Connections in wood and foliage

BY KEVIN T. SMITH

Trees are networked systems that capture energy, move massive amounts of water and material, and provide the setting for human society and for the lives of many associated organisms. Tree survival depends on making and breaking the right connections within these networks (photo, right). Although many of these connections also occur in herbaceous plants, they are even more important in trees due to their potentially great size and age.

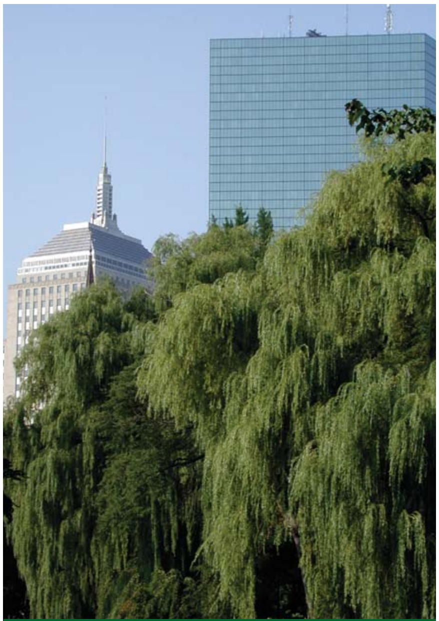
Connections support the flow of water, biomolecules and essential elements from where they are obtained or produced to where they are stored and used. Within each living tree, these connections occur across a wide range of scales, such as between individual living cells; between tissues, like phloem (inner bark) and sapwood; and among plant organs, like leaves, branches, stems and roots. This article outlines a few of the connections in healthy wood and foliage, and how breaking these connections can also be part of healthy maturation and seasonal cycles.

Symplast importance. As seed germinate, living cells in growing roots and shoots become interconnected by strands of cytoplasm (cell contents) and form a single web or symplast.

The symplast links the energy-capture system — primarily in foliage — to the transport, storage and utilization systems throughout the tree.

During development from seedling to mature tree, the symplast continues to expand and link living cells, including those in sapwood. Sapwood is usually light in color and contains symplast and apoplast (the nonliving system of cell walls and wood pores that conducts the flow of water and some essential mineral elements). The living symplast regulates flow through the pores, stores energy (frequently as starch) and actively responds to injury and infection. The symplast distributes some of the mineral elements, as well as carbohydrates, that fuel living cells. It also provides the communication pathway to carry signals and growth regulators from one plant part to another.

Some trees, such as oak, walnut and many conifers, convert living sapwood into nonliving heartwood as they mature. This breaks the symplast connection and frequently darkens or discolors the heartwood (photo, below right). Before living cells die in the conversion of sapwood to heartwood, their metabolism shifts to form chemicals that resist wood decay. This conversion often involves the plugging of wood cells that previously conducted sap. The tree reduces its "overhead," or maintenance cost of living cells, while gaining decay resistance to the central core of the stem. Part of the cost or tradeoff for the



Mature trees in the Boston Public Garden connect people to the city.

The longitudinal section of a red maple shows compartmentalization of wood decay in the center of the tree and at a branch stub.

Black locust wood in a cross-section shows dark heartwood surrounded by light-colored sapwood and crossed by prominent rays.

PHOTOS COURTESY OF KEVIN T. SMITH; COURTESY OF KENNETH R. DUDZIK, USDA FOREST SERVICE

A maple leaf with autumn coloration is loading biomolecules and nutrients into the veins to transport into the tree.

tree is the reduced volume of living wood available for energy storage and water conduction. As long as the vascular cambium continues to add new cells to existing wood, a tree can remain healthy as it loses living sapwood to healthy heartwood formation.

Breaks in symplast connection. The dynamic symplast also has a key role in compartmentalization, which is the process that resists the spread of destructive microorganisms in living wood (photo, opposite). During much of the year, the water in the apoplast of the stem and branches is under tension. When a tree is wounded by storms, wildlife, human activity and so on, the column of water in each pore of the apoplast snaps and pulls away from the wound. This introduces air bubbles into the apoplast, and the wood begins to dry. The drying and aeration of sapwood kill living cells and reduce the extent of the symplast.

Soon after wounding, the wood pores are plugged by the tree. This breaks the apoplast connection and tends to limit the aeration, drying and spread of infection to as small a volume as possible. At the living margin adjacent to the killed wood and infection, the cells shift their metabolism and deposit phenolics, terpenes and waterproofing lipids that can further resist the spread of infection. After injury, the vascular cambium produces an anatomically and chemically distinct barrier zone that resists the outward spread of infection and helps protect the integrity of the living tree. Although the tree may not be able to prevent infection, compartmentalization enables the tree to continue to grow and thrive.

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Another obvious break in the symplast connection occurs during leaf fall. In one simple model for broad-leaved trees, such as maple, birch and poplar, some combination of day length and cooling temperatures reduces the production of the auxin hormone in leaves and growing tips. This reduction in auxin both slows growth and increases the sensitivity of the leaves to naturally occurring ethylene, a second plant hormone. This increase in sensitivity, as well as the additional production of ethylene by aging leaves, stimulates the breakdown and reassimilation of lipids, carbohydrates and essential elements back into the branches and stems.

Recent research suggests that the red-to-purple anthocyanin pigment in autumn foliage protects these essential processes while the materials are moved back into the twig and branch (photo, above). An anatomically distinct and "corky" abscission layer forms at the base of the leaf petiole, allowing the leaf to fall away from a waterproof seal. Although differing in timing and regulation, similar processes occur in other broad-leaved and conifer tree species. Premature shedding of foliage can occur in response to leaf infection by a wide variety of fungi. Although infection can occur early — even as the leaf is expanding in the spring — leaves may develop normally until the fungal demand for nutrition and surface area compromises the value of the leaf for the tree. Then, the leaf is shed. Leaf shedding that is premature, yet late in the growing season, usually does not cause lasting damage to an otherwise healthy tree (photo, above).

A silver maple leaf has black masses of fungus tissue, which is a characteristic of tar spot disease — a dramatic, but rarely threatening, disease.

Living connections do not stop with the individual tree, as trees are connected at greater distances through root grafts and fungal infections that can be beneficial (mycorrhizae) or damaging (root rots). Connections with people and society spread even further, through our landscape use and history.

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