Tree Hormones and Why They Matter

Joseph Murray

The hormone pathway runs from roots to branch tips in trees such as this *Stewartia pseudocamellia*.

Trees are the oldest, largest, and perhaps the most complex organisms on earth. Increasingly, society has moved beyond simply appreciating trees for the beauty and shade they offer, and now recognizes the significant societal, environmental, and economic benefits trees provide. These benefits can be especially important in urban areas, yet many urban sites present very difficult situations for growing trees. Most tree species should be able to live and provide benefits for several hundred years, but urban trees—often plagued by poor soil, restricted root zones, and limited care—rarely achieve even a fraction of their potential life spans. The more we (arborists, city foresters, growers, etc.) know about the biology of trees, the better we will be able to apply proper arboricultural practices to help trees help themselves.

Plant hormones and their effect on tree behavior is an often overlooked aspect of arboriculture. Plant hormones—generally defined as substances produced in very small amounts in the plant that influence the plant's physiological processes—play a crucial role in helping the plant to make adjustments in a changing environment. Knowing more about how plant hormones work in trees helps in understanding the implications of such common arboricultural practices as pruning, planting, fertilization, and irrigation.

What Do We Know About Plant Hormones?

Prior to 1950 in the United States, this article would only have addressed two hormones, auxin and ethylene, which were then considered responsible—by their presence, absence, concentration, or interaction—for everything happening in trees. Today, most plant science textbooks describe five major plant hormones: auxin, cytokinin, gibberellins, abscisic acid, and ethylene. However, there are more than five hormones in plants and research is ongoing.

Plant hormones present a number of challenges to the physiologists attempting to understand how they operate. Plant hormones are produced, and are active, in very small concentrations. At different times during the growing season, different parts of the plant produce specific hormones that influence dis-

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Hormones and Tropisms

An interesting example of a hormone causing a plant response is auxin's role in phototropism. A tropism in plants is any growth response resulting in the curvature of a plant organ toward or away from stimuli. Phototropism in plants typically consists of new growth in the shoot system growing toward light. Light striking the side of new growth at the end of branches stimulates the tissues to produce auxin, which then migrates to the opposite (dark) side of the stem where it triggers a physiological response loosening longitudinal cell walls, allowing those cells to expand in length, thus resulting in the curvature of the stem toward the light. Similarly, gravitropism also results in the curvature of the new growth in the root system downward to gravity in response to the unequal cell expansion in the tissue just behind the root tip. In addition to light and gravity, there are many other forms of stimuli that elicit a growth response.

This *Hippeastrum* exhibits phototropism—plant growth bending toward light. Charles Darwin was one of the first to research the mechanics of phototropism and, with his son Francis, published a summary of their observations in the book *The Power of Movement in Plants* in 1880. Later researchers identified auxin as the plant hormone involved in phototropism.

tant tissues that are receptive for brief periods of time. Furthermore, the same hormone may cause two different responses in the same receptive tissues, depending upon the concentration of the hormone.

Hormones are signal transducers, converting an environmental stimulus into a physiological or anatomical response. As an example, let's look at how sunlight makes roots grow in the spring, via a simple pathway using the plant hormone auxin. It makes sense for a tree to invest resources into the root system before the shoot system, so early in the spring sunlight on the shoot apical meristem (bud) and young leaves results in these tissues producing auxin, which travels down to the roots. Hormones in plants may travel throughout the plant but will only affect tissues composed of cells that have special receptors to receive that particular hormone. These target cells may perform a number of functions in response to the arrival of the plant hormone. In a physiological response similar to that described for phototropism (see textbox), auxin stimulates cells at the root tips to release hydrogen ions into the surrounding cell walls. In response to the decreasing pH, enzymes become activated and begin loosening bonds between cellulose microfibrils, thus softening the cell walls. Inside the plant cell is an organelle, the central vacuole, full of water that is continually pressing against the cell wall resulting in turgor pressure. The collective action of softened cell walls expanding in response to the central vacuoles results in the elongation of the root tips. The signal transduction is complete. The hormone auxin allowed the tree to translate an environmental stimulus into a physiological and anatomical response. Simply put, sunlight made roots grow.

The Auxin-Cytokinin Pathway

Many gardeners are familiar with a common technique to produce bushier plants; by simply pinching off the end of a growing stem,

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Removal of the branch tip (center of photo) disrupted the auxin-cytokinin pathway, allowing lateral shoots to develop just below the removal point.

there is a proliferation of branch development below the area that was removed. This growth response demonstrates what happens when the auxin-cytokinin pathway is disrupted.

The downward flow of auxin creates a pathway from the terminal buds to the root tips. As mentioned, the auxin acts as a signal transducer, notifying the roots that it's spring and it would be in the best interest of the tree to begin growing roots for the season. In addition to growth, the tissues in the root tips produce the hormone cytokinin. Cytokinin, like auxin, is going to stimulate growth as well, but in a different location—at the ends of the very branches that originally established the auxin pathway. Each spring, the auxin-cytokinin pathway promotes the timely growth of the root and shoot systems.

Like a male insect following a pheromone trail produced by a receptive female insect, cytokinin follows the increasingly stronger gradient of auxin directly to the shoot tips responsible for the auxin's production. Left out of this pathway are the numerous lateral buds, especially those near the end of the branch. Without receiving the spring wake-up call from cytokinin, these lateral buds become dormant. Although they are no longer visible at the surface, each year the dormant buds move outward with the vascular cambium so that they remain close to the surface. Should something happen to disrupt the auxin-cytokinin pathway, then they may emerge and grow into branches, setting up their own auxin-cytokinin pathways with the root system.

It's also important to recognize that there are specific enzymes located at the shoot and root tips to destroy the arriving hormones after they have had their effect. These hormone-destroying enzymes are produced in the same tissue near the shoot and root tips. In the root tips, an enzyme is produced that will destroy auxin, just as in the shoot tips, an enzyme is made to destroy cytokinin. Should these enzymes not perform their tasks, the concentration of hormones will increase and cause a different response in the receptive tissues.

Common Tree Care Practices and the Impact of Hormone Pathways

Knowing that plants have internal mechanisms helping them with an ever-changing environment should make us pause and attempt to understand what is happening in the plant before beginning to actively "care" for the plant. Sometimes our efforts at achieving short term goals (e.g., darker green foliage, more growth, controlled shape) may be aggravating the tree's ability to achieve optimal health. Trees' hormone pathways are involved in the arboricultural practices described below:

Transplanting

Regardless of how carefully balled-and-burlapped or container-grown trees are transported and installed, some roots will be damaged and die. The roots that are particularly susceptible to damage are the very fine root tips. And it is these same roots that are to produce cytokinin and transport it up to the shoot tips to stimulate elongation of branches. This is why newly transplanted trees are so slow at developing significant shoot growth during

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Auxin accumulates at the base of stem cuttings, stimulating root initiation. Exogenous auxins, in the form of rooting powders or dips, are often applied to the bases of woody plant stem cuttings before sticking in propagation beds (rooted *Microbiota decussata* cuttings seen here).

the first year or two after transplanting. The loss of the root tips also means the loss of the ability to produce the auxin-destroying enzymes. As a result, the auxin concentration increases until the surrounding tissue responds by generating adventitious root growth. This kind of root proliferation can be observed when an African violet leaf stem is placed in water. Auxin moves down the base of the stem until it builds in concentration at the point the stem was severed from the plant, changing stem tissue into actively growing root tissue.

Fertilization

So long as there is adequate nitrogen available in the soil, tree roots will continue producing cytokinin at the appropriate times of the year in response to the establishment of the auxin pathway. However, when the nitrogen level is inadequate, the root system will suspend cytokinin production. Auxin will then be the dominant hormone directing the majority of resources to continue root growth, and a larger root system enables a search through a greater soil volume for nutrients. In nutrient poor soil, it is in the tree's best interest to invest its limited resources in root growth and not shoot growth. But if a fertilizer is applied, the root system is fooled into thinking it is in a nutrient-rich environment and the production of cytokinin increases, resulting in a larger shoot system relative to the root system. If this nutrient subsidy ceases, the tree is caught with a shoot system that cannot be sustained with the current root system.

Irrigation

Cytokinin also functions in the opening of stomata on the underside of leaves, allowing the steady movement of water from the roots to the leaves. The arch-rival of cytokinin is another root-derived hormone called abscisic acid. Abscisic acid is responsible for the closure

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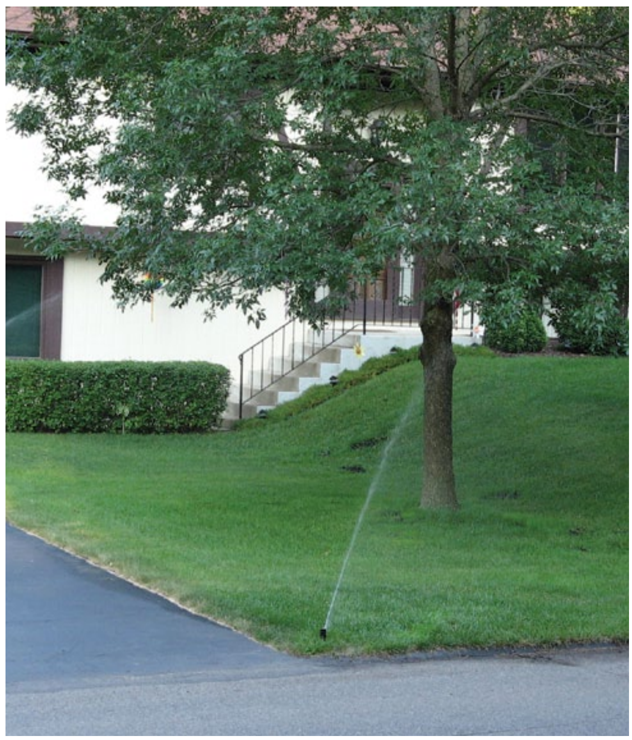

When trees receive environmental subsidies, such as supplemental water from lawn irrigation systems, their internal regulatory mechanisms can be disrupted resulting in imbalanced root-to-shoot growth.

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Topping, an improper pruning practice in which tree trunks and major branches are drastically cut back, results in a proliferation of weakly attached lateral shoots at the pruning points.

of the stomata when there is not enough soil moisture to perform photosynthesis. As long as the fine roots are in contact with soil and able to absorb water, cytokinin is being produced and traveling to the leaves to keep the stomata open. Should the soil begin to dry and soil particles pull away from the roots, the root system will produce abscisic acid and send it to the foliage to shut the stomata. Periodic episodes of landscape irrigation disrupt this internal regulatory mechanism, possibly placing those irrigated trees at risk for more severe damage. If periodic irrigation stops (perhaps from failure of an irrigation system or institution of municipal watering bans) the trees are suddenly exposed to drought conditions made even more acute because the shoot system has developed at a faster pace than the root system.

Improper Pruning Cuts or Storm Damage

Similar to the response observed in trees following transplanting, the loss of shoot (branch) tips will also disrupt the auxin-cytokinin pathway. Should the shoot tips be removed, the timely production of auxin and its transport to the roots will not occur in the spring. This means the cytokinin produced in the roots will not know where to travel to stimulate the growth at the end of the branch. The concentration of cytokinin will increase at the point where the branch broke or was cut because the tissue responsible for producing the cytokinin-destroying enzymes is gone. As a result, cytokinin will spread through this new truncated terminal end of the branch, finding and releasing the latent buds. This is why there is a proliferation of watersprouts emerging at the end of branches damaged by storms or by the ill-advised practice of topping trees.

Lessons Learned

Trees have existed for over 300 million years. The evolution of a hormone system allowed early plants to deal with a changing environment and to coordinate their parts in time and space. And for venerable trees, these hormone systems are particularly important. As caretakers of trees in urban areas, it is our duty to first understand these subtle internal mechanisms before blithely applying a treatment that we believe is in the tree's best interest.

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