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## AGE-RELATED CHANGES IN TREES

by James R. Clark<sup>1</sup>

One characteristic that distinguishes trees from other plant species is the presence of long-lived shoots. While woody shrubs and herbaceous perennials may appear to be long-lived, the longevity of a single shoot is relatively short; ranging from a few months to a few years. The long life spans attributed to shrubs and perennials reflect the replacement of 'older' shoots with new ones on a continuing basis. Trees, on the other hand, retain a single main growing shoot throughout their life cycle with the attainment of massive size as a result. Indeed, trees are among the largest and most long-lived organisms on earth (Table 1). The bristlecone pine, *Pinus aristata*, is generally recognized as the longest-lived organism on earth with recorded life spans of over 4,000 years. Numerous North American forest tree species have life spans of 500 years or more (Fowells 1965). Trees in landscape situations do not live nearly as long as those under native conditions. Horticulturists speak of "useful life span" or "landscape life span."

While the life span of individual plants can be quite long, the longevity of genotypes, as measured by clonal material, can be even longer. Clones are defined as "genetically identical organisms derived from one individual, propagated by asexual means" (Hartmann and Kester 1975). Clones of such species as banana, fig, Chinese yam, and date palm have been reputed to be over 2,000 years old (Mobius 1897). A clone of *Populus* native to Utah has been reported to be over 8,000 years old (Cottam 1954). Such tree fruit clones as 'Winter Pearmain' apple (introduced

ca. 1200), 'Reine Claude' plum (ca. 1500), 'Bartlett' pear (1770), and 'Delicious' apple (1870) have outlived the original genetic parent.

What implications does the longevity of clones have for the process of aging in trees? One implication concerns the influence of the overall system on longevity. Clearly, a given genotype can be perpetuated for long periods of time, while an organized system of dividing cells containing that genotype does not survive as long. There is good evidence that those animal cells which appear to be continuously dividing throughout the life of an organism possess a finite life span *in vitro* (Hayflick 1975). Romberger (1976) related such evidence to plants, suggesting that meristematic cells may be limited in the number of cell divisions they may undergo and thus possess limited life spans. If meristematic tissues possess finite life-spans, then the life-span of intact trees must also be limited.

### Changes in size and complexity

As a direct result of their long life span, trees have the potential to become extremely complex. This ever-increasing complexity may play a significant role in the gradual decline of the individual over time. Meristematic areas are good examples of the development of this complexity. A mature oak may possess 500,000,000 root tips, all of which must act and react in some coordinated fashion. In shoot systems, the potential complexity is even greater. If a tree produced but one shoot per year for every existing shoot, by the end of the fiftieth year there would be  $1.1 \times$

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$10^{15}$  shoots. This potential to produce an enormous number of shoots in 10-30% of the life span of many forest trees is never fully expressed. Apical dominance, apical control, shedding of branches, and other mechanisms prevent the release of many buds.

It is striking enough that meristematic regions become numerous. Yet, it is even more astonishing that all of these areas are related and interacting. We tend to think of a separate root and shoot system, yet, these two are components of one system. The transport of nutrients, assimilates, hormones, and other materials does not occur at random, but in a coordinated manner within this system. As trees grow larger, the demands of the transport system for assimilates also grows larger.

Any list of long-lived trees (for North America at least) is composed mostly of gymnosperms (Table 1). It may be that a fundamental difference between gymnosperm and angiosperm trees is the level at which each group is able to organize and maintain the large plant structure. Perhaps gymnosperms are more efficient in 'coordinating' the interactions between root and shoot, especially over long periods of time. Most gymnosperms possess a growth habit with a strong central leader and strong apical control leading to one main stem with all other branches being secondary to it. Perhaps this growth habit has some inherent advantages in terms of transport of assimilates, maintenance requirements, etc. over the more diffuse form that most angiosperms possess. While not an entire answer, the observa-

**Table 1. Longevity of some tree species.**

<i>Pinus aristata</i>	2000-4000 years
<i>Sequoiadendron giganteum</i>	2000-3000
<i>Chamaecyparis nootkatensis</i>	1000-3500
<i>Sequoia sempervirens</i>	1000-2200
<i>Thuja plicata</i>	1000+
<i>Picea sitchensis</i>	750+
<i>Pseudotsuga menziesii</i>	750-1200
<i>Larix occidentalis</i>	700+
<i>Quercus garryana</i>	500+
<i>Quercus alba</i>	500+
<i>Tsuga heterophylla</i>	500+
<i>Fagus</i> spp.	300
<i>Quercus</i> spp.	300
<i>Carya</i> spp.	300
<i>Betula alba</i>	50

Taken from Fowells (1965).

tion about form and efficiency may be an important factor.

Concomitant with these changes in structure are changes in overall size. The root and shoot systems must remain in 'functional balance' while increasing in size. Borchert (1975, 1976) has developed some interesting evidence on the interdependence of root and shoot activity, especially growth. He suggested that a feedback mechanism between root and shoot regulates growth and maintains this balance. As the tree grows larger, the ability of the shoot to respond to changes in the root decreases, and vice versa, (i.e., the response time increases). As an example, if a decrease or cessation of shoot growth is a way of compensating for severe drought, Borchert suggests that the time it takes to invoke and develop this response greatly increases with increasing tree age. Changes in ability to respond to environmental stimuli or timing of that response may help to explain why older trees in landscape situations are much more sensitive to site disturbances.

Borchert (1976) noted also the changes in water potential that occur with increasing tree height. He suggested that the decreases in water potential with increasing height (0.1 atm/m) may be an important factor in the dynamics of tree growth, especially in tall (> 10m) trees.

### Maturation, aging and senescence

Although we speak of 'aging' of trees, a number of developmental processes are taking place simultaneously. Three types of 'aging' phenomena have been distinguished (Fortanier and Jonkers 1976): chronological, physiological and ontogenetical. Chronological aging refers to time since germination measured in days, years, etc. 'Young' and 'old' are terms commonly used to describe this type of aging. Physiological aging refers to the development of a plant from zygote to adult. Horticulturists use 'juvenile' and 'mature' in this context.

Whenever the term 'aging' is being discussed, it is important to make clear precisely which type of aging or phenomenon is being examined (the literature can be quite confusing in this area). Wareing (1959) suggested that we distinguish between maturation and aging. Maturation refers

to phase change, a part of ontogenetical development, and describes the transition from the juvenile (vegetative) to mature (reproductive) phase. Aging is the loss of vigor associated with increased complexity. These definitions have been generally accepted by plant scientists. Zimmerman (1973) noted that maturation occurs to seedlings or juvenile plants, whereas aging occurs to mature material. A redwood becomes mature at 20 years of age, but continues to age for 2,000 years. We might think of maturation as being a part of ontogenetic aging, and 'aging,' in Wareing's view, to be physiological aging.

### Ontogenetical aging-maturation and phase change

One of the most critical developmental changes to occur in all woody plants is phase change. While the presence of the juvenile phase appears to be universal among woody plants, the length of this phase is quite variable and ranges up to 20-30 years (Table 2).

At first glance, possessing such a juvenile, non-reproductive period would seem to run counter to the individual plant's 'goal' of perpetuating the species. However, under natural conditions there may be a distinct advantage to the plant to allocate its resources to vegetative growth, perhaps as a way of competing successfully with surrounding vegetation, especially when viewed in the context

**Table 2. Length of juvenile period in some woody plants. Juvenile period based on the appearance of the first flower under natural conditions.**

Rosa (Hybrid tea)	20-30 days
Vitis spp.	1 year
Prunus spp.	2-8 years
Pyrus spp.	4-8 years
Citrus spp.	5-8 years
Sequoia sempervirens	5-15 years
Pinus monticola	7-20 years
Malus spp.	8-10 years
Hedera helix	10 years
Thuja plicata	15-25 years
Pseudotsuga menziesii	20 years
Pinus aristata	20 years
Sequoiadendron giganteum	20 years
Tsuga heterophylla	20-30 years
Picea sitchensis	20-35 years
Quercus robur	25-30 years
Abies amabilis	30 years
Fagus sylvatica	30-40 years

of a life span of hundreds of years. 'Investment of resources' in building a structure early in the life cycle allows for a long-term 'return' in an advantage over surrounding plants.

Morphological differences which have been observed for juvenile and adult forms may give clues as to the basis of any adaptive advantage. Such morphological and/or physiological differences include the characteristics of leaf morphology, phyllotaxy, shoot orientation, seasonal leaf retention, thorniness, ability to form adventitious roots, disease resistance, losses of tissue through animal browsing, as well as the presence or absence of flowers.

Although we have observed the changes that may distinguish juvenile from adult, little is known about the precise nature of the mechanism that regulates maturation (see reviews by Hackett 1976, Zimmerman 1972, and Wareing 1959 for detailed discussions). It is generally recognized that maturation results from an accumulation of changes within the apical meristem (Sussex 1976). However, there is also evidence the meristem can repond to external influences as well. Hackett (1976) summarized the available evidence and suggested that control of maturation is related to the:

1. Relative plant size and/or number of cell divisions in the apical meristem.
2. Hormone levels (specifically, gibberellin and abscisic acid).
3. Substrate availability at the apex.

Precisely how these lines of evidence are related is not clear.

Two additional aspects of phase change need to be mentioned. One, entire plants do not undergo phase change; only the apical meristem does. Thus, both juvenile and adult tissue can exist in the same plant. Given the differences between the two phases, this proves valuable to horticulturists in terms of ease of propagation. Second, although the development of the mature phase results in a stable form, reversion of the mature to the juvenile phase may occur, induced by some hormonal and environmental treatments.

### Physiological aging

"Aging" usually describes the decline in plant vigor with increased size and complexity. We shall

describe physiological aging in terms of such processes as photosynthesis, respiration, overall growth patterns, and resource allocation; all possible measures of plant vigor.

Changes in the rates of photosynthesis and respiration occur during development. On an organ level, photosynthetic rate declines with age. In deciduous trees, net photosynthetic rate for an individual leaf reaches a peak just after maximal leaf expansion and declines thereafter (Schaedle 1975). In conifers, net photosynthesis is maximal during the first or second year and declines rapidly in succeeding years (Freeland 1952). Although there is little evidence on the long-term changes in photosynthetic rate, leaves of mature English ivy possess photosynthetic rates 1.5 times those of juvenile leaves (Bauer and Bauer 1980). Although net photosynthetic rates for an individual leaf decline with time, in terms of the amount of carbon fixed per year, total plant photosynthesis will increase throughout its life cycle — a direct consequence of continual increases in leaf biomass.

Respiration patterns also change with increasing age, reflecting the large increases in stem volume that take place. Switzer *et al.* (1968) provided an interesting analysis of these stem volume changes. Over time, the ratio of photosynthetic (leaves) to non-photosynthetic (branches) tissues decreases on a dry weight basis from 1:1 to 1:12 in birch, and to 1:8 in pine. Similar but more dramatic changes can be measured in the ratio of leaves to stems. As the amount of non-photosynthetic tissue increases, the amount of respiration also increases. In 25-year-old beech stands, respiration utilized 40% of dry matter fixed (Moller *et al.* 1954). This increased to 50% by 90 years. Given that beech has a life span of 250-300 years, we can only speculate as to the respiration requirements of trees that age. Why would increasing respiration rates be important? Primarily because they represent the amount of energy required to maintain the large, complex structure that trees develop.

On a whole plant level, physiological aging is reflected in the changes in overall growth patterns (see review by Borchert 1976). Observed changes in shoot growth include decline in the duration of shoot elongation (for plants with in-

determinate growth), decline in the number of flushes (for recurrently flushing types), an increase in the formation of sylleptic shoots, and an increase in the proportion of short to long shoots. The rates of cambial (Mikola 1950) and root (Scholtes 1953) growth may also decrease.

Meyer (1938) developed an age versus annual height growth comparison for *Pinus ponderosa*. Shoot growth rate decreased throughout the life span of the individual tree. It is unclear whether or not this is the typical situation — there are few such comparisons. If Meyer's observations are the normal situation, does this mean that declines in growth rate over time are unavoidable?

These changes in both productivity and growth patterns might also be viewed in the context of resource allocation. Ovington (1957) analyzed the dry matter distribution in *Pinus sylvestris* trees of varying ages. When trees were 8 years old, approximately 65% of the total plant dry matter was found in needles and fine roots. By 55 years, approximately 60% of the total plant dry matter was located in the main stem. Needles and fine roots held a minor proportion of the total dry matter.

As emphasized previously, the very structure that sets trees apart from other higher plants has an enormous impact upon the complexity and productivity of an individual. The main trunk and branch system is a large sink for assimilates, both in terms of respiration rates and production of wood. Such a situation leaves a relatively smaller proportion of assimilates available to the rest of the plant. Waring (personal communication) suggested that Douglas fir allocates to meristematic tissues above all others. The observed increase in trunk volume is only a reflection of an active cambium, a meristem that undergoes dramatic increases in size.

Changes in physiological parameters may manifest themselves in ways other than overall growth. Alterations may also be seen in the patterns of susceptibility of trees to insect, disease, or virus attacks. A number of insect pests of forest trees appear to prefer older trees as hosts. Susceptibility to insects such as western pine beetle, spruce budworm, and bronze birch borer increases with time. Similar observations have been made for some disease organisms. In fruit trees, the expression of 'latent' viruses does not

usually occur until the trees are quite 'old' in terms of chronology.

One general suggestion regarding susceptibility and age bases this relationship on overall tree vigor. As trees age, vigor declines and it is this lack of vigor which may cause an increase in susceptibility. This is certainly the case with western pine beetle (Miller and Keen 1960). Waring and Pitman (1980) have developed a vigor index (based upon basal and sapwood areas) to predict the mortality of *Pinus contorta* to bark beetles. The maintenance of tree vigor is a primary control method for bronze birch borer. We need to be aware that these declines in vigor or increases in susceptibility are not always caused by external stresses, but appear to occur as a normal pattern of development.

### Summary

Trees are distinguished from other plants by their large size and long life span. The development of trees over this life span is not static but on-going, with a wide range of changing physiological characters. As time progresses, these changes can be either readily observed, such as the maturation of juvenile plants, or much less obvious, as in an overall decline in vigor. It is clear however, that the myriad of phenomena associated with development do not occur at random but are a normal occurrence in a tree's live cycle.

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Center for Urban Horticulture  
University of Washington  
Seattle, Washington 98195