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Review Article

Net Primary Productivity of Forest Trees: A Review of Current Issue

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ABSTRACT

Forest growth is important both economically and ecologically and it follows a predictable general trend with age. Generally, the growth of all forests accelerates as canopies develop in young forests and declines substantially soon after the maximum leaf area is attained. The causes of this decline trend are multiple. Initially, age- and size-related declines were attributed to photosynthesis-respiration imbalance. Subsequently, several competing hypotheses have been proposed over the years, although nutrient and hydraulic limitation hypotheses appear to be the most likely to have caused it. In this paper, the authors attempt to review these hypotheses and concentrate on one related aspect, as this can set the scene for further examining the issues of age-related versus size-related processes.

Keywords: Forest growth, canopies, photosynthesis – respiration imbalance

GENERAL BACKGROUND

The rate of production of the biomass by both individual trees and forest stands decreases substantially with age (Assmann, 1970). In particular, age-related reduction in biomass accumulation is an important consideration in the mechanistic models which predict the forest growth and determine the capacity of the forests to act as carbon sinks. With the current impetus towards silvicultural approaches that employ uneven-aged systems and extended rotations, understanding the physiological basis for the age-related decline in productivity of dominant species has become increasingly important. Understanding this component of productivity is crucial to quantifying and manipulating carbon fluxes in forest ecosystems and their influence on the global CO_2 cycles.

Despite many studies attempting to explain the age-related decline of forest productivity through a number of theories, the age-related regulation still remains unclear. There is little direct evidence which explains that old forests assimilate less carbon than the young forests. This makes model-based predictions of the carbon sequestration suspect, as most physiological process models predict carbon assimilation were based on the measurements of photosynthesis on young trees (Ryan *et al.*, 1997a). For example, Bond (2000) provided a list of studies exhibiting two contrasting results in the changes in the net photosynthesis with age of trees and shrubs (Table 1).

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TABLE 1

Studies reporting a comparison of the net photosynthesis in differently aged trees and shrubs

Decreased net photosynthesis (A_{net}) with increased ages of trees and shrubs

Species	Comparison	Reference
Chrysothamnus nauseosus	Maximum A_{net} in summer. Juvenile *versus* mature.	Donovan and Ehleringer (1992)*
Juniperus occidentalis	Juvenile *versus* young mature.	Miller *et al.* (1995)*
Larrea tridentate	Daily maximum A_{net}, three summer months. Juvenile *versus* mature.	Franco *et al.* (1994)*
Picea abies	Light-saturated A_{net}, open-grown trees. Juvenile *versus* mature.	Kull and Koppel (1987)*
Picea rubens	Seasonal A_{net}. Mature *versus* relatively old-growth.	Day *et al.* (2001)
Pinus aristata	Light-saturated A_{net}, optimal conditions. Mature *versus* old-growth.	Schoettle (1994)*
Pinus contorta	Light-saturated A_{net}. Mature *versus* old-growth.	Yoder *et al.* (1994)*
Pinus ponderosa	Light-saturated A_{net}. Mature *versus* old-growth.	Yoder *et al.* (1994)*
Pinus ponderosa	Mean morning A_{net}. Juvenile *versus* mature and old-growth.	Kolb and Stone (2000)*
Prosopis glandulosa	Daily maximum A_{net}, after rainfall. Juvenile *versus* mature.	DeSoyza *et al.* (1996)*
Prunus serotina	Growing season average A_{net}. Seedling *versus* sapling *versus* mature.	Fredericksen *et al.* (1996)*
Sequoiadendron giganteum	Maximum A_{net}. Seedlings *versus* juvenile, mature and old-growth.	Grulke and Miller (1994)*

No difference or increased net photosynthesis with increased ages of trees and shrubs

Species	Comparison	Reference
Acer negundo	Maximum A_{net}, during peak of drought period. Juvenile versus mature.	Donovan and Ehleringer (1992)*
Artemesia tridentata	Maximum $A_{net,}$ in mid-summer at a dry site. Juvenile *versus* mature.	Donovan and Ehleringer (1992)*
Chrysothamnus nauseosus	Maximum A_{net}, in mid-summer at a dry site. Juvenile *versus* adult.	Donovan and Ehleringer (1992)*
Prosopis glandulosa	Daily maximum A_{net}. Summer drought. Small (0.5 m) *versus* large (1.1 m).	DeSoyza *et al.* (1996)*
Pseudotsuga menziesii	No clear trend of light-saturated A_{net}. Mature *versus* old growth.	McDowell *et al.* (2002)
Quercus rubra	Light-saturated A_{net}, during growing season. Seedling *versus* mature.	Hanson *et al.* (1994)*

Note: * = cited from Bond (2000).

The causes of this age-related decline are likely multiple, but the most important potential causes which can explain a decline in forest productivity with stand development are nutrient limitation, hydraulic limitation and maturation (genetic programming) hypotheses. According to some authors, the so called "age-related" decline in the forest productivity is primarily a "size-related" decline (Weiner and Thomas, 2001). Ideally, a test should be conducted on the trees of similar size, but different ages or *vice versa*; thereby separating the confounded factors of size and age. An alternative to obtain trees with similar size but with different ages is to graft scions of the different ages onto young rootstocks.

Studies using grafting have been conducted by a few researchers (summarised in Table 2) in relation to the effect of age on the growth, morphology and physiology of grafted scions. However, these studies still yielded contrasting outcomes with the age of scion. Despite the presence of these grafting studies, there are some weaknesses which have never been tackled by the previous researchers. For instance, no study has so far simultaneously compared individuals in the field and genetically identical grafted seedlings. Day *et al.* (2001) conducted a similar study, but the individuals selected in the field were not genetically identical with the grafted seedlings (although they came from the same population). Moreover, most of the published evidences on grafting have been obtained from very young trees. In relation to the studies presented in Table 2, for instance, Hutchison *et al.* (1990) used individuals taken from four age classes, ranging from 1 to 45 years; whereas, Rebbeck *et al.* (1993) used only juvenile and mature (>50 years old) scions. In addition, Greenwood (1984) studied shoot development as a function of age on *Picea taeda*, but the comparisons were only made among scions up to 12 years of age. Furthermore, Greenwood *et al.* (1989) also used grafting approach to study the effect of age on the morphological characteristics and DNA methylation of *Larix laricina*, but the scions involved were taken from juvenile and mature trees, ranging from 1 to 74 years of age.

Mencuccini *et al.* (2005) also used propagated material to separate the relative effects of size and age on tree growth and metabolism. These authors selected four different tree species. Three of them (one conifer, Scots pine and two angiosperms with diffuse-porous wood, sycamore and ring-porous wood, ash) were propagated by grafting, whereas the fourth (poplar) was propagated by direct rooting. Poplar was also chosen because of its clonal nature, which allowed a different approach in the separation of age versus size (cf., Mencuccini, 2007 for further details). The approach adopted in Mencuccini *et al.* (2005) avoided some of the potential artefacts presented in the earlier works (Table 2). For instance, the individuals measured in the field were almost always the exact same donors from where the grafted twigs were taken, thereby avoiding genetic differences between the donor trees and the grafted plants. For the conifer in the study by Mencuccini *et al.* (2005) (Scots pine), the measurements took place five to seven years after the initial grafting, to ensure that enough time had elapsed since grafting had taken place. More importantly perhaps, the grafting technique did not leave any room for competition between shoots of the grafted plant and the shoots of the rootstock, as the canopy of the accepting rootstock was completely pruned away after grafting.

Therefore, additional comparative studies are required to determine whether the different conclusions reached by some of the earlier studies were the results of different species-specific developmental events or whether they are determined by the different experimental protocols.

AGE- AND SIZE-RELATED REGULATION OF THE NET PRIMARY PRODUCTION

Observations have showed that aboveground net primary productivity negatively correlates with the age of tree for both individual trees and single

TABLE 2
Summary of the results showing contrasting trends involving in grafted scions

Species	Results	Reference
Hedera helix	Increased light-saturated A_{net} with increased ages of scions. Juvenile *versus* mature scions grafted to juvenile rootstock.	Bauer and Bauer (1980)
Larix laricina	Height and diameter growth decreased with increased ages of scions. Juvenile *versus* mature scions grafted to juvenile rootstock.	Greenwood *et al.* (1989)
Larix laricina	Total chlorophyll increased with increased ages of scions. Juvenile *versus* mature scions grafted to juvenile rootstock.	Greenwood *et al.* (1989)
Larix laricina (indoor-grown trees)	Increased light-saturated A_{net} with increased ages of scions. Juvenile *versus* mature scions grafted to juvenile rootstock.	Hutchison *et al.* (1990)
Larix laricina (outdoor-grown trees)	No trend observed in light-saturated A_{net} with increased ages of scions juvenile *versus* mature scions grafted to juvenile rootstock.	Hutchison *et al.* (1990)
Larix laricina	Increased xylem diameters with increased ages of scions. Juvenile *versus* mature scions grafted to juvenile rootstock.	Takemoto and Greenwood (1993)
Picea rubens	Decreased A_{net} with increased ages of scions. Juvenile *versus* mature scions grafted to juvenile rootstock.	Rebbeck *et al.* (1993)
Picea rubens	Decreased light-saturated A_{net} with increased age of scions. Mature *versus* old scions.	Day *et al.* (2001)
Picea taeda	Diameter and height growth, leaf area, branch numbers and scion biomass decreased with increased scion ages. Juvenile *versus* young scions grafted to juvenile rootstock.	Greenwood (1984)
Pinus radiata	Diameter and height growth and branch numbers decreased with increased scion ages. Juvenile *versus* mature scions.	Sweet (1973)
Pseudotsuga menziesii	Diameter and height growth, branch numbers and branch length decreased with increased scion ages. Juvenile *versus* young scions grafted to juvenile rootstock.	Ritchie and Keeley (1994)

cohort stands (Assmann, 1970; Whittaker, 1975; Bormann and Likens, 1979; Harcombe *et al.,* 1990). Long-term studies on even-aged forests showed that the maximum bole increment rate occurs shortly after crown closure and declines as trees reach maturity (Assmann, 1970). Yoder *et al.* (1994) suggested that age-related declines in photosynthetic rates for lodgepole and ponderosa pine may be a significant cause of net production decreases in old trees. This is supported by several studies conducted on age-related differences in photosynthetic rates in Scots pine (Kull and Koppel, 1987), bristlecone pines (Schoettle, 1994) and hybrid Englemann x white x Sitka spruce (Richardson *et al.,* 2000). However, photosynthetic rates in the eastern larch have been reported to be higher in grafts from older trees (Hutchison *et al.,* 1990).

Explanations for these age-related differences in the photosynthetic rates are generally centred on the multiple constraints on carbon assimilation. Among the potential constraints on carbon assimilation are genetic-down regulation of photosynthesis, reductions in the whole-tree leaf area per unit biomass, nutrient based limitations on photosynthetic capacity and reductions in hydraulic conductance, together with the changes in micrometeorological factors such as temperature and the availability of light and water. A few hypotheses have been developed based on the aforementioned constraints such as the respiration hypothesis, the nutrient limitation hypothesis, the maturation hypothesis and the hydraulic limitation hypothesis. In the respiration hypothesis, for instance, the allometry of trees must be such to support the vertical mass and resist the bending forces from wind, which increase rapidly with tree height. Nevertheless, these support systems require considerable investment in non-photosynthetic tissues, which increase maintenance respiration. Meanwhile, in the nutrient limitation hypothesis, growth in older trees is limited by nutrient supply with nutrients being tied up in living plants and soil litter. Moreover, the hydraulic limitation hypothesis is based on the increase in tree height, which may increase hydraulic constraints and limit gas exchange in older or taller trees. Another explanation could be the ontogenetic changes (maturation hypothesis) which contribute to reduced growth in older trees. Each of these four (4) hypotheses has been reviewed in greater detail in the on-going discussions.

Respiration Hypothesis

Before the links between respiration and biosynthesis started to become clear in the 1950s, respiration was considered to be an imperfection in the mechanisms which converted substrates into structural dry matters (Lambers, 1985). Since then, a rapid expansion of knowledge has taken place. Gradually, it has become of interest to establish the quantitative relationship between the substrate use and processes, such as the growth and maintenance of plants and plant parts under different environmental conditions (Lambers, 1985). Yoda *et al.* (1965) estimated the total aboveground wood respiration of a tree by sorting all shoot parts into diameter classes and multiplying the biomass in each class with the average respiration rate for that particular class.

For years, many scientists assumed that the most important constraint to large size is the maintenance cost required by living biomass in very large stems and roots systems (Bond, 1998). This respiration consumes the photosynthate and thus leaves less for the new growth in large trees. Hence, this hypothesis is based on the relative importance of various photosynthate sinks and the observed declines in the ratio of photosynthetic to non-photosynthetic tissues as trees and stands age. Over the years, researchers have expressed respiration rates on the basis of different measures of plant size. Rates expressed on a weight (Yoda *et al.,* 1965) or volume (Ryan *et al.*, 1996) bases decline, while surface area based rates increase with increasing diameter.

Carbon may be allocated away from aboveground growth and toward respiration (Yoda *et al.,* 1965) to defend plant against pathogens or insects, reproduction (Ryan *et al.,* 1997b; Becker *et al.,* 2000b) or belowground growth (Grier *et al.,* 1981; Gower *et al.,* 1996; Magnani *et al.,* 2000). However, the tests of the respiration hypothesis in lodgepole pine (Ryan and Waring, 1992) and eucalyptus (Ryan *et al.,* 2004) have failed to support it. This hypothesis has also been weakly supported by modelling studies (Magnani *et al.,* 2000; Mäkelä and Valentine, 2001).

Nutrient Limitation Hypothesis

The nutrient limitation hypothesis has been supported by some previous studies and refuted by others (Ryan *et al.*, 1997a). As forests age, nutrients may become scarce due to the sequestration in biomass and necromass (Gower *et al.*, 1996; Ryan *et al.*, 1997b). Such scarcity may lead to the reduction in the allocation of nitrogen to thylakoid membranes and enzymes, therefore reduces photosynthetic capacity. This is because photosynthetic capacity is strongly correlated with leaf nitrogen content across a wide range of plant species (Field and Mooney, 1986; Pearcy *et al.*, 1987; Lambers *et al.*, 1990). However, this relationship may be complicated by the partitioning between various photosynthetic systems and non-photosynthetic components (Evans, 1989), as well as the occurrence of nitrogenous osmoregulatory and storage substances (Sarjala *et al.*, 1987; Margolis and Vezina, 1988; Lavoie *et al.*, 1992; Billow *et al.*, 1994). Reich and Schoettle (1988) suggested that photosynthetic response may be more strongly linked to the interaction of nitrogen and phosphorus content than to the former element alone. On the contrary, Ryan and Waring (1992), Yoder *et al.* (1994) and Mencuccini and Grace (1996b) found no significant age-related differences in the total foliar nitrogen content for chronosequences of *Pinus contorta*, *P. ponderosa* and *P. sylvestris*. However, their analyses were limited to the first year foliage. Numerous investigations have shown that the content of foliar nitrogen is inversely related to the age of leaf (Lehto and Grace, 1994; Field, 1983; Field and Mooney, 1983; Matyssek, 1986; Lang *et al.*, 1987). In addition, lower nutrient available may lead to increased allocation of photosynthetic products to root production, particularly in older stands and therefore to decreased allocation to aboveground structures (Ryan *et al.*, 1997a). Grier *et al.* (1981) found that the allocation to fine roots was dramatically greater in an old rather than in an adjacent young *Abies amabilis* forest. Similar results have also been reported for the *Pinus elliottii* stand, whereby fine-root biomass was greater in a mature stand than in a younger stand (Gholz and Fisher, 1982).

Aboveground net primary productivity (ANPP) may decline during stand development due to decreasing availability of nutrients, particularly nitrogen. In general, nitrogen mineralization and nitrification rates decrease during secondary succession of forests (Vitousek *et al.,* 1989). The decline is strongly correlated with litter decomposition, which in turn, is controlled by environmental conditions, together with chemical and physical characteristics of litter (Gower *et al.,* 1996). Stand-age effects may contribute in two ways. First, the ratio of leaf to woody detritus input (with low and high C:N ratios, respectively) gradually decreases during stand development. Second, the accumulation of woody litter as stands age will slow decomposition due to its low surface area:volume ratio, as compared to fine litter (Landsberg and Gower, 1997). The reduction in litter quality during stand development increases nitrogen immobilization during litter decomposition, which in turn, decreases the net nitrogen mineralization as stand ages (Davidson *et al.,* 1992; Hart *et al.,* 1994).

Hydraulic Limitation Hypothesis

The hydraulic limitation hypothesis proposes that leaf-specific hydraulic conductance (K_L) declines as trees grow taller, resulting in decreased carbon assimilation (Ryan and Yoder, 1997; Bond and Ryan, 2000). Yoder *et al.* (1994) and Ryan and Yoder (1997) proposed this hypothesis to explain the results of their study on ponderosa pine, which indicated that photosynthesis was limited in older trees relative to younger individuals by reduction in midday stomatal conductance (G_S). This hypothesis was based on older trees having lower hydraulic conductivity in the water path between the roots and shoots, due to longer or more complex hydraulic pathways. Due to this lower conductivity, stomata of older trees show greater sensitivity to evaporative demand and more tightly regulate transpiration to minimize the potential for xylem embolism (Ryan and Yoder, 1997). The rate of xylem water flow is determined by Darcy's law (Tyree and Ewers, 1991; Margolis *et al.,* 1995), in which the flow rate is directly proportional to cross-sectional area of the transmitting structure (sapwood xylem), its permeability and the water potential gradient. As conductivity is equivalent to the combination of area and permeability terms, a decrease in this combined parameter requires an increase in water potential gradient to maintain a constant flow. If xylem conductance is lower in older (larger) trees, a critical water potential for stomatal closure will be reached more rapidly than in younger (smaller) trees, as evaporative demand increases.

Studies of tree hydraulic architecture provide evidences that potential xylem flux decreases with tree size. Darcy's law further states that flow is inversely related to pathway length. Thus, maintaining an equal flow to leaves at greater distance from a root absorption point, as in larger trees, requires either an increase in conductivity or water potential gradient. Leaf specific conductivity (*LSC*) is commonly used as a measure of the ability of a particular section of stem, or a branch to supply water to more distal leaves and values for this parameter have been found to be relatively constant along the length of tree stems (Tyree and Ewers, 1991). However, Ewers and Zimmerman (1984a, b) found that leaf specific conductivity values are much lower in branches, strongly influenced by branch diameter and order, and subject to significant restriction at branch-stem junctions. Although stem leaf specific conductivity values, if strictly height-determined, cannot be expected to differ greatly between younger and older trees of the same height, the longer branches typical of older crowns may provide significantly reduced leaf specific conductivity values.

McDowell *et al.* (2002) found that hydraulic conductance decreased by 44% as tree height increased from 15 to > 32 m and showed a further decline of 6% with the increase in height. The analyses on sensitivity, based on Darcy's Law to quantify the extent to which compensating mechanisms buffer hydraulic limitations to gas exchange, indicated that without the observed increases in the soil-to-leaf water potential differential ($\Delta\Psi$) and decreases in the leaf area/sapwood area ratio, K_L would have been reduced by more than 70% in the 60-m trees, as compared to 15-m trees, instead of the observed decrease of 44%. However, compensation may have a cost; for example, the greater $\Delta\Psi$ of the largest trees is associated with smaller tracheid diameters and increased sapwood cavitation, which may also have a negative feedback on K_L and G_S.

Several studies indicate that larger trees are capable of altering their hydraulic architecture to compensate for the longer, more complex pathways between roots and foliage (Becker *et al.,* 2000b; Bond and Ryan, 2000; Mencuccini and Magnani 2000). These were summarized in a critique of the hydraulic limitation hypothesis by Becker *et al.* (2000b). Critics of the hydraulic limitation hypothesis have pointed out the various mechanisms, by which plants compensate for hydraulic limitation, as it is evident that the increased height and structural complexity of old trees are unlikely to constrain hydraulic conductance and hence assimilation. Although tapered xylem conduits may buffer hydraulic resistance from path length effects (West *et al.,* 1999; Becker *et al.,* 2000a) and such buffering appears to be overdriven by hydraulic constraints in tall trees. Furthermore, other buffering factors, such as greater water storage in sapwood (Becker *et al*., 2000b) and increased xylem permeability to water flow during tree ageing (Mencuccini and Magnani, 2000) may to some extent, compensate for the long path lengths for water movement in tall trees.

In addition, several attempts to provide direct evidence in support of the hydraulic limitation hypothesis by experimental manipulation have been unsuccessful. Hubbard *et al.* (1999) girdled young lodgepole pine trees to reduce leaf specific conductivity and remove foliage from older trees to increase it, but found that manipulation could neither significantly change stomatal conductance nor photosynthetic rates. A similar study (in which foliage of old Douglas-fir was enclosed in plastic bags to reduce transpiration and leaf specific conductivity) was also unsuccessful at increasing gas exchange rates of uncovered foliage on the same branches (Brooks *et al.,* 2000).

Maturation Hypothesis

Genetic regulation of photosynthesis has not been specifically proposed in the literature, nor are there data to test this hypothesis. However, dramatic changes in morphological and physiological attributes of foliage, including photosynthetic capacity, have been described for numerous species during their early development and have been attributed to different challenges to growth and survival, at various life-stages (Greenwood, 1984; Hackett, 1985; Rebbeck *et al.,* 1993; Greenwood and Hutchison, 1993). Although little is known about age-related trends in foliar attributes beyond reproductive maturity or mid-age, there is some evidence which supports the concept of continuous change. Richardson *et al.* (2000) reported that the changes in foliar morphology and gas exchange attributes continue past mid-age in hybrid Englemann x white x Sitka spruce. Similar trends in foliar attributes have been described for Norway spruce (Kull and Koppel, 1987) and in needle morphology of Sitka spruce (Steele *et al.,* 1989). However, none of these studies has directly addressed the potential for ontogenetic changes in meristematic tissue, as a contributing mechanism to age-related declines in productivity, nor do they experimentally separate age from size.

It is important to highlight that the contribution of maturation-related changes in meristem behaviour to age-related decline in forest productivity is still poorly understood. While changes in the morphological and physiological attributes, associated with the transition from juvenile to reproductively-mature phases, have been described for many woody species, only a few studies have examined the maturational changes which occur after the onset of reproductive development (Greenwood *et al*., 1989; Day *et al.,* 2001; Day *et al.,* 2002). In any case, common rootstock studies, in which scions are donated by juvenile and mature trees, hint at the possibility that the differences in morphological and physiological traits associated with those life-stages are inherent in meristems. Such studies have also been carried out on loblolly pine (Greenwood, 1984), eastern larch (Greenwood *et al*., 1989) and red spruce (Rebbeck *et al.,* 1993; Day *et al.,* 2001).

A field study, conducted by Day *et al.* (2001) on *Picea rubens* Sarg., demonstrated significant age-related trends in foliar morphology, including decreasing specific leaf area (*SLA*) and increasing needle width, projected needle area and needle width-to-length ratio. Similar trends were also apparent in foliage from the grafted trees with different scion ages. Both *in situ* foliage and shoots resulting from grafted scions from the oldest cohort showed significantly lower photosynthetic rates than their counterparts from younger trees; however, the differences in stomatal conductance and internal CO_2 concentrations were not significant. They concluded that the lower rates of photosynthesis had contributed to the age-related decline in the productivity of older red spruce and that the decline in photosynthetic rates was resulted from non-stomatal limitations. In addition, a study where scions from juvenile and mature red spruce were grafted onto common rootstock (Rebbeck *et al.,* 1993) clearly showed that maturation-related changes in meristems of red spruce persisted for at least two years after grafting. In their study, the results on scions from mature trees exhibited lower stomatal conductance and net photosynthetic rates than those from the juvenile donors.

In addition, Emebiri *et al.* (1998) and Hutchison *et al.* (1990) have implicated a genetic basis for ontogenetic changes by identifying differential patterns of gene expression related to life-stages. However, the pathways by which genetic changes in meristems and/or the foliage they produce affecting photosynthetic rates have not been described. A possible pathway, by which ontogenetic changes in meristems may affect photosynthetic rates, is by producing tissue in older trees which have an inherently lower growth rate. Shoots resulting from the grafts of meristems from older trees have lower growth rates as than scions from young trees. This was shown for radiata pine (Sweet, 1972), loblolly pine (Greenwood, 1984), eastern larch (Greenwood *et al.,* 1989, Takemoto and Greenwood 1993) and red spruce (Rebbeck *et al.,* 1993). Takemoto and Greenwood (1993) speculated that the older meristems might be weak sinks for resources as compared to shoots arising from the scions taken from younger trees. Stitt (1990) stated that weak sinks for carbohydrate, due to reduced growth, could result in feedback limitations to photosynthesis. Meanwhile, Leverenz (1981) suggested that sink strength limitations might explain differential photosythetic capacity among the branches in the crowns of mature Douglas-fir.

NEW QUESTIONS AND CHALLENGES FOR THE FUTURE

Since 1997, when the idea of 'the hydraulic limitation theory' was first formally presented (Ryan and Yoder, 1997), many steps forward have been made to better characterize the physiological ecology of old and tall trees. Almost every year, a conference session or a workshop is organised around these themes and the attention in the most prestigious scientific journals has also been increased (e.g., Koch *et al.,* 2004; Pennisi, 2005; Penuelas, 2005). The authors' knowledge of the stand and ecosystem development is rapidly expanding and some consensus has emerged over some issues. However, over several other issues, much more work remains to be carried out. Perhaps more importantly, the authors are still not close to the identification of the component or components which are most likely to determine the observed reductions in the GPP and NPP with age. A recent modelling exercise, based on the concept of optimal carbon allocation (Buckley and Roberts, 2005) has clearly highlighted how much work needs to be done to correctly interpret the significance of some of the observed patterns. Therefore, much of the progress thus far could be viewed as useful but marginal to the central question, which was initially posed by Ryan and Waring (1992).

However, on a more positive side, the impetus provided by those initial studies have helped to identify a number of very different research questions that have not been considered at the outset. This review on the issues related to ageing and senescence was attempted to help set the efforts of the stage for future research in this area. An important concept recently emerged has been the demonstration that size per se exerts effects which are clearly independent of age (Mencuccini *et al.,* 2005), a concept which is consistent with the earlier data (e.g. Sweet, 1972). Much of the older literature on ageing in trees confused these two aspects and accepted that characters such as reduced ring width could be taken to indicate senescence processes. Therefore, the newly emerged complexity of tree research, as compared to animal research, is in the current awareness that any symptom or biomarker of ageing must be thought of independently of the size-related effects which occur in large and tall trees. However, other more fundamental questions remain unanswered. These include questions such as: Are trees potentially immortal, but subject to the vagaries of extreme environmental conditions and occasional disturbances, or do they ultimately show senescence processes, like many other life forms? The current evidence points towards a lack of clear senescence processes, but many unclear points still exist and the few investigations on this topic are quite dated. For instance, evidence is required to answer the question on "what are the trade-offs between lifespan, growth and reproduction in long-lived versus short-lived taxa?" At present, the authors have merely had tentative answers to these very fundamental questions. This topic is coming again to the fore of the ecological and environmental sciences debate and the research in this field is likely to yield interesting new information.

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