

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 CO₂ 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
<i>Chrysothamnus nauseosus</i>	Maximum A_{net} in summer. Juvenile <i>versus</i> mature.	Donovan and Ehleringer (1992)*
<i>Juniperus occidentalis</i>	Juvenile <i>versus</i> young mature.	Miller <i>et al.</i> (1995)*
<i>Larrea tridentate</i>	Daily maximum A_{net} , three summer months. Juvenile <i>versus</i> mature.	Franco <i>et al.</i> (1994)*
<i>Picea abies</i>	Light-saturated A_{net} , open-grown trees. Juvenile <i>versus</i> mature.	Kull and Koppel (1987)*
<i>Picea rubens</i>	Seasonal A_{net} . Mature <i>versus</i> relatively old-growth.	Day <i>et al.</i> (2001)
<i>Pinus aristata</i>	Light-saturated A_{net} , optimal conditions. Mature <i>versus</i> old-growth.	Schoettle (1994)*
<i>Pinus contorta</i>	Light-saturated A_{net} . Mature <i>versus</i> old-growth.	Yoder <i>et al.</i> (1994)*
<i>Pinus ponderosa</i>	Light-saturated A_{net} . Mature <i>versus</i> old-growth.	Yoder <i>et al.</i> (1994)*
<i>Pinus ponderosa</i>	Mean morning A_{net} . Juvenile <i>versus</i> mature and old-growth.	Kolb and Stone (2000)*
<i>Prosopis glandulosa</i>	Daily maximum A_{net} , after rainfall. Juvenile <i>versus</i> mature.	DeSoyza <i>et al.</i> (1996)*
<i>Prunus serotina</i>	Growing season average A_{net} . Seedling <i>versus</i> sapling <i>versus</i> mature.	Fredericksen <i>et al.</i> (1996)*
<i>Sequoiadendron giganteum</i>	Maximum A_{net} . Seedlings <i>versus</i> 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
<i>Acer negundo</i>	Maximum A_{net} , during peak of drought period. Juvenile <i>versus</i> mature.	Donovan and Ehleringer (1992)*
<i>Artemisia tridentata</i>	Maximum A_{net} , in mid-summer at a dry site. Juvenile <i>versus</i> mature.	Donovan and Ehleringer (1992)*
<i>Chrysothamnus nauseosus</i>	Maximum A_{net} , in mid-summer at a dry site. Juvenile <i>versus</i> adult.	Donovan and Ehleringer (1992)*
<i>Prosopis glandulosa</i>	Daily maximum A_{net} . Summer drought. Small (0.5 m) <i>versus</i> large (1.1 m).	DeSoyza <i>et al.</i> (1996)*
<i>Pseudotsuga menziesii</i>	No clear trend of light-saturated A_{net} . Mature <i>versus</i> old growth.	McDowell <i>et al.</i> (2002)
<i>Quercus rubra</i>	Light-saturated A_{net} , during growing season. Seedling <i>versus</i> mature.	Hanson <i>et al.</i> (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
<i>Hedera helix</i>	Increased light-saturated A_{net} with increased ages of scions. Juvenile <i>versus</i> mature scions grafted to juvenile rootstock.	Bauer and Bauer (1980)
<i>Larix laricina</i>	Height and diameter growth decreased with increased ages of scions. Juvenile <i>versus</i> mature scions grafted to juvenile rootstock.	Greenwood <i>et al.</i> (1989)
<i>Larix laricina</i>	Total chlorophyll increased with increased ages of scions. Juvenile <i>versus</i> mature scions grafted to juvenile rootstock.	Greenwood <i>et al.</i> (1989)
<i>Larix laricina</i> (indoor-grown trees)	Increased light-saturated A_{net} with increased ages of scions. Juvenile <i>versus</i> mature scions grafted to juvenile rootstock.	Hutchison <i>et al.</i> (1990)
<i>Larix laricina</i> (outdoor-grown trees)	No trend observed in light-saturated A_{net} with increased ages of scions juvenile <i>versus</i> mature scions grafted to juvenile rootstock.	Hutchison <i>et al.</i> (1990)
<i>Larix laricina</i>	Increased xylem diameters with increased ages of scions. Juvenile <i>versus</i> mature scions grafted to juvenile rootstock.	Takemoto and Greenwood (1993)
<i>Picea rubens</i>	Decreased A_{net} with increased ages of scions. Juvenile <i>versus</i> mature scions grafted to juvenile rootstock.	Rebbeck <i>et al.</i> (1993)
<i>Picea rubens</i>	Decreased light-saturated A_{net} with increased age of scions. Mature <i>versus</i> old scions.	Day <i>et al.</i> (2001)
<i>Picea taeda</i>	Diameter and height growth, leaf area, branch numbers and scion biomass decreased with increased scion ages. Juvenile <i>versus</i> young scions grafted to juvenile rootstock.	Greenwood (1984)
<i>Pinus radiata</i>	Diameter and height growth and branch numbers decreased with increased scion ages. Juvenile <i>versus</i> mature scions.	Sweet (1973)
<i>Pseudotsuga menziesii</i>	Diameter and height growth, branch numbers and branch length decreased with increased scion ages. Juvenile <i>versus</i> 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 CO₂ 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 photosynthetic 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.

REFERENCES

- Assmann, E. (1970). *The Principles of Forest Yield Study*. Oxford: Pergamon Press Ltd.
- Bauer, H. and Bauer, U. (1980). Photosynthesis in leaves of the juvenile and adult phase of ivy (*Hedera helix*). *Physiologia Plantarum*, 49, 366 – 372.
- Becker, P., Gribben, R.J. and Lim, C.M. (2000a). Tapered conduits can buffer hydraulic conductance from path length effects. *Tree Physiology*, 20, 965 – 968.
- Becker, P., Meinzer, F.C. and Wullschleger, S.D. (2000b). Hydraulic limitation of tree height: a critique. *Functional Ecology*, 14, 4 – 11.

- Billow, C., Matson, P. and Yoder, B. (1994). Seasonal biochemical changes in coniferous forest canopies and their response to fertilization. *Tree Physiology*, 14, 563 – 574.
- Bond, B.J. and Ryan, M.G. (2000). Comment on 'Hydraulic limitation of tree height: A critique' by Becker, Meinzer and Wullschleger. *Functional Ecology*, 14, 135 – 140.
- Bond, B.J. (1998). *The maximum heights of trees*. McGraw-Hill 1999 Yearbook of Science and Technology (8th ed.) (p. 375 – 378). New York: McGraw-Hill Book Co.
- Bond, B.J. (2000). Age-related changes in photosynthesis of woody plants. *Trends in Plant Science*, 5, 349 – 353.
- Bormann, F.H. and Likens, G.E. (1979). *Pattern and Process in a Forested Ecosystem*. New York: Springer-Verlag.
- Brooks, J.R., Bond, B.J., Coulombe, R., Domec, J.C., Hinckley, T.M., McDowel, N., Phillips, N. and Schulte, P.J. (2000). The effects of transient reductions in functional leaf area on stomatal conductance: branch level experiments on young and old trees (p. 62). In ESA Abstract, *The Ecological Society of America 85th Annual Meeting*, August 6 – 10 2000 Snowbird, UT. Ecological Society of America, Washington, DC. 428p.
- Buckley, T.N. and Roberts, D.W. (2005). How should leaf area, sapwood area and stomatal conductance vary with tree height to maximise growth? *Tree Physiology*, 26, 145 – 157.
- Davidson, E.A., Hart, S.C. and Firestone, M.K. (1992). Internal cycling of nitrate in soils of a mature coniferous forest. *Ecology*, 73, 1148 – 1156.
- Day, M.E., Greenwood, M.S. and White, A.S. (2001). Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. *Tree Physiology*, 21, 1195 – 1204.
- Day, M.E., Greenwood, M.S. and Diaz-Sala, C. (2002). Age- and size-related trends in woody plant shoot development: regulatory pathways and evidence for genetic control. *Tree Physiology*, 22, 507 – 513.
- DeSoyza, A.G., Franco, A.C., Virginia, R.A., Reynolds, J.F. and Whitford, W.G. (1996). Effects of plant size on photosynthesis and water relations in the desert shrub *Prosopis glandulosa* (Fabaceae). *American Journal of Botany*, 83, 99 – 105.
- Donovan, L.A. and Ehleringer, J.R. (1992). Contrasting water-use patterns among size and life-history classes of a semi-arid shrub. *Functional Ecology*, 6, 482 – 488.
- Emebiri, L.C., Devey, M.E., Matheson, A.C. and Slee, M.U. (1998). Age-related changes in the expression of QTLs for growth in radiata pine seedlings. *Theoretical and Applied Genetics*, 97, 1053 – 1061.
- Evans, J.R. (1989). Photosynthesis- the dependence on nitrogen partitioning. In H. Franco, C., DeSoyza, A.G., Virginia, R.A., Reynolds, J.F. and Whitford, W.G. (1994). Effects of plant size and water relations on gas exchange and growth of the desert shrub *Larrea tridentata*. *Oecologia*, 97, 171 – 178.
- Ewers, F.W. and Zimmermann, M.H. (1984a). The hydraulic architecture of balsam fir (*Abies balsamea*). *Physiologia Plantarum*, 60, 453 – 458.
- Ewers, F.W. and Zimmermann, M.H. (1984b). The hydraulic architecture of eastern hemlock (*Tsuga canadensis*). *Canadian Journal of Botany*, 62, 940 – 946.
- Field, C. (1983). Allocating leaf nitrogen for maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia*, 56, 341 – 347.
- Field, C. and Mooney, H.A. (1983). Leaf age and seasonal effects on light, water, and nitrogen use efficiency in a California shrub. *Oecologia*, 56, 348 – 355.
- Field, C. and Mooney, H.A. (1986). The photosynthesis-nitrogen relationship in wild plants. In T.J. Givnish (Ed.), *On the economy of plant form and function* (p. 255). Cambridge, England: Cambridge University Press.
- Fredericksen, T.S., Steiner, K.C., Skelly, J.M., Joyce, B.J., Kolb, T.E., Kouterick, K.B. and Ferdinand, J.A. (1996). Seasonal patterns of leaf gas exchange and xylem water potentials

- of different-sized *Prunus serotina* Ehrh. trees. *Forest Science*, 42, 359 – 365.
- Gholz, H.L. and Fisher, R.F. (1982). Organic matter production and distribution in slash pine *Pinus elliottii* plantations. *Ecology*, 63, 1827 – 1839.
- Gower, S.T., McMurtrie, R.E. and Murty, D. (1996). Aboveground net primary production decline with stand age: Potential causes. *Trends in Ecology and Evolution Research*, 11, 378 – 382.
- Greenwood, M.S. and Hutchison, K.W. (1993). Maturation as a developmental process. In M.R. Ahuja and W.J. Libby (Eds.), *Clonal forestry I: Genetics and biotechnology* (p. 14 – 33). NY: Springer-Verlag.
- Greenwood, M.S. (1984). Phase change in loblolly pine: Shoot development as a function of age. *Physiologia Plantarum*, 61, 518 – 522.
- Greenwood, M.S., Hooper, C.A. and Hutchison, K.W. (1989). Maturation in larch. I. Effect of age on shoot growth, foliar characteristics, and DNA methylation. *Plant Physiology*, 90, 406 – 412.
- Grier, C.C., Vogt, K., Keyes, M.R. and Edmonds, R.L. (1981). Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Canadian Journal of Forest Research*, 11, 155 – 167.
- Grulke, N.E. and Miller, P.R. (1994). Changes in gas exchange characteristics during the life span of giant sequoia: implications for response to current and future concentrations of atmospheric ozone. *Tree Physiology*, 14, 659 – 668.
- Hackett, W.P. (1985). Juvenility, maturation, and rejuvenation in woody plants. *Horticultural Reviews*, 7, 109 – 155.
- Hanson, P.J., Samuelson, L.J., Wullschleger, S.D., Tabberer, T.A. and Edwards, G.S. (1994). Seasonal patterns of light-saturated photosynthesis and leaf conductance for mature and seedling *Quercus rubra* L. foliage: differential sensitivity to ozone exposure. *Tree Physiology*, 14, 1351 – 1366.
- Harcombe, P.A., Harmon, M.E. and Greene, S.E. (1990). Changes in biomass and production after 53 years in a coastal *Picea sitchensis-Tsuga heterophylla* forest approaching maturity. *Canadian Journal of Forest Research*, 20, 1602 – 1610.
- Hart, S.C., Nason, G.E., Myrold, D.D. and Perry, D.A. (1994). Dynamics of gross nitrogen transformations in an old-growth forest – the carbon connection. *Ecology*, 75, 880 – 891.
- Hubbard, R.M., Bond, B.J. and Ryan, M.G. (1999). Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiology*, 19, 165 – 172.
- Hutchison, K.W., Sherman, C.D., Weber, J., Smith, S.S., Singer, P.B. and Greenwood, M.S. (1990). Maturation in larch II: Effects of age on photosynthesis and gene expression in developing foliage. *Plant Physiology*, 94, 1300 – 1315.
- Koch, G.W., Sillett S.C., Jennings G.M. and Davis, S.D. (2004). The limits to tree height. *Nature*, 428, 851 – 854.
- Kolb, T.E. and Stone, J.E. (2000). Differences in leaf gas exchange and water relations among species and tree sizes in an Arizona pine-oak forest. *Tree Physiology*, 20, 1 – 12.
- Kull, O. and Koppel, A. (1987). Net photosynthetic response to light intensity of shoots from different crown positions and age in *Picea abies* (L.) Karst. *Scandinavian Journal of Forest Research*, 2, 157 – 166.
- Lambers, H. (1985). Respiration in intact tissue: its regulation and dependence on environmental factors, metabolism and invaded organisms. In R. Douce and D.A. Day (Eds.), *Higher plant cell respiration* (p. 418 – 473).
- Lambers, H., Freijssen, N., Poorter, H., Rose, T. and VanDerWerf, A. (1990). Analyses of growth based on net assimilation rate and nitrogen productivity: Their physiological background. In H. Lambers, M.L. Cambridge, H. Konings, and T.L. Pons (Eds.), *Causes and consequences of variation in growth rate and productivity of higher plants* (p. 1 – 18). SPB Academic Publishing, the Hague, the Netherlands. 363p.
- Lambers, M., Cambridge, L., Konings, H. and Pons, T.L. (Eds). *Variation in Growth Rate and Productivity* (p. 159 – 174). SPB Academic Publishing.

- Landsberg, J.J. and Gower, S.T. (1997). *Applications of Physiological Ecology to Forest Management*. San Diego: Academic Press.
- Lang, O.L., Zellner, H., Gebel, J., Schramel, P., Kostner, B. and Czygan, F.C. (1987). Photosynthetic capacity, chloroplast pigments, and mineral content of the previous year's spruce needles with and without the new flush: Analysis of the forest decline phenomenon of needle bleaching. *Oecologia*, *73*, 351 – 357.
- Lavoie, N., Vezina, L.P. and Margolis, H.A. (1992). Absorption and assimilation of nitrate and ammonium ions by jack pine seedlings. *Tree Physiology*, *11*, 171 – 183.
- Lehto, T. and Grace, J. (1994). Carbon balance of tropical tree seedlings: A comparison of two species. *New Phytologist*, *127*, 455 – 463.
- Leverenz, J.W. (1981). Photosynthesis and transpiration in large forest grown Douglas-fir: Interactions with apical control. *Canadian Journal of Botany*, *59*, 2568 – 2576.
- Magnani, F., Mencuccini, M. and Grace, J. (2000). Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. *Plant, Cell and Environment*, *23*, 251 – 263.
- Mäkelä, A. and Valentine, H.T. (2001). The ratio of NPP to GPP: Evidence of change over the course of stand development. *Tree Physiology*, *21*, 1015 – 1030.
- Margolis, H.A. and Vezina, L.P. (1988). Nitrate content, amino acid composition and growth of yellow birch seedlings in response to light and nitrogen source. *Tree Physiology*, *4*, 245 – 253.
- Margolis, H.A., Whitehead, O.R. and Kaufmann, M.R. (1995). Leaf area dynamics of conifer forests. In W.K. Smith and T.M. Hinckley (Eds.), *Ecophysiology of coniferous forests* (p. 181 – 223). San Diego: Academic Press.
- Matyssek, R. (1986). Carbon, water and nitrogen relations in evergreen and deciduous conifers. *Tree Physiology*, *2*, 177 – 187.
- McDowell, N.G., Phillips, N., Lunch, C., Bond, B.J. and Ryan, M.G. (2002). An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiology*, *22*: 763 – 774.
- Mencuccini, M. and Grace, J. (1996a). Developmental patterns of aboveground hydraulic conductance in a Scots pine (*Pinus sylvestris* L.) age sequence. *Plant, Cell and Environment*, *19*, 939 – 948.
- Mencuccini, M. and Grace, J. (1996b). Hydraulic conductance, light interception and needle nutrient concentration in Scots pine stands and their relation with net primary productivity. *Tree Physiology*, *16*, 459 – 468.
- Mencuccini, M. and Magnani, F. (2000). Comment on 'Hydraulic limitation of tree height: a critique' by Becker, Meinzer and Wullschlegler. *Functional Ecology*, *14*: 135 – 136.
- Mencuccini, M., Martínez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S. and Michiels, B. (2005). Size-mediated ageing reduces vigour in trees. *Ecology Letters*, *8*, 1183 – 1190.
- Mencuccini, M., Martínez-Vilalta, J., Hamid, H.A., Korakaki, E. and Vanderklein, D. (2007). Methodological considerations on the use of different metrics of tree growth in grafting studies. *Tree Physiology*, *27*, 463 – 473.
- Miller, P.M., Eddleman, L.E. and Miller, J.M. (1995). *Juniperus occidentalis* juvenile foliage: Advantages and disadvantages for a stress-tolerant, invasive conifer. *Canadian Journal of Forest Research*, *25*, 470 – 479.
- Pearcy, R.W., Bjorkman, O., Caldwell, M.M., Keeley, J.E., Monson, R.K. and Strain, B.R. (1987). Carbon gain by plants in natural environments. *Bioscience*, *37*, 21 – 29.
- Pennisi, E. (2005). Tree growth: The sky is not the limit. *Science*, *310*, 1896 – 1897.
- Peñuelas, P. (2005). A big issue for trees. *Nature*, *437*, 965 – 966.
- Rebbeck, J., Jensen, K.F. and Greenwood, M.S. (1993). Ozone effects on grafted mature and juvenile red spruce: Photosynthesis, stomatal conductance, and chlorophyll concentration. *Canadian Journal of Forest Research*, *23*, 450 – 456.
- Reich, P.B. and Schoettle, A.W. (1988). Role of phosphorus and nitrogen in whole plant carbon gain and nutrient use efficiency in eastern white pine. *Oecologia*, *77*, 25 – 33.

- Richardson, A.D., Berlyn, G.P., Ashton, P.M.S., Thadani, R. and Cameron, I.R. (2000). Foliage plasticity of hybrid spruce in relation to crown position and stand age. *Canadian Journal of Botany*, 78, 305 – 317.
- Ritchie, G.A. and Keeley, J.W. (1994). Maturation in Douglas-fir: I. Changes in stem, branch and foliage characteristics associated with ontogenetic aging. *Tree Physiology*, 14, 1245 – 1259.
- Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P. and Senock, R.S. (2004). An experimental test of the causes of forest growth decline with stand age. *Ecological Monographs*, 74, 393 – 414.
- Ryan, M.G., Binkley, D. and Fownes, J.H. (1997a). Age-related decline in forest productivity: Patterns and process. *Advances in Ecological Research*, 27, 213 – 256.
- Ryan, M.G., Hubbard, R.M., Pongracic, S., Raison, R.J. and McMurtrie, R.E. (1996). Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nutrient content. *Tree Physiology*, 16, 33 – 343.
- Ryan, M.G., Lavigne, M.B. and Gower, S.T. (1997b). Annual carbon costs of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *Journal of Geophysical Research*, 102, 28871 – 28883.
- Ryan, M.G. and Waring, R.H. (1992). Maintenance respiration and stand development in a subalpine lodgepole pine forest. *Ecology*, 73, 2100 – 2108.
- Ryan, M.G. and Yoder, B.J. (1997). Hydraulic limits to tree height and tree growth. *Bioscience*, 47, 235 – 242.
- Sarjala, T., Raitio, H. and Turkki, E.M. (1987). Nitrate metabolism in Scots pine seedlings during their first growing season. *Tree Physiology*, 3, 285 – 293.
- Schoettle, A.W. (1994). Influence of tree size on shoot structure and physiology of *Pinus contorta* and *Pinus aristata*. *Tree Physiology*, 14, 1055 – 1068.
- Steele, M.J., Coutts, M.P. and Yeoman, M.M. (1989). Developmental changes in Sitka spruce as indices of physiological age I. Changes in needle morphology. *New Phytologist*, 113, 367 – 375.
- Stitt, M. (1990). The flux of carbon between the chloroplast and cytoplasm. In D.T. Dennis and D.H. Turpin (Eds.), *Plant physiology and molecular biology* (Chap. 21. p. 309 – 326). England: Longman Scientific and Technical.
- Sweet, G.B. (1972). The effect of maturation on the growth and form of vegetative propagules of radiata pine. *New Zealand Journal of Forestry Science*, 3, 191 – 210.
- Takemoto, Y. and Greenwood, M.S. (1993). Maturation in larch: Age-related changes in xylem development in the long-shoot foliage and the main stem. *Tree Physiology*, 13, 253 – 26.
- Tyree, M.T. and Ewers, F.W. (1991). The hydraulic architecture of trees and other woody plants. *New Phytologist*, 119, 345 – 360.
- Vitousek, P.M., Matson, P.A. and van Cleve, K. (1989). Nitrogen availability and nitrification during succession: Primary, secondary, and old-field seres. *Plant Soil*, 115, 229 – 239.
- Weiner, J. and Thomas, D.C. (2001). The nature of tree growth and the 'age-related decline in forest production'. *Oikos*, 94, 374 – 376.
- West, G., Brown, J. and Enquist, B. (1999). A general model for the structure and allometry of plant vascular systems. *Nature*, 400, 664 – 667.
- Whittaker, R.H. (1975). *Communities and Ecosystems* (2nd ed.). New York: Macmillan.
- Yoda, K., Shinozaki, K., Ogawa, H., Hozumi, K. and Kira, T. (1965). Estimation of the total amount of respiration in woody organs of trees and forest communities. *Journal of Biology*, 16, 15 – 26.
- Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W. and Kaufmann, M.R. (1994). Evidence of reduced photosynthetic rates in old trees. *Forest Science*, 40, 513 – 527.