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Origin of Buds, Branches, and Sprouts

*New shoots from young pollarded London plane trees (*Platanus x hispanica*, syn.* P. x acerifolia*). Pollarding is a legitimate technique to maintain the size of trees of some tree species after they have developed the desired structure. The shoots are removed annually, leaving dormant or latent buds to sprout from the pollard head the following year.*

By Kevin T. Smith, Ph.D.

Recent research shows that survivor trees in rural, managed forests rebuild broken crowns with new branches and foliage after ice storm injury (Shortle et al. 2014). Veteran trees in historic parks and landscapes show repeated cycles of crown loss and recovery (Fay 2002). Crown rebuilding or reiteration from sprouts is a physiological response with architectural effects that occur after crown injury or as part of tree aging, or senescence (Meier et al 2012). That a tree would form new shoots and branches to replace lost foliage and photosynthetic capacity makes sense (Shigo 1989). However, arboriculture and the public sometimes seem divided on what to do with branch and stem sprouts (Meilleur 2012).

Some ambivalence about sprouts may come from contributions to community tree care from production forestry and orchard management. The value of sawtimber for wood products is greatest for wood with straight grain and no knots. Stem or epicormic sprouts that form knots in the bole greatly reduce value of otherwise high-quality timber or veneer. In orchard production, epicormic sprouts frequently do not produce flowers or fruit and are considered a wasteful drain on fruit yield.

Arboricultural texts seem to strive for an obvious or sensible balance. It's difficult to deny that young sprouts can be weakly attached to the stem and pose a hazard for climbing and rigging (Beranek 1992). Sprouts that interfere with utility lines or structures should be removed and those that help fill gaps in the canopy should be left (Harris et al. 2004). Sprouts that currently or presently will interfere with existing crown structure should be removed, while leaving most of the rest (Gilman, 2012).

The characteristic arrangement of branches and the pattern of sprouts can be a distinctive feature of a tree species. Branching in the mature tree begins with the pattern established by primary growth at the tip of stem and branch. The emerging shoot tip of a new tree seedling grows from the tip or apex. That growing tip contains the dividing cells of the apical meristem. The core of the apical meristem contains cells that are totipotent, meaning they are capable of differentiation into any type of cell that the plant needs. A slight distance from that core the cells are still meristematic, but are beginning to follow the genetic program of specialization or differentiation into specific types of cells and tissues.

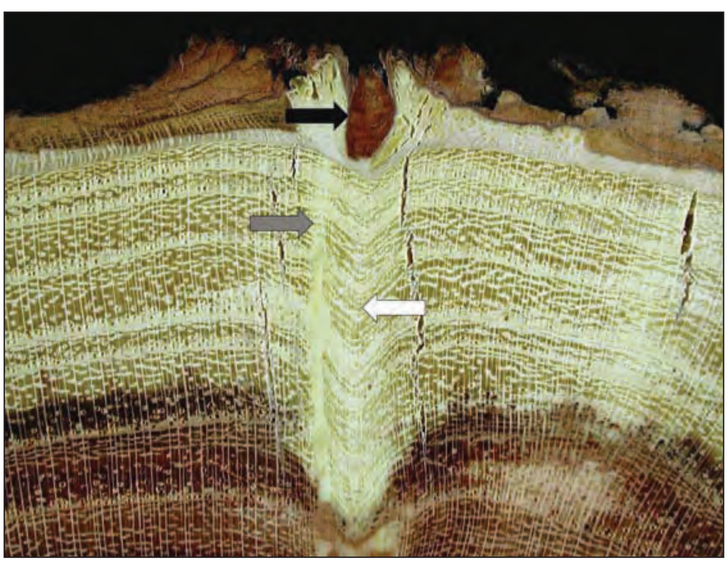
Before detectable changes in cellular structure, the daughter cells produced by the apical meristem lose totipotency and are programmed, or "fated" based on anatomical position, to develop into one or a few types of cells with specific functions. This program includes the organization of the meristematic vascular cambium as well non-dividing cells that comprise distinct tissues for transport, storage, energy capture, and structural support. Many corresponding processes occur in the root as well, which is beyond the scope of this article as are the interactions of plant hormones that direct or influence growth and development.

Normal branch formation is sequential and follows the same general pattern for conifer and broadleaved trees. At the edge of the apical meristem, dividing cells lose totipotency and become specialized as leaf primordia. Divisions of the leaf primordium will differentiate and mature into the specialized parts of the leaf. The physical position of the developing leaf and the connections to the stem constitute a node. This is the point at which the leaves and subsequently the branches are determined to be opposite, alternate, or whorled, a fundamental characteristic for tree identification (Coder 2014).

This is also the point at which phyllotaxy, the distribution or spiral of leaves around the stem, is fixed. As the leaf primordium develops, another small patch of meristem develops in the leaf axil, between the stem and the leaf primordium, and is fated to become the core of the axillary bud. That bud may be dormant until the following growing season, or it may remain latent for years to come.

Forest-grown sugar maple (left) and paper birch (right) that rebuilt their crowns from sprouts after a near complete loss of branches. All images courtesy of the author and Kenneth R. Dudzik, USDA Forest Service, Durham, NH.

All of the above takes place as primary growth, derived from the apical meristem. While these processes are taking place and the apical meristem is adding length to the shoot, the meristematic vascular cambium becomes organized to produce secondary growth. Secondary xylem cells differentiate into wood. Secondary phloem cells differentiate into inner bark that transports sugars and biomolecules. The vascular cambium sets apart the conifer and broad-leaved trees from all other green plants, even those that also grow tall such as bamboo and palm.

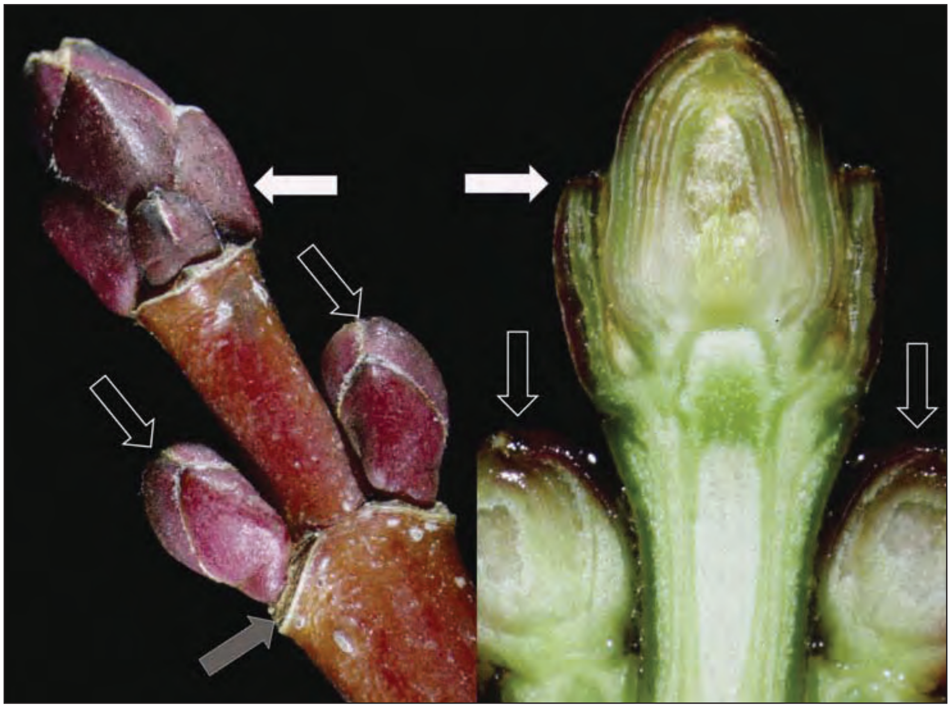


*Transverse section of black locust (*Robinia pseudoacacia*) showing a latent bud (black arrow) immersed in the phloem and bark. The distorted wood associated with the bud trace (white arrow) extends toward the pith. A second bud trace (shaded arrow) indicates a single bud in an epicormic complex or system of latent buds.*

The vascular cambium is formed usually during the first year of growth. Late in the growing season, some of the apical and axillary tips will begin to form flower primordia instead of or in addition to leaf primordia. Also late in the growing season, developing leaves are modified into bud scales that shelter the apical and axillary meristems through the coming dormant season.

After leaf fall, the axillary buds are usually pretty conspicuous, located above the scars formed at the base of shed leaves. The pattern of buds and leaf scars is tightly controlled, which is why tree identification from twigs and branchlets can be so reliable. At the beginning of the next growing season, and in response to external conditions including soil temperature, the dormancy of the apical bud is broken and the apical meristem begins to divide and form new cells. Depending on tree species, flower buds may break dormancy before the buds for new leaves or stems.

The extending shoot tips move away from the bud scale scars that typically circle the shoot. The distance between



*Terminal buds (white arrows), axillary buds (black arrows), and leaf scale scar (shaded arrow) in an intact (left) and dissected (right) twig of red maple (*Acer rubrum*). The bud scales protect the meristematic and primordial tissue that will produce shoots, foliage, and flowers in the growing season.*

successive annual bud scale scars enables the comparison of relative growth rates. A primary shoot with its own apical meristem may develop from the axillary bud the year following bud formation. As with the seedling, the axillary shoot develops a vascular cambium and undergoes secondary growth and wood production. The woody axillary shoot in now considered to be a lateral branch. Careful longitudinal dissection can show the bud trace that connects the primary growth in the pith of the branch to that of the stem.

Either due to the inborn constitutive program or induced by physical injury, sometimes two or more vegetative buds are formed at the shoot apex. Codominant stems result from multiple apical buds breaking dormancy and simultaneously producing new shoots. Alternatively, two or more young shoots may become appressed and grow together to form a codominant stem. As the formerly independent members of the codominant stem increase in diameter, they push against each other. Sometimes the vascular cambium becomes confluent and continuous around the appressed stems and form a strong union. Frequently, however, the vascular cambium does not become confluent or extensive bark is included in the tight crotch between the codominants. As the codominants increase in diameter and weight, the joint may weaken and eventually split.

The vascular cambium is continuous over the surfaces of branch and stem as well as the union of codominant stems. There are key differences, however. Early in the growing season, branch wood forms first, followed later by the formation of wood by the stem. This alternation helps produce a strong branch collar of interlocked branch and stem tissue that provides good structural support (Shigo 1985). Also, the inserted base of a branch contains wood that is chemically modified to resist the spread of infection from the branch into the stem. The union of codominant stems does not produce such interlocking layers and does not contain the protection wood. Although the relative growth rates may be manipulated by removal of foliage and branches from one member of a codominant pair (Gilman 2012), the change in aspect ratio does not result in the same interlocking connections or protection wood found in a natural branch collar.

In addition to lateral branches and latent buds that were initiated from the apical meristem and primary growth, new meristematic growth and shoots may develop from wounded or stressed living wood tissue. The totipotent meristematic tissue can form from cell divisions of callus pads at the edge of wounds or from outgrowths of ray parenchyma that have dedifferentiated. As with development of "normal" buds, the hormonal regulation of these events is complex and likely involves auxin produced near growing tips, cytokinins that regulate cell divisions, and ethylene that induces shifts in metabolism as part of a stress response.

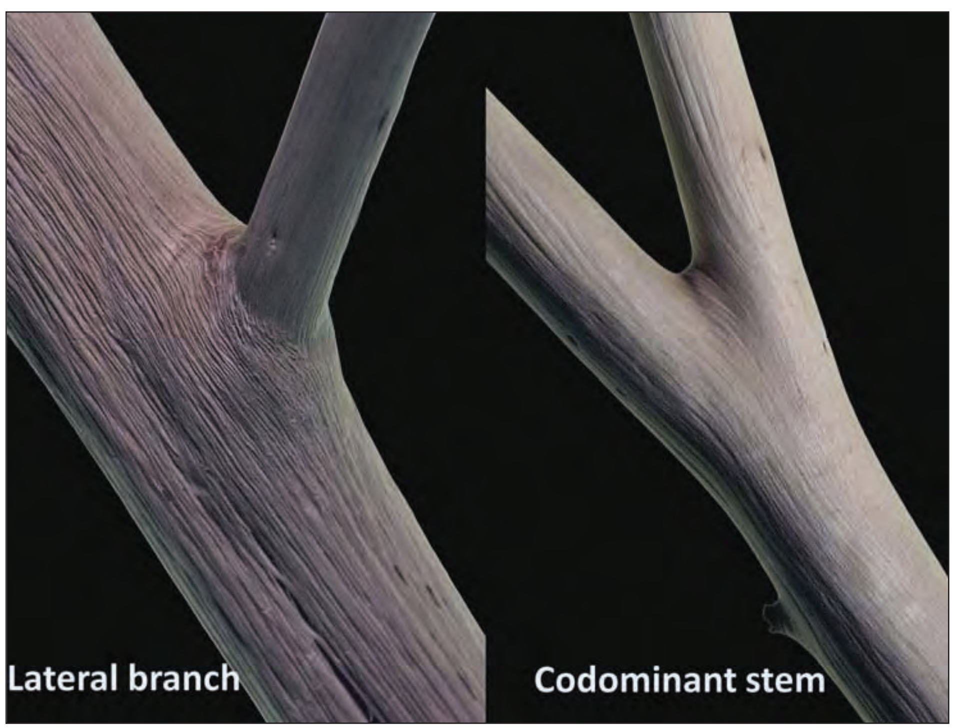
Sometimes these new meristems are encased in scales and properly called buds. Epicormic meristems that are not encased in bud scales are more properly referred to as "meristematic points." These meristems are not located at nodes nor do they follow the usual phyllotaxy. Being formed "out of place," these newly-arising buds and shoots are termed adventitious. The adventitious buds and shoots may be dormant until the next growing season or remain latent for years. The apical meristem of an adventitious shoot may produce its own axillary buds or meristematic points. The assemblage of adventitious buds, meristematic points, and resulting shoots form an epicormic complex.

The regular promotion of adventitious buds and sprouts is the key to pollarding. Successful pollarding requires early training of the tree for structure followed by annual removal of sprouts back to the knob or knuckle formed in response to the repeated sprouting (Shigo 1989). Within a few years the knob contains numerous

*New shoots from the base of a coastal redwood (*Sequoia sempervirens*). Redwood is a vigorous sprouter, from stem burls, stumps, and roots. Redwood sprouts from a single source can result in a "fairy ring" of mature trees many years later.*

latent or dormant buds as a persistent epicormic complex.

Adventitious buds that do not immediately germinate may grow from their base just enough to keep pace with bark growth, just like latent axillary buds (Meier 2012). Consequently, both latent adventitious and latent sequential buds can leave a bud trace in the wood. However, the adventitious bud trace will not link back to the primary tissue in the pith. Once the adventitious bud or meristematic point develops a shoot, that will produce the alternating, interlocked growth at the branch base.



*Branch union of white oak (*Quercus alba*, left) and codominant union of American elm (*Ulmus americana*, right). The bark has been peeled to show the presence (left) and absence (right) of a branch collar.*

Unlike normal sequential branches, the growth will be interlocked with stem only for the period of time after sprouting began. The branch collar may not be conspicuous for several or more years after sprouting.

Trees have highly ordered and very efficient responses to internal needs and external disturbances. Buds are preformed structures that can rapidly sprout when conditions are right. Dormant bud formation allows survival through cold or dry seasons. Latent buds confer the potential to quickly add capacity for energy capture. Arboriculture can learn from these processes to help guide tree treatments. Observation of what works and doesn't work in nature is the first step. Trial manipulations such as sprout pruning or promotion to meet our preferences, expectations, and needs will follow. Attempts to sustain or restore healthy landscapes may have some false starts, but can begin with the fundamental processes of tree biology.

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