Aging, Rejuvenation, and Propagation in Trees

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DEVELOPMENTAL ISSUES: PLANTS VERSUS ANIMALS

Plants and animals are structured along very different lines. Animals are considered determinate and entire in their development, while plants are considered indeterminate and open. Animals are organized around tissue and organ systems and develop at the cellular level, while plants are structured around meristematic zones and develop at an organismal level (Kaplan and Hagemann, 1991). The higher degree of morphological plasticity found in plants relative to animals is a manifestation of their more flexible developmental processes (Arber, 1950).

The challenge facing plant propagators is twofold: first to distinguish the variable, yet synergistic, roles that genetics, environment, and development play in shaping the form of the tree (Halle et al., 1978); and second, to use this knowledge to produce high quality, true-to-type plants for the market place.

AGING IN PLANTS

Plants age from the base to the top and from the inner to the outer. From the chronological perspective, the cotyledonary node is the oldest part of any seed plant but, paradoxically, it is ontogenetically the most "juvenile". In contrast, the flower meristems at the periphery of the tree are chronologically the youngest part of the plant but ontogenetically the most "mature". Researchers have resolved this apparent paradox by describing three different types of aging in plants (Fortaniers and Jonkers, 1976):

1) **Chronological Age**. The amount of time that has elapsed in the course of the life span of the whole plant or a portion of the plant. In clonally reproducing species such as quaking aspen, *Populus tremuloides*, or creosote bush, *Larrea divaricata*, chronological age can either refer to the age the entire organism, measured in thousands of years, or the age of a given stem, measured in hundreds of years.

2) **Ontogenetic Age**. This refers to the process of a plant passing through different "phases" of development. At any point in time, different sectors of a tree can be in different growth phases. The control of the ontogenetical aging process is localized in the meristematic tissues of the plant body. The generalized characteristics of the various phases of tree growth are summarized in Table 1.

3) **Physiological Age**. This refers to the general condition of the entire plant body. In the case of mature trees, it covers the suite of traits circumscribed by the term senescent. Such traits include the loss of growth vigor in the root and/or shoot systems; stress-related decline and general deterioration ("die-back"); or the breakdown of the internal regulatory system that normally controls and coordinates the development of form (Romberger, 1976). In general, the control of the physiological aging process is localized in the differentiated tissues of the plant body.

Rejuvenation. Rejuvenation is the opposite of aging. As such it can either be ontogenetical or physiological, the former being much more difficult to accomplish than the latter.

EXAMPLES OF ONTOGENETICAL AGING IN PLANT PROPAGATION

Numerous cultivars of various tree species have been created by selectively propagating a specific portion of the plant that is in a particular ontogenetic phase. Such cultivars are not genetic mutants per se, but epigenetic selections whose distinctive characteristics are the result of variation in gene expression rather than in gene composition (Brand and Lineberger, 1992; Greenwood, 1993). For propagators, the source location of the propagation material on the parent tree is of crucial importance because it can strongly affect the form of the final product (Hackett, 1983; Warren 1991). Some well-known examples of epigenetic cultivars maintained by selective propagation include:

1) Thornless selections of *Gleditsia triacanthos* ('Elegantissima' syn. 'Inermis') and *Citrus* sp. which are propagated from sexually mature portions of the tree. Seed-raised honeylocust and citrus always have thorns on their trunks.
2) 'Prostrata'-type cultivars among various conifer genera, including *Abies, Araucaria*, and *Taxus*, are propagated from lateral branches. They are essentially stuck in the mature growth phase and maintain a horizontal orientation for many years, a phenomenon technically known as topophysis (Olesen, 1978; Del Tredici, 1991).
3) The vase-shaped, spreading cultivars of various nut-producing species, including pecan (*Carya illinoinensis*), walnut (*Juglans*), and ginkgo (*Ginkgo biloba*), represent the mature growth phase of the tree. When grown from seed, these same species have a juvenile form dominated by a strong central leader (Del Tredici, 1991).
4) Shrub-form cultivars of *Hedera helix* with entire leaves and flowers represent the mature, difficult-to-rooting phase of growth. In its juvenile phase, English ivy has lobed leaves and readily produces adventitious roots.
5) Many dwarf conifers with "immature" foliage and congested growth are stuck in the seedling or juvenile growth phase. Examples include the dwarf Alberta spruce, *Picea glauca* 'Conica', and the so-called "Retinospora" cultivars in the genus *Chamaecyparis*. Among angiosperms, broadleaf evergreen *Eucalyptus* and *Acacia* species provide examples of trees which sometimes retain juvenile foliage for many years (Borchert, 1976).

REJUVENATION OF ONTOGENETICAL AGING

In nature, one commonly finds ontogenetic rejuvenation in trees that produce suckers from the basal portion of their trunk. Such suckering is usually an adaptation to some form of periodic disturbance or environmental stress. Following Groff and Kaplan (1988), the author has identified four basic types of "in vivo" rejuvenation in woody plants: (1) root suckering species such as *Ailanthus* and *Populus* (Del Tredici, 1995), (2) stoloniferous species with specialized underground stems (many shrubs in the Rosaceae are in this category), (3) species with decum-

Table 1. Phases of ontogenetical development in temperate trees.

Phase name	Morphological characteristics	Physiological characteristics	Propagation implications
Seedling	Cotyledons fully functional Heteroblastic leaf development Vigorous tap-root development Anthocyanins in shoot tips	Maximum developmental plasticity Indeterminate growth flushes Polarity of shoot and root systems established	Strong adventitious root formation Propagules vertical Propagules thorny
Juvenile	Large, dimorphic leaves Thorns on stems Anthocyanins in shoot tips Long-shoots dominate crown Prolonged leaf retention	Strong apical control of shoot system Leader shoot strongly vertical Recurrent growth flushes Sylleptic branching	Strong to moderate adventitious root formation Propagules vertical Propagules thorny
Mature	Small, uniform leaves Thornless stems Flower and fruit production Short-shoots dominate crown	Strong apical dominance Horizontal (plagiotropic) orientation of lateral branches Single annual growth flush Root growth horizontal	Moderate to weak adventitious root formation Propagules diagonal and heavily branched Propagules thornless
Senescent[1]	Burl & sprout formation on trunk Sucker growth from root crown Greatly reduced extension growth Crown and/or root die-back	Loss of apical control Reiteration on all parts of tree Sectoring of vascular system (strip-bark development)	Weak adventitious root formation Propagules diagonal and heavily branched
Rejuvenation	Large, dimorphic leaves Thorns on stems Anthocyanins in shoot tips Leaf retention Adventitious root formation	Indeterminate growth Growth strongly vertical Sylleptic branching	Strong to moderate adventitious root formation Propagules vertical Propagules thorny

[1]More a physiological than an ontogenetical phase.

bent lateral branches that produce adventitious roots when they come in contact with the soil (referred to as layering), and (4) basal suckering species that produce vigorous shoots and adventitious roots from the root collar or lignotuber (*Sequoia sempervirens, G. biloba, Eucalyptus,* etc.). In the case of this last group, the root collar buds typically originate from meristems located in the axils of the cotyledons. These are the oldest buds on the tree and yet when they sprout 50 to 100 years after their initiation, the shoots they produce are considered fully juvenile (Del Tredici, 1992).

Shoot cuttings taken from a tree in the mature phase of growth often show partial rejuvenation when artificially propagated by grafting or rooting, particularly if the scions or cuttings originated from vigorous trunk sprouts or basal suckers (Brand and Lineberger, 1992; Cameron and Sani, 1994). Plant propagators learned long ago that such juvenile shoots have a much greater capacity to produce adventitious roots than mature shoots from the same tree and they have developed a variety of pruning techniques, including stooling, hedging, and pollarding stock plants, specifically designed to stimulate the production of vertically oriented, easy-to-root propagation material (Libby and Hood, 1976; Hackett, 1988). In the author's opinion, however, it is an oversimplification to define all adventitious roots as a manifestation of juvenility in the shoot system that produces them. While the statement is true for cuttings propagated under controlled conditions, it is not necessarily true for mature trees in nature, where adventitious root production appears to be as much the cause of shoot rejuvenation as the result of it.

Using modern, in vitro tissue culture techniques, researchers have been able to come much closer to achieving full ontogenetic rejuvenation of mature growth phase tissue than is possible with traditional techniques (Brand and Lineberger, 1992; Huang et al., 1992). However, even under optimal in vitro conditions, measurable differences in maturation state between cuttings taken from the base as opposed to the top of a tree can persist indefinitely (Bon et al., 1994; Greenwood, 1995). Indeed, most available research indicates that the rejuvenation effects associated with sexual reproduction — including apomixis — are qualitatively distinct from those associated with vegetative reproduction. It is for this reason that the seedling phase is separated from the juvenile phase in Table 1.

PHYSIOLOGICAL AGING AND ITS REJUVENATION PHYSIOLOGICAL AGING AND ITS REJUVENATION

In nature one finds the longest-lived trees growing in the most stressful environments. The bristle cone pine (*Pinus longaeva*), which grows at high elevations in California's White Mountains and reaches ages over 4000 years, is a famous example of the apparent paradox that "adversity promotes longevity" (Schulman, 1954). A less well known, but equally remarkable case is the eastern arborvitae, *Thuja occidentalis,* which grows on the steep, limestone cliffs of the Niagara Escarpment in Ontario, Canada. Under extremely exposed conditions, individual arborvitae stems can reach ages over 1200 years, considerably longer than the 300 to 400 years they last on more favorable sites (Larson et al., 1993). As a general rule, the longest-lived individuals within any given tree species are inevitably the slowest growing.

In an extensive survey of the longevity of North American tree species, Loehle (1988) found that the longest-lived species among both gymnosperm and angiosperm genera were those that directed the greatest proportion of their carbohydrate budget into chemical and structural defenses as opposed to vegetative growth. This same trade-off scenario seems to operate within a given species and provides a plausible explanation for why trees growing under extreme, continuous stress live longer than their counterparts growing under more favorable conditions..

For trees in cultivation, intensive pruning is often considered a mechanism for reversing the negative effects of physiological aging. The Asian art of bonsai is a well-known example of such rejuvenation induced by pruning. The techniques used in bonsai, particularly the root pruning, seem to produce a suspension of the physiological aging process that persists as long as the pruning regimen is maintained (Del Tredici, 1989). Pollarding and coppicing are tree pruning techniques of European origin that, when applied to appropriate species (e.g., *Corylus, Platanus, Tilia*, and *Ulmus*), promote greater longevity that one sees in unpruned trees of the same taxa (Rackham, 1976).

By analogy with trees growing on the tops of mountains, one might consider the intensive pruning of cultivated trees to be a form of environmental stress that causes the tree to invest more heavily in chemical defenses than it normally would. In general, pruning seems to bring 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 limited in some way (Bochert, 1976; Fortanier and Jonkers, 1976).

As a final point, one should ask the question, can the root systems of old trees undergo rejuvenation the way that shoot systems can? The practical experience of bonsai masters, as well as companies that specialize in transplanting large trees certainly suggests that root systems can be rejuvenated, but there is no obvious morphological evidence of it the way there is with shoot systems.

CONCLUSION

Many of the practices employed in commercial plant propagation are firmly intertwined with the confusing and poorly understood concepts of juvenility and maturity. Much of this confusion can be clarified with the realization that the ontogenetical and physiological aging processes operate independently of each other and that trees, unlike people, can be simultaneously embryonic and senile.

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