

Aging and Rejuvenation in Trees

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Trees are absolutely fascinating to study, not least because their entire life histories are recorded in their forms. In a sense, the shape of a tree is analogous to the personality of a human, a unique product of the interaction between genetic endowment and environmental influences, "nature" and "nurture." Trees illustrate an idea first enunciated by the German philosopher and poet Goethe, namely, that the external form of plants is a manifestation of their internal physiological processes (Arber 1950). By carefully studying the shape of a tree, for instance, one can literally recreate everything that has happened to it over the course of its life (Hallé et al. 1978).

Plants develop in ways fundamentally different from those of vertebrate animals. By some point during adolescence, all of an animal's body parts have become fully differentiated, and further growth simply increases size without increasing developmental potential. Plants, on the other hand, show continuous development from a network of meristematic tissue that remains embryonic throughout the entire lifespan of the tree.

In all plants, these meristems produce the differentiated tissue that makes up the plant—roots, stems, leaves, and flowers—but remain undifferentiated themselves. There are thousands of meristems on any given tree. Those located at the heart of every bud are called shoot meristems, just as those at the tip of every root are called root meristems. The third category is the vascular cambium, a cylindrical band of meristematic tissue that sheaths the branches and roots and is responsible for their increase in girth. (Annual growth rings are a visible indicator of the activity of the vascular cambium.) Taken together, the meristematic network forms a thin veneer of embryonic tissue at the periphery of the tree's differentiated woody core. Meristems produce new plant tissue throughout

the life of the tree, always expanding outward and upward; any tree that is not expanding is a tree that is dying.

From a chronological perspective, the cotyledonary node of the seedling, produced at the time of germination, is the oldest part of the tree, but paradoxically, from a developmental point of view it is considered the most juvenile. Conversely, the flowering shoots at the periphery of the tree are the youngest part of the plant chronologically but the most mature developmentally. Researchers have resolved these apparent paradoxes by describing three different types of aging in plants (Fortanier and Jonkers 1976).

Types of Aging in Trees

The first type, *chronological* aging, is simply the time that has elapsed in the course of the lifespan of the entire plant or some part of it. In the case of a giant sequoia, a single stem can be as much as two thousand years old. In the case of root-suckering species, such as quaking aspen, chronological age can refer either to the age of an entire organism measured in thou-



A seedling of eastern arborvitae (*Thuja occidentalis*) clearly showing the difference between the juvenile, needle-like foliage along the main stem and the mature, scale-like foliage of the branches.



The retention of foliage through the winter is a common manifestation of juvenility among members of Fagaceae, in this case, American beech (Fagus grandifolia).

sands of years, or the age of a given stem measured in hundreds of years.

The second type, *ontogenetical* aging, refers to the process of a plant passing through different "phases" of development. I distinguish four phases in the life of a tree: the seedling phase extends from the point of seed germination through the end of the tree's first season of growth, as marked by the onset of a dormant period. The juvenile, or sapling, phase begins in a tree's second season of vegetative growth and ends with the production of flowers. The

adult, or mature, phase encompasses the major portion of a tree's lifespan; and the senescent phase begins when the tree starts to deteriorate as a result of damage or disease (Del Tredici 2000). The ontogenetical aging process is controlled by the meristematic tissues of the tree, and it is not uncommon for different parts of a tree to be in different growth phases at any point in time, as when juvenile sucker shoots originate from fully mature trunk tissue.

The third and final type of aging, *physiological*, is related to the general condition of the entire plant body and describes the development as well as the deterioration of the life-support systems of the tree. Specifically, it covers the loss of vigor in the root or shoot system that results from environmental stress or from the damage caused by wind, fire, ice, or snow. In general, the physiological aging process is controlled by the differentiated tissues of the tree (Romberger 1976).

The concept of *rejuvenation* is defined as the opposite of aging. As such, it can be either ontogenetic—a shift of all or part of the tree from an older growth phase to a younger phase—or physiologic—a retardation of the aging process.

Ontogenetic rejuvenation can be thought of as a resetting of the aging clock back to the juvenile stage, whereas physiological rejuvenation involves slowing down the aging clock.

Ontogenetic Rejuvenation

Aging and rejuvenation play important roles in the field of horticulture. Cultivars of various trees have been created by selectively propagating a part of the tree that is locked in a particular ontogenetic phase. The resulting cultivars are not genetic mutants; instead, their distinc-



Thorn production in honey locust (*Gleditsia triacanthos*) raised from seed.

tive characteristics stem from variations in gene expression rather than gene composition (Brand and Lineberger 1992; Greenwood 1993).

For plant propagators, it is crucial to choose the right location on the parent tree for the cuttings because this strongly effects the form of the finished product (Hackett 1983). Some well-known examples of nongenetic cultivars maintained by selective propagation include:

- Thornless selections of the honey locust, *Gleditsia triacanthos* 'Inermis', are propagated from sexually mature portions of the tree and do not produce lots of thorns on their trunks. Seed-raised honey locusts, in contrast, always have thorns on their trunks (Warren 1991).
- 'Prostrata'-type cultivars of various dwarf conifers, such as fir, yew, and spruce, are often propagated from lateral branches. These cultivars are locked into the mature, or horizontal, growth phase, and their branches retain a lateral orientation for many years. Unfortunately, many of these low-growing cultivars

are unstable and eventually produce vigorous vertical leaders (Olesen 1978; Del Tredici 1991).

- The vase-shaped, spreading cultivars of various nut-producing species, including ginkgo, pecan, and walnut also represent the mature growth phase of the parent trees. When grown from seed, these same species show the strong, clearly defined central leader and whorled lateral branches that typify the juvenile form (Del Tredici 1991).
- Shrub-form cultivars of English ivy with unlobed leaves and flowers represent the mature, nonrooting phase of growth. In its juvenile state, English ivy has lobed leaves and readily produces adventitious roots. This pattern of development is typical of vines that, in their natural habitats, must cope with the radical difference between the environmental conditions of the shady forest floor, where they first take root, and those of the sunny canopy, which they reach at maturity (Lee and Richards 1991).
- Many dwarf conifers with "immature" foliage and highly congested growth are propagated from parent trees that are "stuck" in the seedling or juvenile growth phases. Examples include the well-known dwarf Alberta spruce (*Picea glauca* 'Conica') and the many "plumose" cultivars within the genus *Chamaecyparis*. Among angiosperms, the florist's *Eucalyptus* is an example of a flowering tree that retains its juvenile foliage for many years (Borchert 1976). Eventually, all of these cultivars show a tendency to "revert" to the mature form, although the process is clearly more of a developmental advancement than a reversion.

Natural Rejuvenation

In nature, one commonly finds ontogenetic rejuvenation in trees that produce sprouts from the base of their trunks or from their roots. This sprouting usually happens in response to some form of periodic disturbance or environmental stress. Four basic types of rejuvenation sprouting are commonly seen in trees.

- Root suckering—the production of new shoots by the root system—occurs in species such as American beech (*Fagus grandifolia*), the tree

of heaven (*Ailanthus*), and various species of poplars (Del Tredici 1995).

- **Rhizome sprouting**—the production of specialized underground stems, or runners, that send up aerial shoots. These are commonly found among shrubs and trees that are specifically adapted to survive fire.
- **Layering**—the production of adventitious roots by the trunk or by lateral branches when they come in contact with the soil. Branch or trunk layers are most likely to form on trees growing on exposed mountaintops, where harsh conditions promote the retention of lower branches, or on wet sites, where moist, peaty soil facilitates adventitious rooting (that is, roots formed on branches). Among cultivated trees, layering is commonly seen in open-grown specimens whose lower branches have not been pruned.
- **Basal sprouting**—the emergence of vigorous shoots and adventitious roots from the collar. This is seen in several species native to eastern North America, including the American linden (*Tilia americana*) and the red and white oaks. In the West, where fires are much more common than in the East, many trees are adapted to sprout back vigorously after being burned; these include the most prolific sprouter of them all, the California redwood, the madrone (*Arbutus menziesii*), the bay laurel (*Umbellularia californica*), and the tan oak (*Lithocarpus densiflorus*). In the case of *Sequoia*, the root collar originates from cotyledonary buds that were produced at the time of germination; nevertheless, when they sprout

fifty to one hundred years after they were initiated, the shoots they produce are considered fully juvenile (Del Tredici 1999).

Plant propagators learned long ago to mimic trees' natural methods of rejuvenation for their own commercial purposes. For example, it has long been known that juvenile sprouts from the base of a tree will produce adventitious roots much more readily than mature shoots from the



Prolific root-suckering in American beech (Fagus grandifolia) growing at the Arnold Arboretum.



"Layering" of a low lateral branch of the western arborvitae (Thuja plicata) growing at Westonbirt Arboretum in Tetbury, England.

same tree. Over the years, nurseries have developed a variety of pruning techniques designed to stimulate stock plants to produce such vertically oriented, easy-to-root shoots. These techniques include hedging, the annual shearing of shrubs or trees to create a geometrical shape of fixed size; pollarding, annual pruning of the branches to a fixed point to produce an antler-like crown with prominent swellings at the ends of the branches; and stooling, periodic pruning of a woody plant to ground level, causing it to sprout vigorously from the base (Libby and Hood 1976; Hackett 1988).

Unfortunately, rejuvenation effects achieved through propagation by cuttings is never as complete as those achieved through seed propagation. Using modern tissue culture techniques, researchers have come closer to stimulating full rejuvenation of mature-growth-phase tissue than is possible with cutting propagation, but

even here rejuvenation is never complete (Brand and Lineberger 1992). To put it another way, a tree grown from a seed will always be distinguishable from one grown from a cutting, no matter how much technology is applied to the propagation process (Bon et al. 1994).

Physiological Rejuvenation

Physiological rejuvenation—slowing down rather than resetting the aging clock, as occurs in ontogenetic rejuvenation—is best seen in trees that grow in stressful environments like those at the tops of high mountains. Under these conditions, it is common to find individuals of a given species living much longer than they typically would under more favorable conditions. From the human perspective, this seems paradoxical, but among trees adversity promotes longevity. The best-known example of this phenomenon is the bristle-cone pine (*Pinus*

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American linden, *Tilia americana*, sprouting from its basal lignotuber.

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Pollarded lindens, *Tilia vulgaris*, growing in Selborne, England. The trees were planted by the naturalist Gilbert White (1720–1793).

longaeva), which reaches its maximum age of more than 4,000 years at high elevations in the White Mountains of southern California.

A less well-known, but equally remarkable example has been documented in the eastern arborvitae (*Thuja occidentalis*), which grows on the steep limestone cliffs of the Niagara Escarpment in Ontario, Canada, as well as on flooded bottomlands. On exposed cliffs, the trees are extremely stunted—reaching only five to fifteen feet in height—and attain ages of over 1,200 years. In moister, more protected sites, the trees are much larger—forty to fifty feet tall—but live only 200 to 300 years (Larson et al. 2000).

These examples follow a general rule: within any given species, the slowest growing individuals are the longest-lived; or conversely, the biggest trees in a forest are never the oldest. A survey by Loehle (1988) of the longevity of North American trees found that the longest-lived species among both conifers and angiosperms were those that invested the greatest proportion of their carbohydrate reserves in chemical and structural defenses against environmental stress. Put another way, the more energy a plant invests in defense mechanisms as opposed to vegetative growth, the longer it will live.

Horticulturists have also exploited the natural capacity of trees to rejuvenate themselves physiologically. In cultivated trees, the environmental stress that slows physiological aging—analogueous to the stress that trees in nature encounter at high altitudes—is intensive pruning. The Asian art of bonsai is a well-known example of rejuvenation induced by pruning. The techniques used in bonsai, especially periodic root pruning, seem to suspend physiological aging indefinitely (Del Tredici 1989). When applied to appropriate species—hazelnuts, plane trees, lindens, and elms, among others—pruning techniques such as pollarding and coppicing



A ginkgo raised from seed on the left and a grafted ginkgo on the right, both planted at the same time. The differences in form are a manifestation of different growth phases.

also promote greater longevity than one sees in unpruned trees, a clear indicator of physiological rejuvenation (Rackham, 1986).

In general, pruning brings about a measure of physiological rejuvenation by (1) inducing the growth of ontogenetically younger meristems; (2) shortening the internal transport path of water and nutrients; or (3) reestablishing the balance between shoot and root activity when the latter is in some way limited (Borchert 1976; Fortanier and Jonkers 1976).

One final question remains: Can the root systems of old trees undergo rejuvenation in the way that shoot systems can? The practical experience of bonsai masters who recognize the necessity of periodic repotting, as well as arborists who specialize in transplanting large trees, certainly suggests that root systems can be rejuvenated, but given that root systems are underground, morphological evidence for this idea is lacking.

I began by saying that the development pattern of trees differs strikingly from that of animals; in trees, the ontogenetical and physiological aging processes operate independently of each other. This means that trees, unlike people and other animals, can be simultaneously embryonic and senile. When carried to the extreme, this would effectively result in a form of ecological immortality. It is this poten-



A beautiful juniper bonsai (*Juniperus californica*) in the collection of the National Arboretum in Washington DC. The plant was collected from the wild.

tial for immortality that makes trees so fascinating to study and cultivate.

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