree. For carbohydrates there is an addition storage problem with its form — starch or sugar.

University of Georgia Cooperative Extension Service Forest Resources publication FOR98-3

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 across the tree. In the case we are using here, as nitrogen absorption declines, what nitrogen remains is concentrated more in the roots and used preferentially in the root. 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.

A side issue when nitrogen uptake declines is the build-up of carbohydrates under good conditions in the tree. Excess carbohydrate, especially in the sugar transport form, provides a significant pathological risk. This system is sensitive to small changes. 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.

Shoot Example

Moving from the roots to the shoots — a decline in carbohydrate from declining photosynthesis (as 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 and allocated carbohydrate resources to generate more photosynthetic surfaces. 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 the tree to infernally 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 manager does to a tree that effects the equation (model) 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 the 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 the tree. One example is the infected absorbing roots are better protected from surrounding soil microbial populations.

The symbiotic relationship can help minimize energy loss to the environment, allowing for more time to elapse before the root energy loss in the area initiates compartmentalization. This slowing in the root turn-over 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 the tree. The tree receives some of its nitrogen supply already reduced to amino acid form. Another respiration path is made available to the 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 the 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 the tree. Mycorrhizae modify the shoot / root functional balance in a positive sense, and under some severe soil limitations, can 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 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 the end of life. 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.

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 — 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. There can be no shoot / root balance!

Conclusions

Trees exist in a state of internal and external flux. The dynamic interactions of the various tree parts are correlated through growth control regulators and resource allocations. From moment to moment, trees are attempting to solve a series of biological simultaneous equations. The answer for the tree, and for human observers of tree reactions, is a never ending optimalization process played out among a wild and varied mixture of site, tree, and other organisms. Tree managers need to understand how cultural treatments change tree growth regulation patterns and the "functional balance" between top and bottom.

Suggested Literature On Shoot / Root Interactions and Tree Growth Control

Cannell, M.G.R. 1989. Physiological basis of wood production: A review. Scandinavian Journal of Forest Research 4:459-490.

Coder, Kim D. 1998. Growth Control Systems In Trees (Tree Growth Control Systems Series). University of Georgia Cooperative Extension Service Forest Resources publication FOR98-4 . Pp10.

Coder, Kim D. 1998. Pruning Effects On Tree Growth: Growth Regulation Consequences (Tree Growth Control Systems Series). University of Georgia Cooperative Extension Service Forest Resources publication FOR98-5. Pp3.

Coder, Kim D. 1998. Tree Growth Response Systems (Tree Growth Control Systems Series). University of Georgia Cooperative Extension Service Forest Resources publication FOR98-6. Pp7.

Dickson, R.E. 1989. Carbon and nitrogen allocation in trees. In, *Forest Tree Physiology*, E. Dreyer *et.al.* editors, pages 631s-647s suppliment #46, Ann. Sci. For.

Johnson I.R. and J.H.M. Thornley. 1987. A model of shoot:root partitioning with optimal growth. Annals of Botany 60:133-142.

Wilson, J. Bastow. 1988. A review of evidence on the control of shoot:root ratio, in relation to models. Annals of Botany 61:433-449.

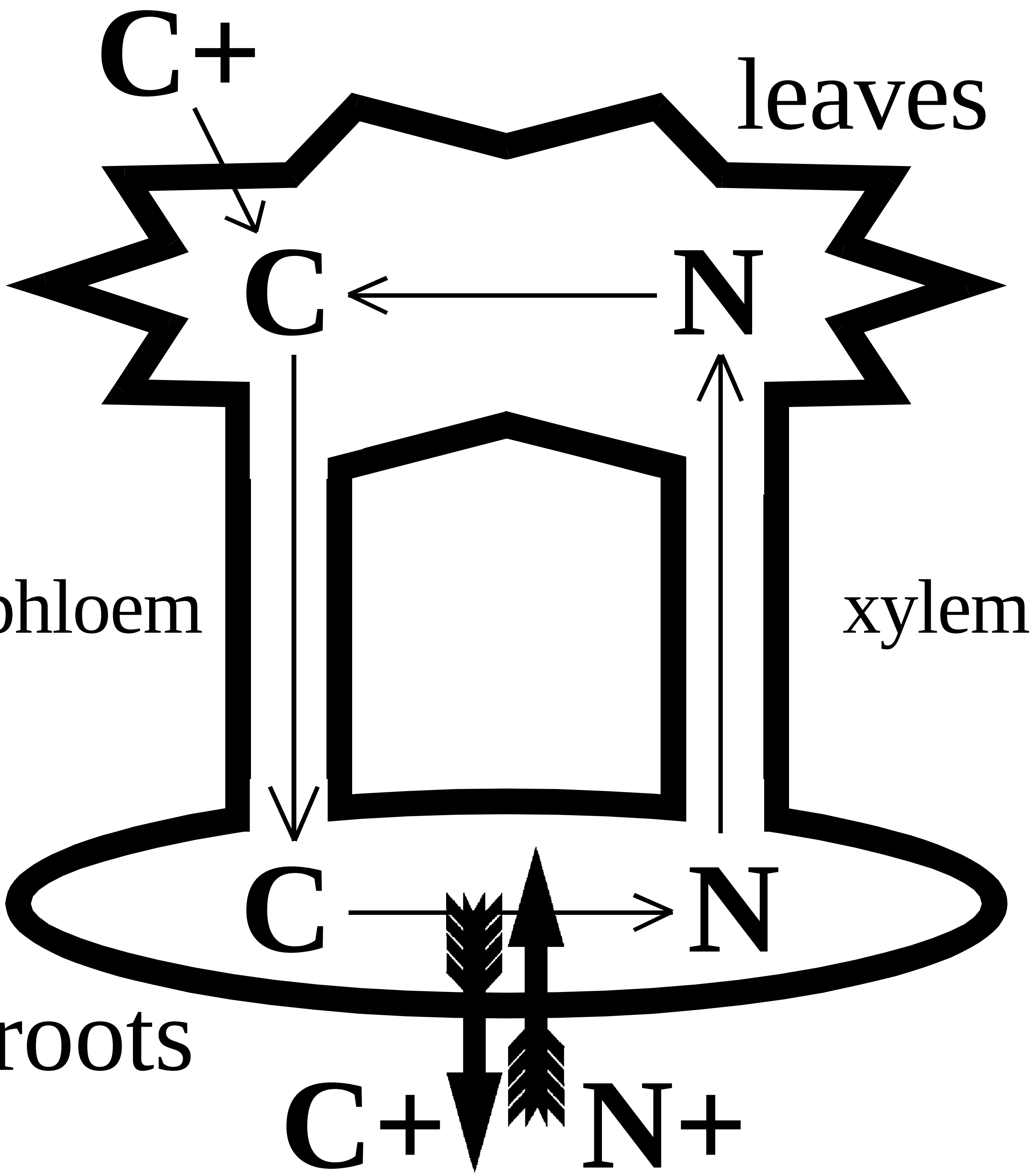

Figure 3A: The capture and use of carbon and nitrogen are critical for tree life. Carbon is captured by leaves and is transported for use in capturing nitrogen. Nitrogen is captured by root and is transported for use in capturing carbon. The shoots are essential for root function, and the roots are essential for shoot function.

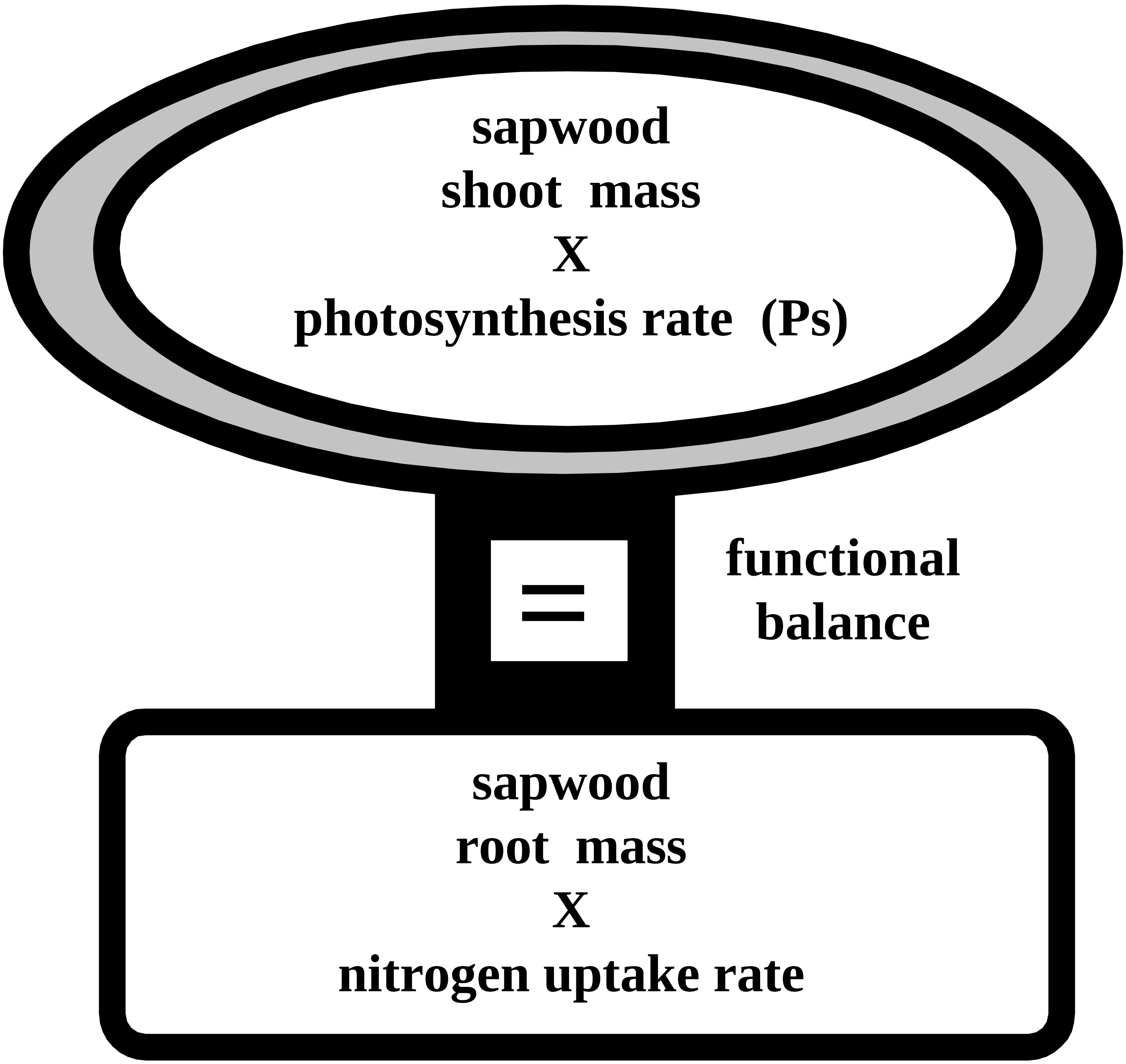

Figure 3B: A tree shoot / root balance equation is graphically shown utilizing four components. As one side of the equation changes, the other side must change in the same direction to maintain the equality. In the literature, this model has been tested and upheld by many researchers. It is generically called a “Thornley” model after its developer.