

Age-related changes in photosynthesis of woody plants

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Woody perennials do not appear to go through a defined senescence phase but do have predictable developmental stages. Reduced photosynthesis and stomatal conductance have been reported at all developmental transitions, although some studies have shown the opposite. What causes these changes and why do results differ among studies? Do these changes result from or cause changes in growth? What are the roles of genetics, size, changing conditions and cumulative environmental stress in aging trees? Definitive answers remain elusive but recent research is helping to clarify some of the processes associated with aging and to point the way for further study.

Compared with our knowledge of senescence processes in annuals and biennials, relatively little is known about age-related changes in woody perennials. It has been known for years that leaf structure and physiology change in many woody species when they become sexually mature¹⁻³ but sexual maturation accounts for only a small portion in the life cycle of woody plants and many changes in growth and development occur long after sexual maturity.

Studies of aging in woody plants have been limited in part by the challenges of working with long-lived organisms that are often large. However, new techniques (e.g. analysis of stable isotopes, improved approaches for measuring sap flow), better field equipment (e.g. field-portable gas-exchange systems) and improved canopy access (balloons, rope climbing, hydraulic lifts and canopy cranes) are helping to make studies of aging trees more feasible. At the same time, the need to understand physiological changes better over the life cycle of woody plants has been increasing. One compelling need is to explain why growth is reduced in aging forest stands: the growth patterns are pronounced and predictable but the underlying mechanisms remain unclear^{4,5}. Pollution and climate-change research have also stimulated new interest in age-related changes in tree physiology because of evidence that older and larger trees might respond differently from seedlings⁶. Similarly, process-based models of carbon fluxes in terrestrial ecosystems are usually performed using measurements of small, young plants. If the rates of gas exchange change as trees age, new information will be needed to account for variation in vegetation age classes across the landscape.

These new measurement capabilities and research imperatives are increasing research on age-related changes in woody perennials but we are far from a comprehensive understanding. In many studies in the current literature, it is not possible to distinguish between the effects of age, size or environmental changes associated with aging, much less the interactions among these factors. The aim of this article is to present emerging information and controversies, and to stimulate further research by pointing out gaps in our knowledge. The focus is on changes in photosynthesis but, to provide a context for understanding age-related changes in leaf physiology, I begin with a discussion of the reproductive and growth phases of woody plants. These characteristic phases in the life histories of woody plants serve as benchmarks of aging, allowing species with different life spans to be compared.

Developmental phases and growth of woody perennials

Juvenility, maturity and old age

One of the clearest indicators of developmental change in woody plants is their reproductive capacity. Prereproductive plants are

considered to be juveniles; the onset of flowering and seed production marks a transition phase, and fully reproductive plants are considered to be mature. However, changes in the structure and function of whole plants continue long after sexual maturity, and old trees and shrubs are quite different in appearance and growth compared with younger mature trees (Fig. 1). Reproductive activity often remains high long after plants display old-growth characteristics (Fig. 2). It is thus useful to identify an additional 'old-growth' phase of development based on changes in plant form and growth rates rather than on changes in reproductive capacity. Physical indicators of old growth are described in more detail below.

The concepts of juvenility and maturity apply to tissues as well as to whole plants, causing some confusion in discussions of age-related change. Individual leaves are 'immature' while they are still developing and 'mature' when fully expanded and developed. It has been known for many years that photosynthetic capacity changes as leaves mature and age⁷. In addition, seedlings of some species (such as many pines) produce 'primary' leaves that are physically and physiologically distinct from both cotyledons and mature leaves; the transition to production of mature leaves is not necessarily concurrent with the transition to reproductive maturity. The focus of this article is on the aging processes of whole plants, and the term 'maturity' is thus used in the reproductive sense. However, many of the studies cited compared different sizes rather than ages or developmental phases of trees and therefore the developmental phases have been inferred.

Growth and productivity through the life cycle of woody plants

In general, the growth phases of woody perennials are not related to reproductive phases, although maturation and fruit production are often associated with temporary increases in photosynthesis and decreases in growth rates. The maximum height increment (the maximum slope of the height curve in Fig. 2) of woody plants usually occurs well before sexual maturity, although the relationships vary greatly with species and site conditions. Subsequently, internode lengths slowly decrease and eventually height growth ceases altogether. The maximum height for a particular species in a particular environment is predictable; indeed, foresters classify the quality of sites based on expected heights for a specified species at a specified age. In trees (but not necessarily shrubs), the production of new primary branches generally stops when maximum height is achieved and branch extension also slows down. This is when the characteristics of old growth emerge. Leaf-bearing stems tend to be thicker and the leaves themselves are often thicker and smaller on old growth compared with on younger mature trees (Fig. 1); in species with multiple age classes of

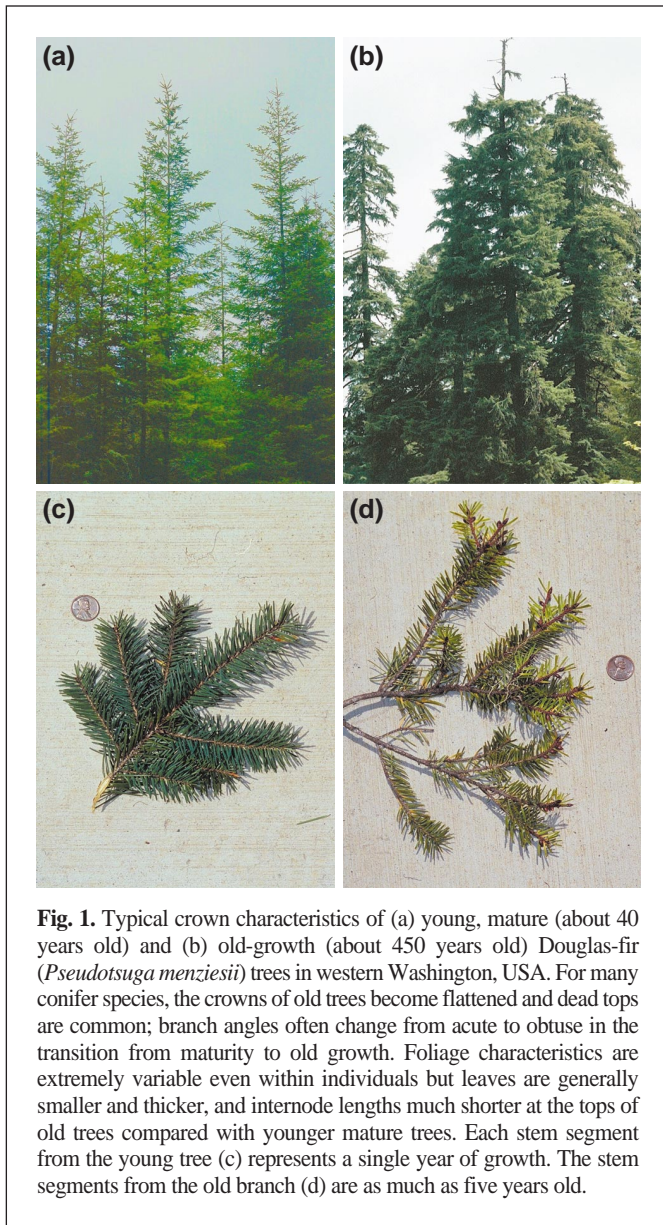


Fig. 1. Typical crown characteristics of (a) young, mature (about 40 years old) and (b) old-growth (about 450 years old) Douglas-fir (*Pseudotsuga menziesii*) trees in western Washington, USA. For many conifer species, the crowns of old trees become flattened and dead tops are common; branch angles often change from acute to obtuse in the transition from maturity to old growth. Foliage characteristics are extremely variable even within individuals but leaves are generally smaller and thicker, and internode lengths much shorter at the tops of old trees compared with younger mature trees. Each stem segment from the young tree (c) represents a single year of growth. The stem segments from the old branch (d) are as much as five years old.

foliage, leaf longevity tends to be greater on old trees⁸. In many species, the form of the crown also changes (Fig. 1).

The productivity of individual trees (as measured by, for example, the volume of wood produced each year) follows a similar pattern to height growth but usually lags behind in time. In young plants that have access to light and soil resources, productivity increases rapidly. This is primarily as a result of crown expansion and increased capture of light. The subsequent growth trajectory is strongly dependent on competition with neighbors. On a stand level, productivity increases initially after a stand-replacing disturbance and then declines after the site achieves maximum leaf area⁴, but recent studies have shown that the productivity of low-density, old-growth stands can be greater than that of high-density, young stands with similar species composition and site conditions⁹. We lack a good understanding of the potential productivity of old trees in a competition-free environment.

Age-related change in photosynthesis and stomatal conductance

Most studies of photosynthesis in woody plants of different ages were not designed to isolate variation caused by age from all other sources of variation (e.g. that owing to size or environment). Well-controlled

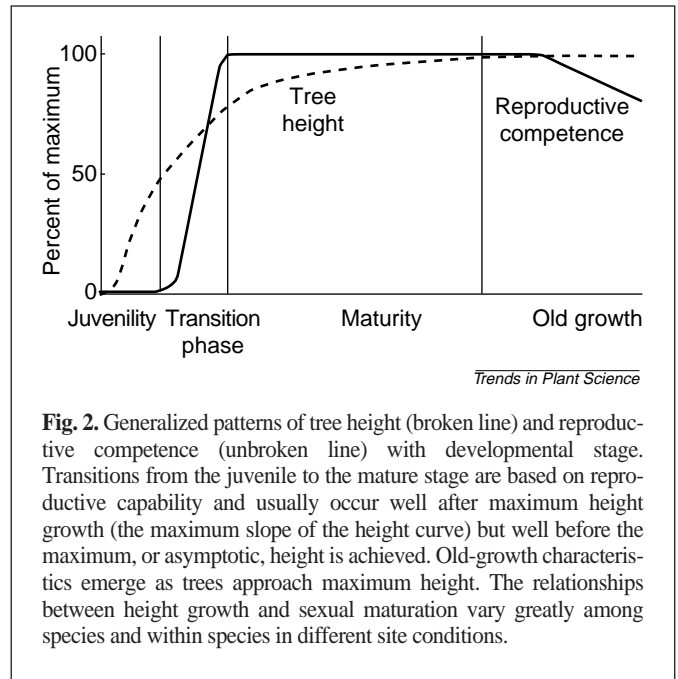


Fig. 2. Generalized patterns of tree height (broken line) and reproductive competence (unbroken line) with developmental stage. Transitions from the juvenile to the mature stage are based on reproductive capability and usually occur well after maximum height growth (the maximum slope of the height curve) but well before the maximum, or asymptotic, height is achieved. Old-growth characteristics emerge as trees approach maximum height. The relationships between height growth and sexual maturation vary greatly among species and within species in different site conditions.

experiments to separate these effects are sorely needed. Nevertheless, published studies from a variety of experimental situations generally indicate that both photosynthesis (Table 1) and stomatal conductance⁶ are reduced with the age of shrubs and trees. These increases have been reported at all phases of development: seedlings versus older plants¹⁰, seedlings versus juveniles versus mature plants¹¹, juvenile versus mature and/or old growth¹²⁻¹⁸, and mature versus old growth^{8,19}. However, there are exceptions to the general trends (Table 2)^{18,20-23}. The following sections take a closer look at potential causes of age-related change in photosynthesis and the differences in results among these studies.

Influence of extrinsic factors

Rates of photosynthesis are highly sensitive to environmental conditions, both in the growth environment and during measurement. For example, shaded plants in the forest understory generally have low photosynthetic capacity compared with sun-adapted plants²⁴. Thus, photosynthesis increases as trees emerge from the understory into the canopy, irrespective of age²⁵. Accumulating live biomass and woody debris might immobilize nitrogen in some aging forests, making it less available for new growth⁵. Reduced photosynthesis is a likely consequence because the nitrogen content of leaves is closely correlated with photosynthetic capacity²⁶.

Water might become more available with age if the roots of larger trees can tap deeper water sources, allowing them to have higher rates of transpiration and photosynthesis than smaller trees^{27,28}. This could explain many of the studies in Table 2 that show increased photosynthesis with age. For example, access to deep water explained why mature box elder (*Acer negundo*) had a higher maximum photosynthesis and stomatal conductance than young trees²⁷, why photosynthesis and stomatal conductance were higher in large than in small mesquite (*Prosopis glandulosa*) when soil water was low¹⁸, and, probably, why photosynthesis was higher for mature than for juvenile *Chrysothamnus nauseosus* on a dry site²⁰. It also explained the greater transpiration rates in large than in small sugar maple (*Acer saccharum*) trees²⁸.

Is aging of woody plants genetically controlled?

Because a plant's microenvironment is often more severe during the establishment phase, natural selection might favor different

physiological strategies^{12,13,18,20}. In young plants, a 'go for broke' strategy of higher rates of photosynthesis and transpiration in more-severe conditions might provide the growth potential they need for establishment, but with a greater risk of mortality. If the strategy improved the overall reproductive fitness of the species, this would result in a greater probability of a genetically programmed switch evolving that changed the plant's strategy from high rates of gas exchange in seedlings and saplings to lower rates in mature plants.

This might explain why seedlings of some species produce distinctive 'primary' foliage, which often has higher rates of photosynthesis than mature foliage, and why older individuals sometimes revert to primary foliage in response to stress²⁹. However, it would be difficult actually to prove that natural selection of woody plants favors risk taking in youth followed by a more-conservative adulthood. One prediction from this hypothesis is that water-use efficiency (carbon fixed per unit water transpired) should increase with age and this has indeed been shown for several species through carbon-isotope analysis or direct gas-exchange measurements^{12,13,19}. However, the same outcome could result from other causes (see discussion on hydraulics, below).

Although the evolutionary rationale and causal mechanisms remain unclear, some of the changes in leaf structure and physiology that occur during the transition from juvenility to maturity are linked to changes in gene expression. In larch (*Larix*) and English ivy (*Hedera helix*), genes associated with chlorophyll binding, anthocyanin production and proline-rich proteins are expressed differently in juveniles and adults³. Shifts in the relative concentrations of plant hormones also occur at maturation, and gibberellins can promote flowering or cause mature tissues to revert to juvenile conditions³. Grafting experiments also imply the existence of genetic controls over maturation: when scions from mature plants are grafted onto seedling or juvenile rootstock, they retain most of their mature characteristics, at least initially³. However, it is also possible that the meristems maintain a 'memory' from their environmental history, perhaps causing meristems of mature plants to be poor competitors for nutrients when grafted onto juveniles. It is extremely difficult to separate causes from effects in all of these observations and there is currently no firm evidence that maturation is genetically controlled³.

At the other end of the age continuum, there is essentially no information about possible changes in gene expression in the transition from maturity to old growth³⁰. Also, there is no evidence to link reproduction with

Table 1. Studies reporting decreased net photosynthesis with increased age of trees and shrubs^a

Species	Comparison	Ref.
<i>Chamaecyparis obtusa</i>	Annual P_n from whole tree measurements or from leaf area from the same age trees (17 yr) of different sizes (5.3–6.7 m).	26
<i>Chrysothamnus nauseosus</i>	Maximum P_n in summer. Juvenile versus mature.	12
<i>Juniperus occidentalis</i>	Juvenile versus young mature.	13
<i>Larrea tridentata</i>	Daily maximum P_n , three summer months. Juvenile versus mature.	14
<i>Picea abies</i>	Light-saturated P_n , open-grown trees. Juvenile versus mature.	15
<i>Picea rubens</i>	Mean seasonal P_n . Juvenile versus mature scions grafted to juvenile rootstock.	16
<i>Pinus aristata</i>	Light-saturated P_n , optimal conditions. Mature versus old-growth.	8
<i>Pinus contorta</i>	Light-saturated P_n . Mature versus old-growth.	19
<i>Pinus ponderosa</i>	Light-saturated P_n . Mature versus old-growth.	19
<i>Pinus ponderosa</i>	Mean morning P_n . Juvenile versus mature and old-growth.	17
<i>Prosopis glandulosa</i>	Daily maximum P_n , after rainfall. Juvenile versus mature.	18
<i>Prunus serotina</i>	Growing season average P_n . Seedling versus sapling versus mature.	11
<i>Sequoiadendron giganteum</i>	Maximum P_n . Seedlings versus juvenile, mature and old-growth.	10

^aMeasurements are from instantaneous measurements of net uptake of CO₂ per unit leaf area unless noted otherwise. Abbreviation: P_n , decreased net photosynthesis.

Table 2. Increased net photosynthesis with a increased age of trees and shrubs^a

Species	Comparison	Ref.
<i>Acer negundo</i>	Maximum P_n during peak of drought period. Juvenile versus mature.	20
<i>Artemisia tridentata</i>	Maximum P_n in mid-summer at a dry site. Juvenile versus mature.	21
<i>Chrysothamnus nauseosus</i>	Maximum P_n in mid-summer at a dry site. Juvenile versus adult.	21
<i>Hedera helix</i>	Light-saturated P_n . Juvenile versus mature scions grafted to juvenile rootstock.	22
<i>Larix laricina</i>	Light-saturated P_n . Juvenile versus mature scions grafted to juvenile rootstock.	23
<i>Prosopis glandulosa</i>	Daily maximum P_n . Summer drought. Small (0.5 m) versus large (1.1 m).	18
<i>Quercus rubra</i>	Light-saturated P_n during growing season. Seedling (in pots) versus mature.	24

^aMeasurements are from instantaneous measurements of net uptake of CO₂ per unit leaf area unless noted otherwise. Abbreviation: P_n , decreased net photosynthesis.

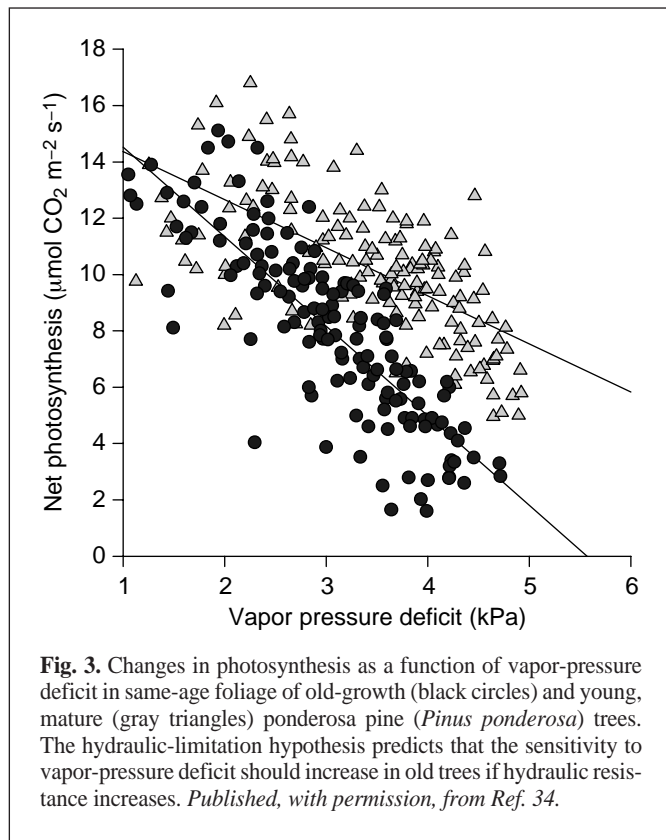


Fig. 3. Changes in photosynthesis as a function of vapor-pressure deficit in same-age foliage of old-growth (black circles) and young, mature (gray triangles) ponderosa pine (*Pinus ponderosa*) trees. The hydraulic-limitation hypothesis predicts that the sensitivity to vapor-pressure deficit should increase in old trees if hydraulic resistance increases. Published, with permission, from Ref. 34.

the transition to old-growth in perennial plants, either directly (through hormone action) or indirectly (through general stress arising from the costs of reproduction). Individuals (as opposed to clones) have a maximum life span that is characteristic of the species and genetic factors, which, in concert with environmental conditions, clearly regulate longevity. However, the determinants of life span might result from varying resistance to environmental stresses rather than from any inherent 'aging' factors³⁰. In other words, although the parts of woody plants can age, senesce and die, whole individuals might not senesce the way that monocarpic plants do³⁰. This is an area that is ripe for further research.

Size and complexity

Because size usually increases with age, it is difficult to separate age responses from size responses. In an experiment with hinoki cypress (*Chamaecyparis obtusa*), whole individuals in a forest were enclosed in 'chambers' and their annual net photosynthesis was measured and calculated on a unit-leaf-area basis²⁵. These trees were of the same age (17 years) but different sizes. When the non-suppressed trees were compared, annual net photosynthesis was found to be inversely related to size.

Researchers have speculated for decades about the loss of vigor that appears to be associated with increasing size and complexity. As early as the 1960s, for example, it was speculated the distance between shoot apices and roots in large woody plants might be too great to allow efficient transport between them, which would cause a decline in growth with increasing size³¹. A variation on this hypothesis was proposed in the 1980s: the growth of large trees might be limited by the transport of water and nutrients if xylem failure (owing to cavitation) was not adequately replaced by refilling or the production of new xylem³².

A more recent version of these ideas has been articulated as the 'hydraulic limitation hypothesis' to explain decreased productivity in aging trees³³. This proposes that the total resistance of the

hydraulic pathway increases as trees approach their maximum height owing to a combination of factors including gravity, a longer hydraulic path length through stems and branches, greater 'tortuosity' of the hydraulic path (e.g. branch junctures) and reduced allocation to roots. Increases in hydraulic resistance could reduce the supply of liquid water for transpiration, which in turn could limit stomatal conductance and photosynthesis.

Several studies have documented increased hydraulic resistance with size and age when environmental conditions are similar²⁹. However, age, size, species and environment can all interact to influence hydraulic architecture, and therefore it is possible that a small tree in a poor environment might have greater total resistance than a large tree of the same species in a better environment. Field studies that controlled for environmental variation have found lower levels of stomatal conductance and photosynthesis in young, mature than in old ponderosa pine (*Pinus ponderosa*) in central Oregon^{19,34} (Fig. 3), in sapling than older ponderosa pine in northern Arizona¹⁷ and in young than in old creosote bush (*Larrea tridentata*)¹⁴.

The hydraulic limitation hypothesis is appealing because it helps to explain why maximum heights are highly predictable for particular species in particular sites, why the same trees would not grow as tall on a poor site and why maximum heights and productivity are closely correlated. However, critics of the hydraulic limitation hypothesis³⁵ rightly point out that woody plants are able to compensate, wholly or partially, for potential hydraulic effects caused by large size. The structure of xylem cells might change as trees grow to make the wood less resistant to water flow, the sapwood area per unit leaf area might increase and the sapwood of large trees might store large amounts of water, 'buffering' the effects of hydraulic resistance. Again, clear answers await further research.

Where do we go from here?

The current literature shows that photosynthesis generally decreases in aging woody plants and that, for many of the exceptions (but not all), there are explanations, such as greater access to water in larger plants with deeper roots. However, the amount of information to date is small and different accounts might emerge as more controlled experiments are conducted. Is photosynthetic decline in aging woody plants an indication of senescence? Probably not – there is no evidence that the physiological or morphological changes in aging woody plants are genetically programmed, especially in the mature to old-growth transition. This conclusion, too, might change with time but, for now, it is better to use the term 'aging' (a passive, non-programmed process) than 'senescence' to describe age-related change in woody plants³⁶.

The study of aging processes in trees is itself at a youthful stage; there are many questions and few definitive answers. In almost all of the research to date, it is impossible to disentangle the effects of age from those of size or varying environment, or to determine whether observed correlations between photosynthesis and growth or gene expression represent causal relationships. Many investigations also suffer from the possibility of genetic and cultivation differences between the age groups that are investigated. This is especially a problem with managed species, in which younger individuals might be propagated from seed sources that have been selected for commercial purposes whereas older plants occur naturally. Experiments that compare potted seedlings or saplings with naturally occurring older trees are extremely difficult to interpret owing to the effects of the pot itself and should be avoided.

There is a need for more cross-disciplinary collaboration in studies of aging. To date, most research has been conducted either by geneticists and molecular biologists, who focus primarily on sexual maturation, or by ecologists, who typically study adaptations to

environmental variations among age classes. Stronger research would result from a combination of these disciplines. A common terminology is necessary to distinguish between maturation stage (seedling, juvenile, mature, old-growth) and size, which might be best expressed as proportion of maximum height for trees or proportion of maximum crown dimensions for shrubs, with the 'maxima' specified for particular sites.

Carefully designed, manipulative experiments are needed to isolate causal factors. These might include adapting bonsai techniques to isolate the effects of age and size on photosynthesis, long-term reciprocal-grafting experiments across the developmental stages, thinning experiments and other manipulations in old-growth stands to understand better the effects of competition with neighbors and investigations of genetic expression in chronosequences of wild plants. Also, more attention should be directed toward the carbon economy of whole plants, including the effects of changing canopy architecture and leaf-age distributions on net annual carbon assimilation.

The physiological changes that occur in aging woody perennials appear to be fundamentally different from the senescence processes in monocarpic plants or mammalian systems. A better understanding of age-related changes in photosynthesis of woody plants could have profound implications for basic biology as well as significant practical applications.

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