Age-Related Decline in Forest Productivity: Pattern and Process

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I. SUMMARY

An understanding of the pattern of forest growth is fundamental for determining the role of forests as sources and sinks in global carbon budgets. Such knowledge is also important for constructing mechanistic models of forest growth, for predicting the response of forests to changing climate, and for understanding the production and sustainability of commercial forests.

In even-aged forests, growth and biomass accumulation decline after reaching a peak (generally coinciding with the peak in stand leaf area) relatively early in a stand's life. The literature shows that this decline nearly always occurs, but the amount and timing of the decline vary. In general, more productive stands show an earlier peak growth and a steeper growth decline.

Initial work suggested that the fraction of assimilates available for wood production declined as woody biomass and respiration of the living cells increased. However, recent direct and indirect tests do not support this respiration hypothesis. Other potential causes include: (1) reduced photosynthesis because of the increasing hydraulic resistance of taller trees; (2) decreasing nutrient supply as a result of nutrient immobilization in living and decaying biomass, leading to lower leaf area, a shift in carbon allocation to root production, or reduced photosynthetic capacity; (3) reduced leaf area from abrasion in the crowns of taller trees with longer branches; (4) increased mortality of older trees; (5) physiological changes associated with changes in genetic expression (i.e, maturation of tissues); and (6) increased reproductive effort.

Reductions in wood production coincide with reductions in stand leaf area, and reduced leaf area is likely to be responsible for a portion of the age-related growth decline. Reduced growth efficiency (wood production per unit of leaf area) also coincides with growth decline and points to the existence of other mechanisms.

Foliage on older trees shows lower photosynthetic capacity and lower diurnal assimilation than foliage of younger trees. Either increased hydraulic resistance or reduced nutrient availability may decrease photosynthesis; current evidence supports the hydraulic mechanism. Allocation to fine roots may increase in older stands, but information is too limited for any general insights. While reduced leaf area, reduced photosynthesis, and increased fine-root allocation implicate reduced nutrient availability in older stands, the few available studies of nutrient availability show no clear trend of increasing or decreasing nutrient supply with stand age.

Juvenile and mature shoots differ in form and physiological behavior, and these differences generally cause grafted shoots from mature trees to grow less than those from juvenile trees. The bulk of maturational changes occur early in a tree's life, while declines in growth and growth efficiency occur in mature trees. Therefore, maturation may play only a limited role in age-

related growth decline. Reproductive effort may increase with increasing tree age, but reproduction is sporadic, and the carbon costs of reproduction appear to be only a small portion of annual assimilation.

A syndrome of changes in structure and function are associated with age-related growth decline, but reduced leaf area and reduced photosynthetic capacity appear to be the most consistent features of the pattern. The causes of these reductions need direct examination and experimentation.

II. INTRODUCTION

The growth of forests typically changes with forest age, reaching a peak relatively soon in stand development followed by a substantial decline. Foresters have long been interested in these changes because they affect the economies of wood production. More recently, issues of global carbon cycling have focused the attention of scientists from many fields on the carbon fluxes of forests and how these fluxes change with forest age. These age-related changes in forest growth (and C flux) are fundamental to discussions of whether tropical forests are net sources or sinks for C (Lugo and Brown, 1992), whether conversion of old-growth forests to young plantations will increase rates of C storage (Harmon *et al.*, 1990), and whether deposition of N will increase C storage in temperate forests (Kauppi *et al.*, 1992).

Biomass accumulation and growth of even-aged forests follows a universal pattern as the trees increase in size. Growth is slow initially, increases as leaf area develops, peaks as leaf area reaches its maximum, and then declines for the majority of the stand's life span (Figure 1). The pattern was first identified in studies of forest growth and yield (Assmann, 1970), but also from ecological studies (Forrest and Ovington, 1970; Turner and Long, 1975; Tadaki *et al.*, 1977; Gholz and Fisher, 1982; Long and Smith, 1992; Ryan and Waring, 1992). Mechanisms responsible for early growth and the growth peak may be well understood, but there is a lack of agreement about the cause of growth decline.

While much of the research in forestry and forest ecology has focused on aggrading forests, forests change in structure (Spies and Franklin, 1991) and function (Grier *et al.*, 1981; Yoder *et al.*, 1994) after dry matter production and leaf area reach their peak. Understanding why growth declines after reaching a peak is important for several reasons. First, mechanistic models of forest production require knowledge of changes in leaf area, nutrition, carbon allocation, and physiology to predict forest growth and function in varied environments (Ryan *et al.*, 1996b). These models are an important tool for assessing the role of forests as terrestrial carbon sources and sinks in the global carbon budget and for understanding the response of forests (and terrestrial carbon storage) to global changes in climate and atmospheric CO_2. Second, regional or global estimates of forest productivity may be possible

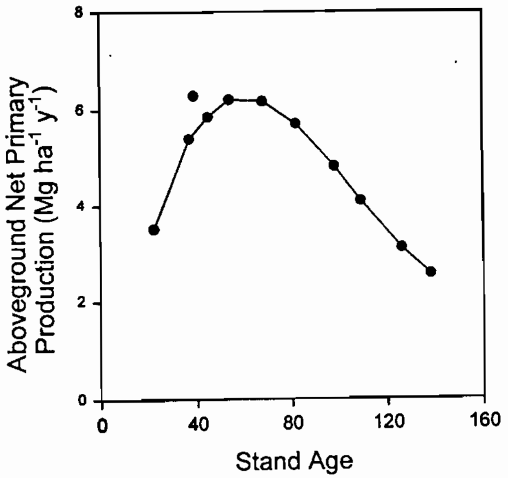

Fig. 1. Growth of *Picea abies* with stand age. Stands were in the vicinity of Karelia, USSR (62°N 34°E). Growing season length was 150 days, mean temperature during the growing season was 11.9°C, and growing season precipitation was 380 mm. From data in DeAngelis *et al.* (1980).

using remotely-sensed estimates of leaf area and climate coupled to models that estimate the efficiency of the conversion of absorbed energy to biomass (Landsberg *et al.*, 1996). Conversion efficiency varies with forest age, and understanding this variation will be vital for the success of these models. Third, because of their slower growth, older forests may be more susceptible to insects and pathogens (Waring, 1987), and may respond differently to changes in climate (Ryan *et al.*, 1996c). Finally, growth decline may be linked with the sustainability of commercial forest production (Murty *et al.*, 1996).

In this review, we re-examine the evidence for the pattern of growth decline with age and summarize the evidence for the mechanisms that may be responsible. We start with an overview of the proposed mechanisms. We then present a framework for understanding the changes in stand productivity with age, because many of the proposed mechanisms are linked and affect carbon allocation. We present the available information on the importance of various mechanisms behind growth decline, in the context of the stand carbon cycle. We conclude with suggestions for experiments that can distinguish among alternative hypotheses.

III. CAUSES OF DECLINING PRODUCTIVITY AS FORESTS AGE

The changes in productivity over time in a forest must derive from changes in components of:

$$NPP = \sum_{i=1}^{n} \varepsilon_i P_i S_i - R \qquad (1)$$

where NPP is net primary production, S_i is the supply rate of a required resource (light, nutrients, water), P_i is the proportion of S_i obtained, ε_i is the conversion efficiency for the resource, and R is respiration (Scurlock *et al.* 1985). Changes in NPP and stem growth may derive from a variety of processes that underlie the production equation, including changes in nutrient supplies, allocation among tree tissues, and stand structure; the hydraulic resistance to water flow through stems; and perhaps some genetic limitation of the physiology of older individuals.

The decline in growth rates as forests age has been commonly attributed to a changing balance between photosynthesis and respiration (Yoda *et al.*, 1965; Whittaker and Woodwell, 1967). This hypothesis argues that leaf area will reach a plateau (limited by light, water, and nutrient supply), stand photosynthesis will remain constant (because of constant leaf area), but respiration will continue to increase as respiring biomass accumulates. Although the photosynthesis/respiration explanation of this pattern has received almost no verification for forest ecosystems, it is accepted almost as universally as the pattern itself (Kramer and Kozlowski, 1979; Waring and Schlesinger, 1985; Aber and Melillo, 1991; Oliver and Larson, 1996).

The focus on respiration as the key to growth declines assumed that the first three components of the production equation (supply of resources, acquisition of resources, and efficiency of resource use) remained constant as trees grew larger, leaving only respiration to balance observed declines in net primary production or stem growth. This argument can be traced back to early ecosystem research when woody biomass was found to be many times larger than leaf biomass. Respiration was thought to be a major fraction of gross primary production (60–65% according to Möller *et al.*, 1954; Yoda *et al.*, 1965), and later dimension analysis clearly showed that woody biomass and wood surface area increased much faster than leaf area per tree or stand (Whittaker and Woodwell, 1967).

Recent evidence does not support increasing respiration as the cause of growth decline. Careful estimates of woody-tissue respiration for a chronosequence of lodgepole pine stands suggested that increased maintenance respiration in older stands was too small to account for decreased growth rate. In fact, decreases in growth respiration resulted in lower total stem respiration in the oldest stand (Ryan and Waring, 1992). In addition, S.T. Gower *et al.* (unpublished data) found that woody-tissue maintenance respiration was similar across a chronosequence in a temperate deciduous forest. Indirect evidence against the respiration hypothesis has come from growth analysis of spacing studies, where trees at wider spacings continued to accelerate in growth rate while supporting higher wood:leaf ratios than closer spacings already in growth decline (Fownes and Harrington, 1990; Harrington and Fownes, 1996).

A variety of other explanations are possible, and several may be more consistent with available information:

(1) *Increased hydraulic resistance*. The total hydraulic resistance between the soil and leaves increases as trees grow taller (Mattson-Djos, 1981; Yoder *et al.*, 1994; Mencuccini and Graces, 1996) and branches lengthen (Waring and Silvester, 1994; Walcroft *et al.*, 1996). Increased resistance may force closure of stomata earlier in the day or earlier in a drought cycle (to prevent cavitation in xylem) and lower time-integrated photosynthesis (Yoder *et al.*, 1994; Ryan and Yoder, 1996).

(2) *Decreased nutrient supply*. The supply of nutrients from the soil may decline as available nutrients accumulate in biomass (Binkley *et al.*, 1995; Schulze *et al.*, 1995) or become immobilized during the decomposition of wood (Murty *et al.*, 1996; Gower *et al.* 1996a). Reduced nutrient supply can lower photosynthetic capacity (Waring and Schlesinger, 1985) and leaf area (Gower *et al.*, 1992, 1995, 1996b) and increase carbon allocation to fine roots (Gower *et al.*, 1995), all of which reduce carbon available for wood growth.

(3) *Reduced leaf area caused by crown abrasion*. Crown interaction increases with tree height, and such interaction may increase gaps between crowns and stand lower leaf area (Putz *et al.*, 1984; Long and Smith, 1992).

(4) *Increased mortality of older trees*. If the mortality of individuals increased after stand leaf area reached peak, net biomass production of the stand would decrease even if the growth of surviving trees was unaffected.

(5) *Increased reproductive effort*. The carbon costs of reproduction can be up to 15% of that of annual wood growth (Linder and Troeng, 1981). If seed production increases with tree age, the increased carbon sink might lower the carbon available for wood production.

(6) *Genetic changes with meristem age*. Genetic expression may change as tissue ages and the number of cell divisions increases (Greenwood and Hutchinson, 1993). These changes in 'maturation' may slow growth in both height and diameter.

The current paradigm that respiration accounts for declining production in older forests has rarely been tested, but the available evidence indicates that respiration changes probably account for only a small portion of the decline in growth (Ryan and Waring, 1992). Management of forests for wood production is often based on expected rates of productivity, and expectations of changes in those rates with stand age. If the decline in growth in older forests results from respiration increases or maturation, then the decline may be unavoidable unless tree genetics are changed. If the decline depends in part on changes in soil nutrient supply, then management activities that increase or decrease soil nutrient supply could substantially alter forest production, optimal rotation ages, and other aspects of stand management. Further, the response of existing forests to changing climate or increased nitrogen deposition may depend strongly on which components dominate the pattern of declining productivity with age. Rates of photosynthesis, respiration and soil nutrient mineralization are interdependent, but respond differently to changes in temperature, and soil moisture. Accurate predictions of forest responses to changing climate will require a functional understanding of the causes of declining forest growth in older stands.

IV. EMPIRICAL EVIDENCE FOR CHANGES IN STAND GROWTH

That growth declines in the latter stages of the life of a forest is a general principle in forestry. However, a systematic examination of the data to support growth decline and to identify mechanisms is lacking. In this section, we examine evidence for growth decline in studies of forest growth and yield, in ecological studies of forest production, and in ecological studies of individual trees.

A. Growth and Yield Studies

The classic pattern of stand growth decline was first identified in early studies of forest growth (see Assmann, 1970, for background). These 'growth and yield' studies used measurements of biomass in chronosequences of forest stands, together with the past growth of individual trees, to estimate standing biomass and growth of ideal stands under a variety of growing conditions. In our small survey of growth and yield studies, net growth rate measured between 30 and 100 years after the peak was, on average, 57% of the peak rate (Table 1; range = 19–100%). In another study, Grier *et al.* (1989) summarized biomass and growth information for 75 second-growth forests of Douglas-fir in the Pacific Northwest U.S. They concluded that biomass increment increases sharply during the first 20 years of stand development, then drops by 20–50% in the next 20 years, reaching a sustained level for the next 60 years.

Because tree height growth peaks earlier and declines more rapidly on higher-quality sites (Beck, 1971), we expected that biomass growth would also decline more rapidly on sites with higher quality. This pattern was found in four of the eight studies we examined (*Betula papyrifera*, *Pinus banksiana*, *Pinus ponderosa*, *Populus tremuloides*). In other studies, the rate of growth decline was unaffected by site quality (*Picea mariana*), increased with site quality (*Pinus contorta* var *latifolia*), or varied with site quality, but showed no consistent pattern (*Quercus alba*).

Table 1
Growth decline and site quality in forestry growth-and-yield studies

Species	Age at maximum Growth (year)	Reference age[1] (year)	Growth at reference age (% of peak growth)		Reference
			High site quality	Low site quality	
Betula papyrifera	55	90	19	62	Gregory and Haack (1965)
Picea mariana	70	110	24	24	Perala (1971)
Pinus banksiana	30	60	85	69	Rudolph and Laidly (1990)
Pinus contorta var. *latifolia*	30	110	71	28	Dahms (1964)
Pinus ponderosa	25	125	24	33	Meyer (1938)
Populus tremuloides (Lake States)	30	60	86	92	Perala (1977)
Populus tremuloides (Alaska)	40	90	100	100	Gregory and Haack (1965)
Quercus alba	30	60	48	50	Gingrich (1971)

[1] Age when a medium-quality site would be harvested under normal management. Further declines in growth occurred in all studies except *Populus tremuloides* (Alaska).

Yield tables are typically constructed using data from relatively few stands and are very subjective (Meyer, 1938). In these studies, growth is estimated from differences in accumulated biomass in different stands and not measured directly. Nonetheless, yield tables based on forest stand data overwhelmingly show that woody biomass accumulation slows as stands age.

Silvicultural studies of spacing and thinning effects are other sources of information on the pattern and controls of growth decline. Generally, the peak and decline in annual volume increment follows canopy closure (Evans, 1982) and occurs sooner at higher tree densities (Harrington and Fownes, 1996). Coppice stands, having many shoots per stump, may peak in biomass accumulation in one year or less under favorable year-round growing conditions (Harrington and Fownes, 1993). These and other plantation studies (Dudley 1990) support the universality of the pattern of peak and decline in even-aged stand growth.

B. Ecological Studies

A survey of chronosequence studies (Table 2, Figure 2) shows that wood production for all stands declines after reaching its peak coinciding with the peak in stand leaf area. Wood production at the end of the studied chronosequence was lower than 50% of peak for eight of the 12 studies (Table 2).

In section VI.A, we show that the declines in wood production often coincide with reductions in stand leaf area, and also that declining leaf area is normal as stands age. Because reduced leaf area will lower carbon assimilation, we wondered if the declines in wood production were solely caused by reduced leaf area. The influence of leaf area on production can be assessed by estimating the growth efficiency (Waring, 1983), or wood production per unit leaf area. If growth efficiency declines with stand age, then the reduction in wood growth exceeds the reduction in leaf area. Also, because light absorption varies exponentially with leaf area, marginal reductions in leaf area may actually improve growth efficiency. For 10 of the 12 chronosequences surveyed (the exceptions were *Pinus elliottii* and *Pinus radiata*), growth efficiency was lower at the end of the chronosequence than when the stand had maximum leaf area (Figure 3). For *Larix gmelinii* and *Eucalyptus grandis* (good site), the peak in growth efficiency did not coincide with the peak in stand leaf area. In high-density stands of fast-growing tropical trees, growth efficiency declined continuously with stand leaf area at leaf area indices above 1.0, both before and after peak biomass growth (Fownes and Harrington, 1990; Harrington and Fownes, 1996). These declines in growth efficiency convincingly show that reduced leaf area is not solely responsible for declines in wood production.

Table 2

Chronosequence studies: length of chronosequence, age at maximum leaf area, maximum leaf area or leaf biomass, and maximum annual above-ground wood production

Species	Range of chronosequence (years)	Age at maximum leaf area (years)	Peak leaf area (m^2 m^{-2})	Peak leaf biomass (Mg ha^{-1}))	Peak annual above-ground wood production	Reference
Abies balsamea	5–60	20		15.5	4.9 Mg ha^{-1}	Sprugel (1984)
Abies veitchii	3–127	37		6.8	6.2 Mg ha^{-1}	Tadaki *et al.* (1977)
Eucalyptus grandis (good site)	1–6	3.1		8.5	23.5 Mg ha^{-1}	Reis *et al.* (1985)
Eucalyptus grandis (poor site)	2–6	2.7		4.2	5.5 Mg ha^{-1}	Reis *et al.* (1987)
Eucalyptus regnans	50–230	50	3.4			Dunn and Connor (1993)
Larix gmelinii	49–380	49		4.3	3.3 mol m^{-2}	Schulze *et al.* (1995)
Picea abies	22–138	68	3.8		6.3[1] Mg ha^{-1}	DeAngelis *et al.* (1980)
Pinus contorta var. *latifolia* (Colorado)	40–245	40	3.8		168 g C m^{-2}	Ryan and Waring (1992)
Pinus contorta var. *latifolia* (Wyoming)	10–120	35	4.0		9.5 m^3 ha^{-1}	Long and Smith (1992)
Pinus elliottii	3–34	14		5.7	6.5 Mg ha^{-1}	Gholz and Fisher (1982)
Pinus radiata	3–12	7		11.6	17.6 Mg ha^{-1}	Forrest and Ovington (1970)
Pinus taeda	10–60	30		4.6	7.3 Mg ha^{-1}	Switzer *et al.* (1966)
Prunus pennylvanica	1–14	6	3.1		16.6[1] Mg ha^{-1}	Marks (1974)

[1] Above-ground net primary production (includes foliage production of <25% of total).

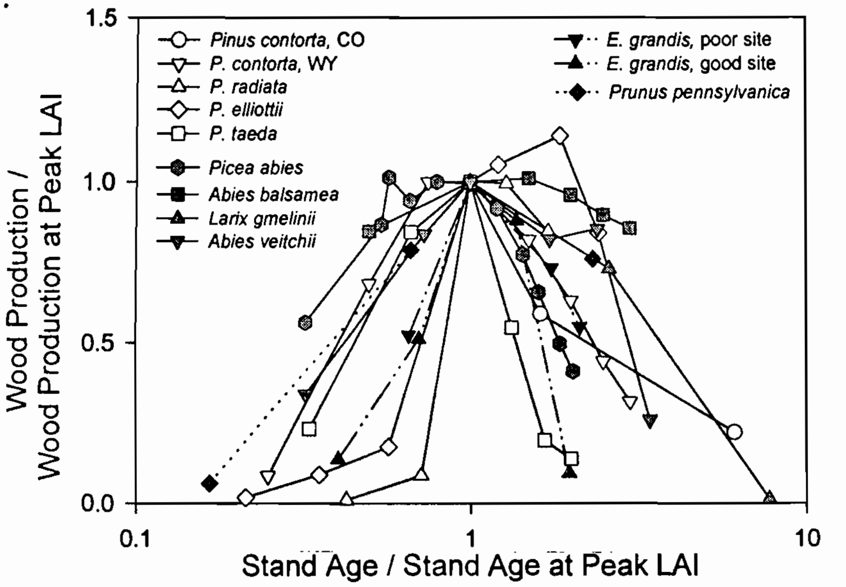

Fig. 2. Wood production relative to wood production when the stand had maximum leaf area plotted against stand age divided by stand age at stand maximum leaf area for 12 chronosequence studies. Actual values of wood production, length of the chronosequence, tree age at peak stand leaf area, and references for the chronosequence studies are given in Table 2.

C. Individual Trees

Comparing the growth of trees of different ages and sizes is difficult because larger trees have more leaf area, larger root mass, and generally produce more wood than smaller trees. Comparing growth efficiencies removes the effect of tree size. Kaufmann and Ryan (1986) found that growth efficiency of individual subalpine conifer trees declined with age in *Pinus contorta* var. *latifolia*, *Picea engelmannii*, and *Abies lasiocarpa*. Of the three species, *Pinus contorta* had the highest growth efficiency when young, but showed the greatest decline with age. Yoder *et al.* (1994) also found substantially lower growth efficiency in older *Pinus ponderosa* compared with adjacent younger trees.

D. Conclusions

We conclude that strong evidence exists (from both the forestry and ecological literature) for a decline in wood production relatively early in the development of stands. The decline in wood production coincides with a decline in leaf area, but concurrent declines in growth efficiency show that leaf area is not solely responsible for declining wood production. The timing and magnitude of declines in growth and growth efficiency vary widely, as may the processes underlying these changes.

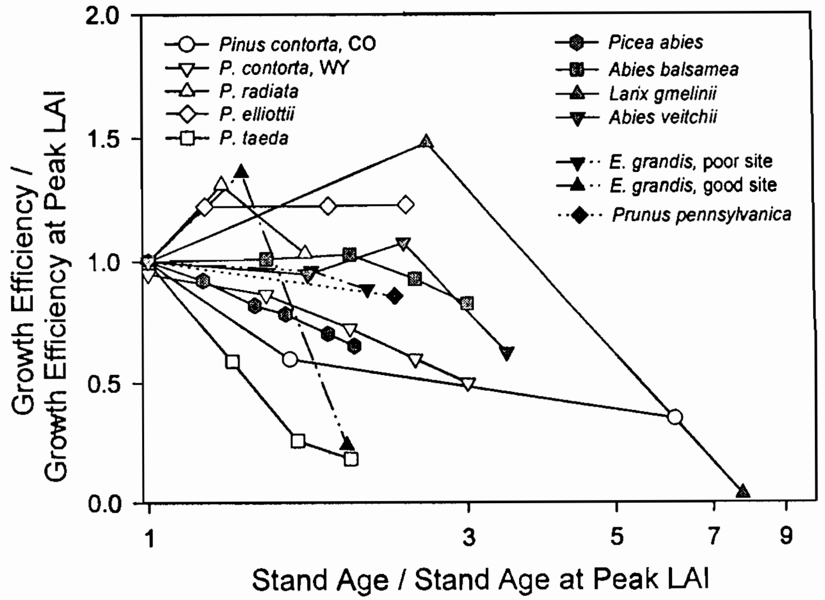

Fig. 3. Growth efficiency relative to growth efficiency when the stand had maximum leaf area plotted against stand age divided by stand age at stand maximum leaf area for 12 chronosequence studies. Only values after the stand reached maximum leaf area are plotted. Actual values of leaf area or biomass, wood production, length of the chronosequence, tree age at peak stand leaf area, and references for the chronosequence studies are given in Table 2.

V. CONTROLS OF BIOMASS PRODUCTION

In sections VI–X, we discuss the changes in function and structure that occur with forest stand development. Although we focus on specific processes, such as photosynthesis, nutrient supply, and respiration, we recognize that the processes are linked and can change in concert. To put these linkages in perspective, we briefly review the carbon cycle and its controls (Figure 4; see also Cannell, 1989; Cannell and Dewar, 1994; Waring and Ryan, 1995).

The ability to capture and use solar energy determines the amount of photosynthesis and plant carbon gain. Leaf area supplies the surface to absorb radiation, and leaf protein content, plant water status, and climate

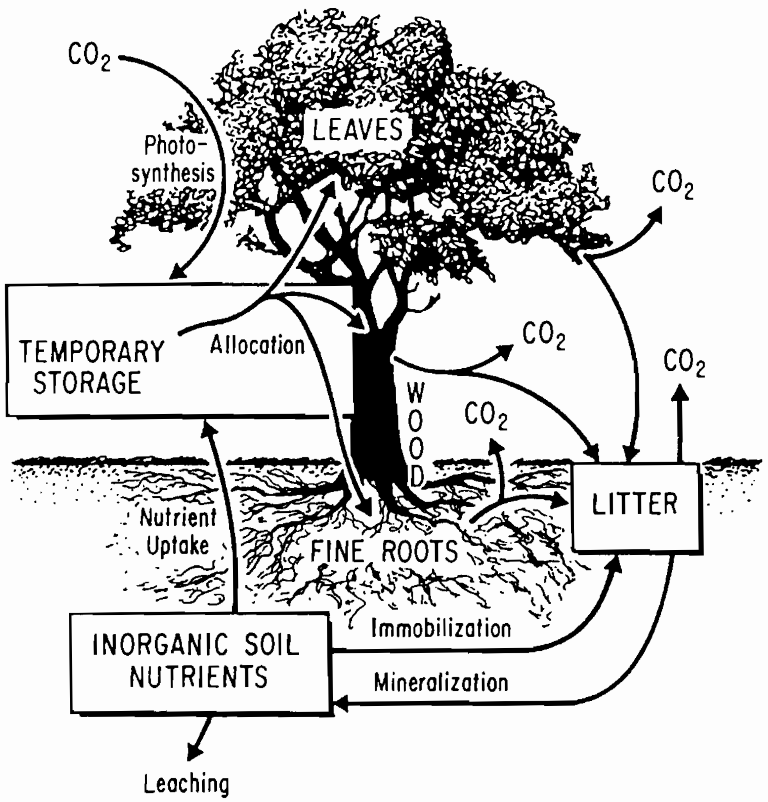

Fig. 4. Carbon balance of a forest ecosystem.

(temperature and humidity) largely determine the rate of photosynthesis. Maintaining existing cells and supporting growth of new cells requires energy, and a large portion of the energy fixed in photosynthesis is lost to respiration. Biomass production, therefore, results from the balance between photosynthesis and respiration. Only a small portion of the energy incident upon leaves is converted into sugars and then to biomass. For forests, 1 MJ of absorbed photosynthetically active radiation yields 1 g biomass, an efficiency of about 1.8% (Harrington and Fownes, 1995; Landsberg *et al.*, 1996). Of the carbon fixed in photosynthesis in forests, roughly 50–70% is lost to respiration of foliage, woody tissue, and fine roots and associated symbionts (Ryan, 1991).

The carbon remaining after respiration can be allocated to support (coarse roots, stemwood, branches), light capture (leaves), nutrient uptake (fine roots, root exudates, mycorrhizas), reproduction (seeds and fruiting structures), and storage (carbohydrates in ray parenchyma cells, fine roots and foliage).

Storage and reproduction may be qualitatively different than 'utilization sinks', such as tissue growth (Cannell and Dewar, 1994). The structural parts of a tree are interdependent; for example, leaves require water and nutrients from roots and a conducting system to supply them. Allocation is constrained by this functional interdependence so that plant parts are maintained in balance.

Carbon allocation is poorly understood, particularly in woody plants where storage and structure are large (Cannell and Dewar, 1994). Most of the attention of modellers has focused on root:shoot partitioning, and mechanistically based models can reproduce observed responses (Thornley, 1972a, b). The mechanistic approach assumes that relative growth of a sink (roots, shoots, cambium) is co-limited by carbon and nitrogen concentrations at the point of phloem unloading. Differential allocation occurs because the carbon and nitrogen concentrations at the shoot or root are a function of the supply rate (e.g., photosynthesis) and transport resistance. The mechanistic approach has been extended to trees with wood growth treated similarly to roots and shoots (Rastetter *et al.*, 1991; Thornley, 1991; Thornley and Cannell, 1992).

Other models (FOREST-BGC; Running and Gower, 1991) use a priority approach, where foliage and fine roots have the highest priority for carbon and wood production has the lowest priority for fixed carbon (Waring and Pitman, 1985; Oliver and Larson, 1996). Wood production might also be regulated by the structural requirements of supporting the canopy and transpirational demand (Cannell and Dewar, 1994). Wood production is a large fraction of net above-ground production (e.g., 80% in *Pinus radiata*; Ryan *et al.*, 1996a), but a relatively small portion of annual photosynthesis (e.g., 15–30% in *Pinus radiata*; Ryan *et al.*, 1996a). Changes in photosynthesis, respiration, or allocation could all potentially alter wood production.

The carbon cycle is strongly linked to water and nutrient cycles and any change in soil moisture or nutrition with forest development will likely alter both carbon uptake and allocation. Water and nutrient availability largely control leaf area and leaf photosynthetic capacity, and climate controls the soil moisture, temperature, and atmospheric humidity whic constrain photosynthesis. In addition to influencing carbon acquisition, nutrition can also alter carbon allocation by promoting changes in fine root biomass or turnover. Given the small fraction of the carbon budget used for wood production, many processes could interact to yield lower wood production with stand development.

VI. CHANGES IN PHOTOSYNTHESIS WITH STAND DEVELOPMENT

If photosynthesis declines as trees and stands develop, and the carbon costs of respiration and root and foliage production remain constant, wood production will also decline. Three mechanisms could lower photosynthesis in older trees and stands: (1) reduced leaf area, (2) reduced photosynthetic capacity, and (3) reduced photosynthetic performance. With lower leaf area, less surface area is available to absorb energy and fix carbon. Photosynthetic capacity controls the amount of carbon fixed per unit of light absorbed, so a lowered capacity will yield less carbon fixed under the same light regime. Photosynthetic 'performance' is the diurnal integration of photosynthesis for a leaf. Leaf area and photosynthetic capacity may be similar for leaves on young and old trees, but the leaves might show different patterns of assimilation if the soil to leaf hydraulic pathways differ. Photosynthesis is strongly linked with nutrition (because nutrition may control leaf area and photosynthetic capacity) and with respiration (because foliage respiration and photosynthetic capacity are coupled, and because the balance between photosynthesis and respiration determines dry matter production).

A. Reduced Leaf Area

Kira and Shidei (1967) defined the model of growth of leaf area after forest establishment for even-aged stands; a similar pattern was found in a model analysis of hardwood succession (Bormann and Likens, 1979). Leaf area develops slowly as stems build supporting structure and plant canopies occupy available space. Leaf area peaks relatively early in the life of a stand at a level greater than the final equilibrium value. In hardwood succession, the initial peak may result from co-existance of early-successional, short-lived species before full establishment of shade-tolerant, longer-lived species (Covington and Aber, 1980). In even-aged stands, a lower leaf area at equilibrium than at peak may result from crown abrasion in taller trees or intense competition. At equilibrium leaf area, mortality is matched by growth of new trees or crown expansion of existing trees.

Leaf-area data from chronosequence and monitored plots often shows a pattern that differs from the concept presented above. For example, most developing forests show a gradual, persistent decline after reaching a peak relatively early in the life of a stand, rather than a rapid post-peak decline in leaf area followed by equilibrium (Figure 5). Even though forests differ greatly in growth rates and peak leaf biomass, nearly all of the chronosequences in Figure 5 show a remarkably consistent *relative* pattern in leaf area development and decline. *Eucalyptus* and *Pinus radiata* (selected for commercial use) build leaf area very rapidly compared with other species, but leaf area also declines relatively more rapidly.

Decline in leaf area with stand development appears to be the rule, and equilibrium leaf area the exception. Of the 13 chronosequences plotted, only one (*Abies balsamea:* Sprugel, 1984) maintained relatively constant leaf area after reaching the peak. Another exception appears to be high-density stands of tropical trees, which decline in stand biomass growth without a decrease in stand leaf area (Harrington and Fownes, 1993, 1996). Extensive analysis of woody biomass and leaf area allometry rule out the possibility that these findings resulted from inappropriate extrapolation of leaf area equations (Fownes and Harrington, 1992; Harrington and Fownes, 1993), which could explain the lack of leaf area decline in some other studies (Fownes and Harrington, 1990).

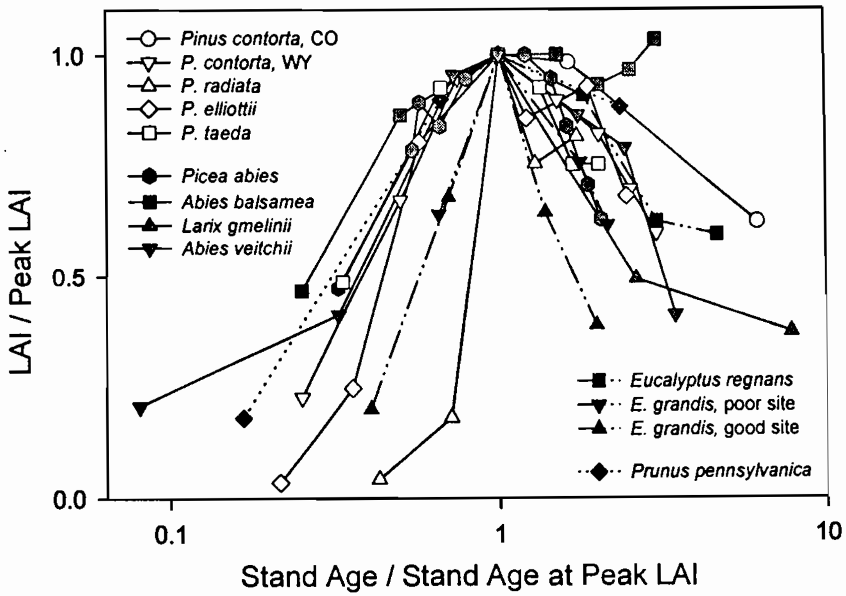

Fig. 5. Stand leaf area or biomass relative to maximum stand leaf area or biomass plotted against stand age divided by stand age at stand maximum leaf area for 13 chronosequence studies. Actual values of leaf area or biomass, wood production, length of the chronosequence, tree age at peak stand leaf area, and references for the chronosequence studies are given in Table 2.

A decline in leaf area through time will lower photosynthesis, decrease litterfall, increase light in the understory, and perhaps alter the understory microclimate. Because the relationship between leaf area and energy absorption is nonlinear, carbon fixation would not be expected to decline at the same rate as the decline in leaf area. For example, if a forest has a peak leaf area index of 4 (e.g., 40-yr-old lodgepole pine), a 25% decrease in leaf area may yield only a 9% decline in absorbed radiation (Ryan and Waring, 1992) if the light extinction coefficient remains constant. Increased radiation in the understory could increase the growth of understory plants that may compete with the trees for water and nutrients. Altered litter inputs and microclimate could affect decomposition and nutrient availability.

Three mechanisms could lower leaf area in a stand after the leaf area peak: altered nutrition, increased mechanical abrasion of crowns, and mortality – either as increased death of individuals or lack of replacement of dead individuals by new seedlings.

Several studies have shown that nutrient availability can fall in the late stages of the life of an even-aged stand (Grier *et al.*, 1981; Binkley *et al.*, 1995; Schulze *et al.*, 1995). Nutrient availability may decline if nutrient capital becomes bound in vegetation (primarily in wood) and unavailable for new growth (Schulze *et al.*, 1995). Because ratios of carbon to nutrients in woody tissues are much higher than in soil organic matter (> 200 versus 20–30), decomposition of woody litter (more common in the latter stages of a stand's life) will immobilize nutrients (Murty *et al.*, 1996).

Leaf area and nutrient availability are tightly linked (Nadelhoffer *et al.*, 1985; Gower *et al.*, 1992, 1995; Herbert and Fownes, 1995), but the precise mechanism is less clear. Reduced nitrogen availability generally increases allocation below-ground which increases the tree's ability to acquire nutrients (Gower *et al.*, 1995). Poor nutrient availability may also lower concentrations of photosynthetic enzymes in foliage which would lower photosynthetic capacity and annual carbon fixation. As carbon fixation declines or the carbon that is fixed is allocated to root production, less carbon may be available to build new foliage.

As tree height increases, crown interaction increases because the arc described by the top of a crown moving in the wind is larger. The resultant mechanical abrasion will prune crowns so that their shape becomes narrower and the gaps in between crowns widens (Putz *et al.*, 1984; Long and Smith, 1992). Foliage depth may be greater as gaps form between crowns, but increasing crown length may not compensate for the foliage lost in gap creation (Long and Smith, 1992). We speculate that crown abrasion may be a larger factor in sparser canopies because denser canopies should lessen the force of wind on individual trees.

A third possibility for explaining reductions in leaf area for an ageing stand is mortality coupled with a lack of replacement. In the earlier stages of stand development, survivors can occupy the space vacated by the death of a neighbor by increasing their crown radius. As trees grow larger, death may result in gaps so large that mechanical constraints on branch length prevent trees from fully exploiting the newly available resources. Seedlings may take many years to develop leaf area and reach the canopy in gaps. These unfilled gaps will lower stand leaf area.

B. Reduced Photosynthetic Capacity

Few studies have compared gas exchange in young and old trees, but those studies suggest that photosynthetic capacity or foliar nitrogen content (closely related to photosynthetic capacity; Field and Mooney, 1986) are often lower in foliage from old trees. Schoettle (1994) found that old bristlecone pine (*Pinus aristala*) trees had lower photosynthetic capacity, stomatal conductance, and foliar nitrogen in 1-year-old foliage than in young trees. For sequoia (*Sequoiadendron giganteum*), Grulke and Miller (1994) found declines in maximum assimilation, dark respiration, stomatal conductance, and the ratio of intercellular to ambient CO_2 concentration on same-aged foliage from tree ages of < 1 to 2000 years. Kull and Koppel (1987) also found lower photosynthesis in Norway spruce (*Picea abies*) foliage from older trees, accompanied by lower foliar nitrogen content.

With a reduced photosynthetic capacity, older forests will fix less carbon per unit of light absorbed. Litter quality may also be poorer, and litter with a high C:N ratio may immobilize more nitrogen as it decomposes. Lower nitrogen availability may promote lower foliar nitrogen and further decrease photosynthetic capacity. Lower photosynthetic capacity could therefore initiate positive feedback that will continue to force itself downward. This hypothesis has not been tested experimentally, and the mechanism for initiating reduced photosynthetic capacity remains unknown. We note, however, that differences in litter quality within species have not been demonstrated to influence nutrient supply (Prescott, 1995).

C. Reduced Photosynthetic Performance

Foliage from young and old trees can have similar maximum photosynthesis rates but a different diurnal pattern of photosynthesis. For example, Yoder *et al.* (1994) observed that the diurnal pattern of photosynthesis differed between same-aged foliage from young and old trees in two species of conifers (Figure 6). The differences in photosynthesis did not appear to be caused by differences in photosynthetic capacity because foliar nitrogen contents and peak photosynthesis rates were similar. However, stomata on the needles from old trees closed earlier in the day, leading to a lower diurnal total carbon assimilation. Fredericksen *et al.* (1996) found that the diurnal pattern of photosynthesis also differed between foliage from young and old cherry (*Prunus serotina*) trees.

Differences in water use or carbon fixation between young and old strands have also been measured. In a study of 40- and 140-year-old Norway spruce, whole-tree sapflow measurements showed that transpiration was about 25% lower for the older trees in dry air (Tenhunen *et al.*, 1996). These differences between individual young and old trees scale to substantial differences at the stand level and are even more striking because the leaf area was about 50% greater in the older stand. The lower transpiration and higher leaf area in the old forest indicate a lower stomatal conductance. If stomatal conductance is lower, photosynthesis will also be lower. Another recent study (Sellers *et al.*,

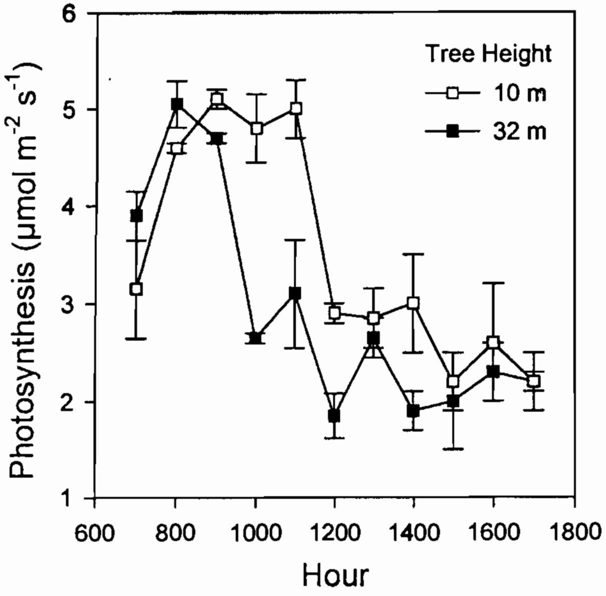

Fig. 6. Diurnal pattern of photosynthesis of 1-year-old foliage from 55-year-old (10 m tall) and 229-year-old (32 m tall) *Pinus ponderosa* foliage from the upper one-third of the canopy. Redrawn from Yoder *et al.* (1994).

1995) compared eddy-correlation measurements of CO_2 and energy fluxes between young and old *Pinus banksiana* forests in northern Canada. Preliminary results from this study indicate that midday net CO_2 uptake and latent energy loss (i.e., transpiration for a dry canopy) were consistently higher for the young stand. Again, the older stand had higher leaf area, suggesting that the flux differences resulted from differences in photosynthetic performance or capacity.

Yoder *et al.* (1994) speculated that differences in photosynthetic performance between young and old trees might be caused by increased hydraulic resistance in taller trees with longer branches. The link between stomatal conductance and the hydraulic resistance of a tree's vascular system has been demonstrated (Sperry *et al.*, 1993; Whitehead *et al.*, 1996) and there is evidence that hydraulic resistance increases with height (Yoder *et al.*, 1994) and branch length (Waring and Silvester, 1994). Sperry and colleagues (Sperry and Pockman, 1993; Sperry *et al.*, 1993; Sperry, 1995) showed that stomata will close to maintain leaf water potential above a level that would cause irreversible cavitation in xylem. Experimental increases in hydraulic resistance have induced stomatal closure without affecting leaf water potential (Sperry and Pockman, 1993). These lines of evidence indicate that stomata may close

to restrict transpiration, not simply in response to dry air (see Monteith, 1995). Photosynthesis declines as stomata close (Ball *et al.*, 1987), so any diurnal reduction in stomatal opening caused by a hydraulic limitation in the vascular system decreases daily carbon assimilation by the canopy.

Hydraulic limitation could contribute to the slowing of the growth of individual trees as size increases. Hydraulic resistance increases with the overall path length (height of tree and length of branches) and decreases as the permeability of the sapwood increases. As a tree grows, hydraulic resistance increases as the tree gains height and branches lengthen (Mattson-Djos, 1981; Mencuccini and Grace, 1996). Because of the link between hydraulic resistance and stomatal opening, and the link between stomatal opening and photosynthesis, a larger hydraulic resistance will likely promote different diurnal and perhaps different seasonal patterns of carbon assimilation – patterns that result in lower total assimilation. If foliage on older trees photosynthesizes less, wood growth will be lower because the other carbon costs (respiration, foliage production, root growth) are similar to or slightly greater than those in younger trees (Ryan and Waring, 1992).

Hydraulic limitation also suggests a positive feedback that could ultimately limit tree height: if trees lose a portion of sapwood each year (to heartwood formation) and less new xylem is built as trees gain height (because less carbon is fixed), sapwood permeability and the effective conducting area of sapwood will be reduced. Therefore, the hydraulic resistance might progressively deteriorate to slow and ultimately stop vertical growth. We can speculate that reduced diurnal photosynthesis near the tops and branch tips of older trees promotes reduced allocation of nitrogen to that foliage and lower photosynthetic capacity.

D. Conclusions

In general, increases in the size and age of trees and stands lead to a syndrome of changes that tend to reduce carbon assimilation. At the stand level, leaf area decreases after reaching a peak rather early in a stand's life, leading to less light absorption and lower photosynthesis. At the tree level, leaf area may still increase as trees grow in size, but photosynthetic capacity or performance may decrease. These changes in photosynthesis result in less carbon being available for wood production.

VII. CHANGES IN NUTRIENT SUPPLY

Larger forests tend to have more nutrients accumulated in biomass and many case studies have documented that the rate of increase in nutrient storage in biomass decreases in older stands. For example, Pearson *et al.* (1987) showed that accumulation rates for nitrogen and other nutrients peaked near the time of peak stemwood increment and then declined. The declining rate of accumulation of nutrients in older forests could result from a declining ability to use the nutrients, or from a declining nutrient supply.

Nutrients are most usually available at the initiation of an even-aged stand because of reduced plant uptake, soil disturbance, or fertilizer application (Binkley, 1986). Soils may also be warmer (from increased insolation) and wetter (from decreased interception and transpiration) early in stand development, favoring microbial activity. In addition, litter inputs are decreased, therefore decreasing the microbial immobilization of N and resulting in less competition between trees and microbes for available soil N. Nutrient availability may decline with stand age as soils become cooler and drier, heterotrophic microbes compete more effectively with trees for nutrients, and nutrients become increasingly stored in the heartwood of live trees, in dead trees, and in woody litter.

Nutrient supply and NPP are linked (Miller, 1984; Nadelhoffer *et al.*, 1985; Waring and Schlesinger, 1985) and changes in nutrient supply often result in changes in NPP (Gower *et al.*, 1992). Any decrease in nutrient supply with stand age may reduce wood accumulation rates both by decreasing assimilation (through reductions in leaf area and leaf area efficiency) and by reducing allocation to wood growth as root production increases to scavenge for nutrients.

Does nutrient supply decline with stand age? In a review of biogeochemical budgets and ecosystem succession, Gorham *et al.* (1979) assumed that declining net ecosystem production in older stands would lead to increased outputs of nutrients as the ability of the stand to use nutrients declined. Vitousek and Reiners (1975) documented higher nitrate concentrations in some streams draining old stands of red spruce (*Picea rubens*) relative to younger stands, suggesting that either the nutrient supply was higher in the old stands, or that the forests were indeed less capable of using nutrients. Chapin *et al.* (1986) noted that old individuals may have a lower ability to respond to increasing nutrient supply than younger individuals of the same species; old aspen (*Populus tremuloides*) stands did not respond as well to fertilization as younger stands. These data contradict the expectation of increasing nutrient limitation in older stands.

Many studies have examined changes in soil nutrient supplies shortly after major disturbances (such as clearcutting), and a few chronosequence studies have documented patterns that might occur with stand development. In this section, we discuss a wide variety of case studies and then discuss the extent to which changes in nutrient supply might explain declines in stemwood production.

A. Comparisons of old and regenerating forests

Several studies have found that nutrient mineralization rates in regenerating forests can be equal to or greater than that in adjacent old forests (Vitousek

and Denslow, 1986; Matson *et al.*, 1987; Zou *et al.*, 1992). Vitousek and Denslow (1986) examined net N mineralization and acid-fluoride-extractable phosphate in intact lowland rainforests and forest gaps at La Selva Biological Station in Costa Rica. They found no evidence of differences in N supply and only slight, nonsignificant increases in phosphorus in the gaps. Matson *et al.* (1987) also examined net N mineralization following logging and burning at another site in Costa Rica. In the first year after treatment, net N mineralization was elevated, but a 5-year post-cutting site showed little difference from the old-forest site. Zou *et al.* (1992) examined N mineralization in two adjacent forests in the La Selva and found no differences in net or gross mineralization or nitrification between the old-growth forest and a 4-year-old successional forest.

Several case studies have documented greater nutrient mineralization in regenerating forests than in old forests. For example, Frazer *et al.* (1990) compared net N mineralization in an old-growth mixed-conifer forest in the Sierra Nevada of California with adjacent stands of 5- and 17-year-old trees. The youngest site had the highest net N mineralization rates, followed closely by the 17-year-old site. The old-growth forest had less than 20% of the net N mineralization rate of the younger forests. In wind-created gaps, net N mineralization 3 years after gap formation declined by about 15% in sugar maple (*Acer saccharum*) forests but increased 20% in hemlock (*Tsuga canadensis*) forests (Mladenoff, 1987).

Clearcutting and site preparation (e.g. burning, plowing) tend to elevate nutrient availability compared with adjacent, older forests. Studies in loblolly pine (*Pinus taeda*) found that *in situ* rates of net N mineralization (Vitousek and Matson, 1985; Fox *et al.*, 1986) and nitrification (Vitousek and Matson, 1985) increased substantially with the intensity of logging disturbance. Krause and Ramlal (1986) used ion exchange resin bags to examine the effects of clearcutting and site preparation on nutrient supply in a balsam fir and black spruce (*Picea mariana*) stand. In the first summer after treatment, the resins collected about twice as much nitrate and phosphate in the cut site than in the uncut forest. In British Columbia, Binkley (1984) compared adjacent cut and uncut stands at three elevations on Vancouver Island. Laboratory incubations indicated no differences in net N mineralization between cut and uncut sites, but on-site resin bags indicated much greater N availability in cut sites. Burger and Pritchett (1984) examined the effects of clearcut logging of slash pine (*Pinus elliottii*) and longleaf pine (*Pinus palustris*) in Florida with a range of subsequent site preparation activities. Aerobic laboratory incubations showed that potential net N mineralization decreased in the sequence from uncut forest to cut-and-burned treatment, to the cut, burned-and-plowed treatment. However, simulations based on differences in soil temperature and moisture suggested that *in-situ* rates of net N mineralization may not differ among treatments.

B. Comparisons of Age Sequences of Forests

Measurements of nutrient mineralization in forest chronosequences show varied patterns of nutrient availability with stand age. Nutrient availability can decrease (Matson and Boone, 1984; Davidson *et al.*, 1992; Binkley *et al.*, 1995), increase (Sasser and Binkley, 1989), or be lowest in middle-aged stands, compared with younger or older stands (Ryan and Waring, 1992; Olsson, 1996).

Matson and Boone (1984) examined net N mineralization in a wave-pattern regeneration sequence in a mountain hemlock (*Tsuga mertensiana*) ecosystem in Oregon, an ecosystem with very low soil N content. Net mineralization doubled from the old-growth stage into the dead-forest zone, and then declined back to the old-growth stage over the next several decades. Ion exchange resin bags also showed declining soil N supply with age, while K and P supplies appeared to increase (Waring *et al.*, 1987). In this case, the decline in soil N may lead not only to declining growth, but to increasing susceptibility to root pathogens because of lack of carbon with which to fight infection.

Binkley *et al.* (1995) examined relationships between nutrient availability, nutrient limitation, and stem growth in a replicated age sequence of lodgepole pine (*Pinus contorta*) in Wyoming. Net nitrification in in-field incubations was more than four times greater in stands younger than 43 years than in older stands. The oldest stands (112–117 years) had significantly lower net N mineralization than younger stands. No trends were apparent in measures of soil P, Ca, Mg, or K. Single-tree fertilization trials indicated that nutrient supply did not limit leaf area or stem growth of forests less than 43 years old, whereas N supply limited leaf and stem growth in older forests. Olsson (1996) used ion exchange resin bags to examine soil N supply over a longer age sequence in lodgepole pine in the same area, and found that N supply was high in forests younger than 50 years, low in forests between 50 and 100 years, and increased in forests older than 200 years. Ryan and Waring (1992) found a pattern similar to that of Olsson (1996) for lodgepole pine in Colorado. While no statistical difference in nitrogen availability existed among adjacent 40-, 60-, and 245-year-old stands, mean N availability was greater in the 245-year and 40-year stands than the 60-years stand. Foliar N reflected N availability, with the 60-year stand having the lowest foliar N.

Sasser and Binkley (1989) examined net N mineralization in two age sequences of fir (*Abies fraseri* and *A. balsamea*) generated by a wave-pattern regeneration sequence. In an environment with high rates of N deposition from the atmosphere (> 10 kg N ha^{-1} yr^{-1}), net N mineralization was high in the dead zone, low to moderate in the regeneration and juvenile stages, and high in the mature (*c.* 80 year old) stands. Sprugel (1984) found that aboveground NPP remained high in balsam fir forests for at least 60 years; bole respiration remained constant, and N supply remained high.

Davidson *et al.* (1992) provided one of the most thorough examinations of the processes behind changes in N turnover in forests of different ages. Net mineralization rates were somewhat higher in a 10-year-old mixed conifer plantation than in a nearby old-growth mixed conifer forest. This higher rate of net mineralization resulted from lower microbial immobilization of the mineralized N (based on ^{15}N pool dilution) in the younger stand, rather than from a higher rate of N release from organic pools. The rate of gross mineralization (total N released from organic pools) was about two to three times higher in the old-growth forest. The younger forest also had four to ten times as much net nitrate production as the old-forest, but again this resulted from lower microbial immobilization of nitrate rather than from greater production of nitrate.

Herbert (1984) followed the productivity of black wattle (*Acacia mearnsii*) plantations through three rotations with and without supplemental fertilization. In all rotations, the rate of basal area (and volume) growth declined after about the first five years. Fertilization increased growth rates but had no effect on the overall pattern of growth with stand age.

C. Old-field Succession Sequences

No clear pattern of nutrient availability and forest age emerges from the literature on old-field succession. Montes and Christensen (1979) examined an age sequence in North Carolina of an abandoned agricultural site (old-field), a 40-year-old loblolly pine stand, and an old-growth oak-hickory stand. Rates of net mineralization and nitrification were higher in the old-field and in the old-growth stand than in the intermediate-aged pine stand. A more thorough, replicated study by Christensen and MacAller (1985) found no consistent trend in soil N supply with successional stages from old-fields through hardwood stages. Pastor *et al.* (1987) examined four old-field sites in Minnesota ranging in age from 16 to > 100 years after agricultural abandonment. Net N mineralization increased through the age sequence. The proportion of total soil N mineralized declined with time, however, suggesting a declining quality of organic matter over time. Robertson and Vitousek (1981) examined net mineralization and nitrification rates in an old-field succession sequence in New Jersey. Both rates tended to increase with time, reaching a maximum in the old-growth forest stage. Thorne and Hamburg (1985) examined an old-field sequence in New Hampshire. They found no relationship between several chemical measures of labile N pools with stand age, although net nitrification did decline with stand age.

D. Conclusions

Nutrient supply (particularly N) does increase after disturbances in most cases, but this is not a universal pattern. Beyond the initial disturbance responses, no clear trend of increasing or decreasing nutrient supply was apparent in the case studies we examined. Two case studies with fir forests in the eastern United States showed increasing N supply with stand age (Sasser and Binkley, 1989), and case studies with lodgepole pine in the Rocky Mountains showed higher N supply in young and old forests than in intermediate-aged forests. The ^{15}N tracer work of Davidson *et al.* (1992) demonstrated that commonly measured indexes of soil N supply may miss important dynamics in the soil N cycle. We conclude that, in some cases, changing nutrient supply plays a role in the declining growth of older forests, but this explanation is not universal.

VIII. CHANGES IN RESPIRATION

Respiration by the living cells in foliage, fine roots, and wood (ray parenchyma cells in sapwood) can use 50–70% of the carbon fixed in photosynthesis (Ryan, 1991; Ryan *et al.*, 1994b). Because of the large respiration costs reported in forests, early hypotheses about the decline of wood production with forest age focused on respiration. The reasoning was: (1) leaf area, and presumably the capacity of a forest canopy to assimilate carbon, peaks early in a stand's life, but (2) wood production declines as woody biomass increases, and (3) respiration increases with biomass in crop plants (Thornley, 1970). Therefore, respiration of the woody biomass was thought to use an increasing fraction of assimilation, and wood production declined (Yoda *et al.*, 1965; Kira and Shidei, 1967). A similar reasoning was used by Whittaker and Woodwell (1967), except they used surface area rather than woody biomass. The 'respiration hypothesis' is the textbook explanation for productivity decline (Kramer and Kozlowski, 1979; Waring and Schlesinger, 1985; Cannell, 1989), although only indirect evidence exists (Whittaker and Woodwell, 1967; Waring and Schlesinger, 1985) to support the explanation.

Direct measurements and estimation from published respiration rates argue against the role of woody-tissue respiration in causing age-related productivity decline. Respiration costs were similar (Ryan and Waring, 1992) for an old lodgepole pine forest and an adjacent younger stand (88 g C m^{-2} year^{-1} in a 245-year-old stand versus 103 g C m^{-2} year^{-1} in a 40-year-old stand), even though wood production was substantially lower in the old forest (37 g C m^{-2} y^{-1} in a 245-yr-old stand versus 168 g C m^{-2} yr^{-1} in a 40-year-old stand). Similarly, S. T. Gower *et al.* (unpublished data) found little difference in woody-tissue respiration costs in a chronosequence in a temperate deciduous forest. Another study (Sprugel, 1984) used published respiration rates and allometric equations to estimate branch and bole respiration for a balsam-fir chronosequence and found nearly constant woody-tissue respiration after age 25 years, while bole wood production declined from 325 to 210 g m^{-2} yr^{-1}. In the balsam-fir chronosequence, bole surface area actually declined with stand age as fewer (but larger) trees and branches replaced the more numerous smaller trees and branches. Finally, maintenance respiration for woody tissue in old and young stands of *Tsuga heterophylla* and *Pseudotsuga menziesii* on highly productive sites was similar, and respiration was not implicated in the low wood production in the old stand (Runyon *et al.*, 1994).

Other indirect evidence argues against woody-tissue causing productivity decline. If respiration is partitioned into the functional components of growth and maintenance (see Amthor, 1986), growth respiration will decline along with wood growth. Maintenance respiration rates of woody tissues generally appear to be low (Ryan *et al.*, 1994b), and maintenance respiration of wood uses a small fraction (5–12%) of annual carbon fixation (Ryan *et al.*, 1994a, 1995). Growth analysis of spacing studies showed that trees at wider spacings (with higher wood:leaf ratios) continued to grow and have higher growth efficiency, while trees with narrower spacings declined in growth and growth efficiency (Fownes and Harrington, 1990; Harrington and Fownes, 1996). Finally, extrapolating rates based on surface area may be biased because of the variability caused by the underlying sapwood (Ryan, 1990).

Maintenance respiration rates are low for woody-tissues, because the stems contain few living cells and these have low activity (Ryan, 1990); also, in many trees the fraction of sapwood (which contains the living cells) can be only a small portion of the total woody biomass. The sapwood fraction appears to be high in small, drought-tolerant trees and low in large, drought-intolerant trees. Because of this trend, little of the woody biomass in forests with high biomass is in sapwood. For example, the above-ground sapwood fraction for a tropical wet forest was estimated as 23% of total above-ground biomass (Ryan *et al.*, 1994a).

Although respiration rates for foliage and fine roots are much larger than those of woody tissue (Ryan *et al.*, 1994b; Sprugel *et al.*, 1995), the fraction of assimilation used by foliage and fine root respiration is unlikely to change with forest development. If leaf area and photosynthetic capacity remain constant after canopy closure, foliage respiration is unlikely to change. If leaf area declines (see section VI.A), foliage respiration as a fraction of assimilation is likely to decline, not increase (Ryan *et al.*, 1994b). Fine root biomass and nutrient content largely determine fine root respiration (Ryan *et al.*, 1996a), but potential changes in fine-root biomass with stand development remain largely unknown. At a coarse (global) scale, fine root biomass may correlate with foliage (Raich and Nadelhoffer, 1989), but at the ecosystem level, relationships between foliage and fine roots are strongly dependent on nutrition and water (Gower *et al.*, 1996b). In forest development, changes in root turnover or carbon allocation to root exudates and mycorrhizas may be more important than changes in respiration of fine roots (see section IX.B).

IX. CHANGES IN ALLOCATION

A peak and decline in stem growth with stand age could also result from a constant rate of net primary production but reduced allocation to stem production. For example, a comparison of young and old *Abies amabilis* stands showed allocation to fine roots increased as a fraction of NPP (Grier *et al.*, 1981). A similar trend was observed for an age sequence of slash pine (Gholz *et al.*, 1986), where both the relative and absolute allocation to roots increased with stand age.

Another possibility is that other turnover processes increase with stand age. When biomass accumulation rates are estimated by successive stand inventories, stem mortality is often not included, resulting in an underestimation of actual stem production. As tree crowns converge during canopy closure, lateral branches may become suppressed, resulting in a rearrangement of the leaf area distribution within crowns (Ford, 1984). In a model of *Eucalyptus globulus* growth, the fractional leaf turnover rate increased from 0 to 0.5 year^{-1} at 6 years (unfertilized) and 4 years (fertilized) to simulate this effect (Linder *et al.*, 1985). Patterns in NPP allocation also may interact strongly with nutrient availability.

A. Per Tree

The factors that directly control the allocation of photosynthate in individual trees remain largely unknown; important factors include genetic, biochemical, and physiological regulation of transport from sources and sinks (Cannell and Dewar, 1994; Gower *et al.*, 1995), and competition among trees (Nilsson and Albrektson, 1993). At a coarser scale, a great deal is known about biomass production of stems, leaves, and in some cases roots. Growth of stemwood raises the tree's canopy above competitors; stem growth also responds to wind stress (Coutts, 1983). Allocation to leaf production depends in part on availability of site resources, such as water and nutrients (Cannell and Dewar, 1994; Gower *et al.*, 1995), and the acquisition of these resources depends on allocation to fine roots and mycorrhizas. Young trees allocate more photosynthate to foliage production than wood production, and this ratio declines as canopy closure develops. Allocation to large support roots often follows a simple allometric relationship, such as 20% of total tree biomass (Jackson and Chittenden, 1981; Gower *et al.*, 1995). Trees that experience strong competitive stress may allocate larger fractions of assimilate to stem wood production. For example, Nilsson and Albrektson (1993) found that suppressed Scots pine (*Pinus sylvestris*) trees showed greater stem growth per gram of needle mass than dominant trees, whereas allocation to needles and branches did not differ between competitive classes. Higher wood growth for suppressed conifers was also found by Kaufmann and Ryan (1986).

B. Changes in Fine Root Production and Longevity

Fine root production is difficult to measure, and the strengths and weaknesses of the major approaches have been debated extensively (Fairley and Alexander, 1985; Nadelhoffer *et al.*, 1985; Kurz and Kimmins, 1987; Santantonio and Grace, 1987; Raich and Nadelhoffer, 1989). Most studies that focused on root production omitted the photosynthate requirement for root construction and maintenance respiration (Ewel and Gholz, 1991), which may be 50% of below-ground allocation (Ryan, 1991). Some generalizations about root production appear to be supported from research over the past two decades, and these patterns depend strongly on scale. At a global scale, the allocation of photosynthate to fine root production and respiration generally increases with increasing ecosystem productivity (Raich and Nadelhoffer, 1989). At a regional scale, fine root production (and probably respiration) may (or may not) increase with increasing N availability. For example, Nadelhoffer *et al.* (1985) used estimates of net mineralization and N uptake and allocation to above-ground tissues to estimate what fine root production must have been to balance the N budget. Across nine stands (and nine species) in south-central Wisconsin, they estimated that root production must increase with increasing rates of net N mineralization in the soils. This calculation, coupled with decreases in standing biomass of fine roots on high N sites indicated that root longevity must be much shorter on richer sites (a finding confirmed by Pregitzer *et al.*, 1993).

Within single species, the pattern of root production appears to be the opposite of the regional and global patterns. Studies of fine root production that compared the same species growing in high and low productivity sites generally found equal or greater fine root production and increased relative below-ground allocation on the poorer sites (Keyes and Grier, 1981; Santantonio and Hermann, 1985; Beets and Pollock, 1987; Comeau and Kimmins, 1989; Gower *et al.*, 1996a; but see Nadelhoffer *et al.*, 1985). Most of these studies attribute differences in site productivity to water supply, but nutrient supply may also be important. Greater nitrogen availability appears to reduce allocation to fine roots even if plants become deficient in other nutrients (Ericsson 1995).

Several intensive experiments have also demonstrated lower absolute and relative below-ground production following fertilization of Scots pine (*Pinus sylvestris*; Linder and Axelsson, 1982), Norway spruce (*Picea abies*, Persson *et al.*, 1995; Clemensson-Lindell and Persson, 1995), Douglas-fir (*Pseudotsuga menziesii*; Vogt *et al.*, 1990; Gower *et al.*, 1992), and loblolly pine (*Pinus taeda*; H.L. Allen and P. Dougherty, personal communication). None of these fertilization experiments examined patterns with stand age; however, if soil fertility changes with stand development (and the evidence is mixed, see section VII), below ground allocation would also likely change.

Only a few studies examined root biomass and production with stand age. Berish (1982) found that fine root biomass (production was not examined) increased from 220 to 1300 to 1550 kg ha^{-1} in an age sequence of 1-, 8- and 70-year-old successional forests in Costa Rica. Vogt *et al.* (1983) looked at fine root biomass (but not production) on two age sequences of Douglas fir. Stands younger than 15 years had low fine root biomass on both types of sites, but no further trends were evident with stand age. Grier *et al.* (1981) compared 23-year-old and 180-year-old stands of Pacific silver fir (*Abies amabilis*) and found that ecosystem NPP was similar between the stands (about 17 to 18 Mg ha^{-1} yr^{-1}), as was total below-ground NPP (about 12 Mg ha^{-1} yr^{-1}). The major difference between the stands was the greater contribution of shrubs in the production budget of the younger stand. Comparing only tree production, the younger stand showed much greater above-ground production and lower below-ground production (especially of fine roots) than the older stand. Fine root production by trees in a 27-year-old slash pine (*Pinus elliottii*) stand was substantially higher than in younger stands (Gholz *et al.*, 1986). However, the total below-ground production (trees + understory) of the younger stand matched that of the older stand.

Some current work in lodgepole pine forests in Wyoming has found that below-ground allocation (as measured by the difference between soil respiration and above-ground litter inputs) declines substantially in old stands, but the timing of the decline does not match the timing of the decline in above-ground NPP (S. Resh and F.W. Smith, personal communication, 1996). Recent work with loblolly pine in South Carolina is demonstrating a strong response of proportional allocation below-ground in response to fertilization and irrigation, but very little response in actual below-ground NPP (NCSFNC, 1995; H.L. Allen and P. Dougherty, personal communication, 1995). Irrigation increased NPP of a young plantation by about 11%; allocation to roots declined from 41% in control plots to 34%. Fertilization increased NPP by 65%, with just 26% going below-ground. Fertilization plus irrigation more than doubled NPP, with just 21% allocated below-ground. The actual below-ground NPP (Mg ha^{-1} yr^{-1}) varied little (±10%) among treatments.

The paucity of studies on root production with stand age allows no generalization of trends. Any decrease in soil N supply with stand age would probably increase relative allocation to fine root production, but the evidence for a decline in N supply with stand age is mixed. Studies with Pacific silver fir (Grier *et al.*, 1981) and slash pine (Gholz *et al.*, 1986) indicated a major role for root dynamics of understory species; changes in root production by competing species can alter resource supplies to trees and presumably alter allocation patterns of the overstory.

C. Allocation to Symbionts

Most tree species develop obligatory or facultative symbioses with mycorrhizal fungi (Allen, 1991), and a few genera are capable of symbiotic N fixation in association with prokaryotic bacteria (Werner, 1992). The mycorrhizal

symbioses are usually viewed as mutualistic associations where fungi receive carbohydrates from the trees and the trees receive resources such as N, P, and water. The carbohydrate cost of sustaining the mycorrhizal network can be substantial and probably varies among species and across resource gradients (such as soil P supply). While complete carbon budgets for mycorrhizas have not been developed, allocation to symbionts will change with stand age only if mycorrhizal growth is sensitive to soil nutrition and if soil nutrition changes with stand age.

Mycorrhizas can use up to 20% of assimilation (Soderstrom, 1991; Ryan *et al.*, 1996a), but the carbon cost can be offset by increased assimilation. For example, Reid *et al.* (1983) provided $^{14}CO_2$ to Scots pine seedlings with and without mycorrhizas. After 10 weeks, the mycorrhizal seedlings had fixed 2.5 times as much C as the non-mycorrhizal seedlings and accumulated 2.1 times as much biomass. Respiration as a fraction of total assimilation was much greater in the mycorrhizal seedlings (30%) than in the non-mycorrhizal seedlings (18%).

Early work on mycorrhizas suggested that mycorrhizal associations declined as the external supply of nutrients increased (Marx *et al.*, 1977), but the solution concentrations of nutrients were often one or more orders of magnitude higher than those encountered in forest soils. Mycorrhizal associations probably remain important across normal ranges of soil fertility, but low supplies of soil P may increase proportional allocation of C to mycorrhizas (cf. Ekblad, 1995). Termorshuizen (1993) examined the effects of N fertilization (at rates up to 60 kg N ha^{-1} yr^{-1}, for 3 years) on mycorrhizas, and concluded that high supplies of N reduced production of fungal fruiting bodies, but did not change the frequency of mycorrhizal infection of root tips or the volume of mycorrhizal hyphae per unit of soil volume. Similarly, Soderstrom (1991) found that fertilization with up to 600 kg N ha^{-1} did not alter the proportion of root tips colonized by mycorrhizas.

We know of only one study that attempted to characterize the C allocation to mycorrhizas across stand age. Vogt *et al.* (1982) estimated the biomass production of mycorrhizal fungi in a 23-year-old and a 180-year-old stand of Pacific silver fir (*Abies amabilis*). For both stands, the production of the mycorrhizal mantle and sporocarps accounted for about 15% of NPP; inclusion of the extramatrical hyphae that permeate the soil would raise the estimate of both total NPP and proportional allocation to mycorrhizas. In addition, the turnover rates of mycorrhizal tissues are commonly more rapid than those of plant tissues (Allen, 1991), so inclusion of respiration losses may further increase the proportion of GPP allocated to developing and sustaining the mycorrhizal association. Termorshuizen (1993) suggested that mycorrhizal diversity should change with ecosystem development because diversity declined with stand age in Scots pine forests. However, reviews by Brundrett (1991) and Molina *et al.* (1992) do not support generalizations about changes in diversity with ecosystem development.

Over 600 tree species have been documented to be capable of symbiotic N-fixation (MacDicken, 1994), including dozens of genera of legumes and several notable non-legume genera such as *Alnus*. Rates of N fixation are typically about 75–200 kg N ha^{-1} yr^{-1} in monoculture stands, representing a C cost of about 400–1000 kg C ha^{-1} yr^{-1} (Binkley *et al.*, 1994; Binkley and Giardina, 1996). However, the investment of C to aid symbionts in fixing N substantially increases assimilation. Some greenhouse studies have shown that high concentrations of ammonium or nitrate can impede N fixation by symbionts. However, little if any feedback inhibition of N fixation is found where the supply rate of N is high but soil concentrations are realistically low (Binkley *et al.*, 1994). All studies that examined N fixation in old (> 50 year) stands of red alder (*Alnus rubra*) have found rates that match those of younger stands (Binkley *et al.*, 1994). The situation is less clear for leguminous trees; declining N fixation with stand age has been suggested for several field studies (J. Sprent, personal communication, 1995).

Considerably more work is needed to quantify the role of mycorrhizas in the C budgets of forests. However, current evidence does not suggest that changes in mycorrhizal associations account for the decline in above-ground forest production with age. Similarly, there seems to be no reason to speculate that changes in the N-fixing symbiosis could account for the age-related decline in productivity.

D. Allocation to Foliage and Branches

As described earlier (section VI.A), the allocation of photosynthate to leaf production is high in young stands (before canopy closure) and typically declines later. This shift in allocation to foliage can partially explain the early increase in stem production, but is generally in the wrong direction to account for any decline in stem production in later stages. Although total canopy leaf area declines in older stands, reductions in the number of trees typically leads to increased leaf area per tree, and this concentration of more leaves on each stem requires more substantial branch development. This increase in the branch biomass:leaf area ratio has not been examined widely as a possible mechanism for reduced stem production, but at least one study indicated an important role for this change in canopy structure (Long and Smith, 1992).

E. Allocation to Reproduction

The carbon cost of reproduction (seeds, supporting fruiting structures, and associated respiration) is typically a low fraction of annual assimilation. For example, Linder and Troeng (1981) estimated that cone production and respiration in a 120-year-old Scots pine (*Pinus sylvestris*) stand required 157 kg C ha^{-1} y^{-1}, roughly 10–15% of the carbon allocated to annual above-ground wood production and woody-tissue respiration. Respiration of cones is low (< 3% of net photosynthesis in *Pinus contorta*) because cone biomass is relatively low and cone photosynthesis lowers carbon loss (Dick *et al.*, 1990). Reproduction can lower the growth of foliage and wood (Eis *et al.*, 1965; Tappeiner, 1969). In *Pseudotsuga menziesii*, heavy cone crops reduced diameter increment up to 25% (Eis *et al.*, 1965; Tappeiner, 1969) and also reduced shoot growth (*c.*50%; Tappeiner, 1969) and needle length (40%; Tappeiner, 1969).

Little information exists about whether reproductive effort changes with stand development. In a literature review, Greene and Johnson (1994) found that seed production generally increased with tree size up to a stem diameter (at 1.4 m height) of 0.36 m. Seed production in trees larger than 0.36 m diameter showed a variety of responses to increasing tree size (modal, asymptotic, and increasing linear). Seed production is sporadic (Eis *et al.*, 1965) while growth decline is not (Figures 2 and 3), so reproductive costs alone could not account for declines in stand growth with age. The lack of data on changes in reproductive effort with stand development and the impact of reproduction on diameter growth suggest that further work is needed in this area.

X. OTHER CHANGES IN STRUCTURE AND FUNCTION

A. Maturation

Woody plants undergo changes in developmental behavior (termed maturation or phase change) as they age (Haffner *et al.*, 1991; Greenwood and Hutchinson, 1993; Greenwood, 1995), and these changes can alter physiology and growth. The effects of maturation can be observed on intact trees of different ages and on rooted cuttings or grafted scions taken from different-aged trees. Evidence is sketchy, but observations such as the persistence of mature characteristics in scions grafted onto juvenile rootstock (Greenwood, 1984) suggest that maturation involves genetic changes in the meristematic tissue of plants (Greenwood and Hutchinson, 1993). Changes in gene expression in grafted scions did vary with parent age in eastern larch (*Larix laricina*; Hutchinson *et al.*, 1990b), but no causal relationship between genetic expression and maturation has been established.

The developmental changes associated with maturation are quite varied. Maturation affects branching, foliage morphology, physiology, and biochemistry, and these changes generally slow shoot height and diameter growth (Greenwood and Hutchinson, 1993). For example, in loblolly pine (Greenwood, 1984), Douglas fir (Ritchie and Keeley, 1994), and larch (Greenwood *et al.*, 1989), diameter growth, shoot length, and the number of branches decreased in grafted scions as the age of the parent increased (Figure 7). Photosynthesis may increase (Hutchinson *et al.*, 1990b) or decrease (Hutchinson *et al.*, 1990a) in scions grafted to juvenile rootstock, but differences in leaf area were more important than changes in photosynthesis in determining growth. Mature branches are also more likely to flower, and the proportion of male cones increases as branches age (Greenwood and Hutchinson, 1993). Finally, the ability of scions to root decreases with parent age (Greenwood *et al.*, 1989; Steele *et al.*, 1989) and with branch height in individual trees (Foster and Adams, 1984).

Because of the reductions in growth with parent age in grafted scions, maturation may explain the decrease in vertical growth with age (Greenwood, 1989), and the abrupt decline in vertical growth for fast-growing trees (Greenwood and Hutchinson, 1993). If so, differences in individual tree growth could accumulate to affect stand growth, and maturation may be involved in age-related productivity decline. As judged by the performance of rooted scions, however, transition from juvenility to maturity appears to occur early in the life of a tree, before the age at which peak stand leaf area would occur. For example, the greatest maturational changes occur between 1 and 4 years or loblolly pine (Greenwood, 1984) and Douglas fir (Ritchie and Keeley, 1994), and between 1 and 20 years in larch (Greenwood *et al.*, 1989). Slowing of growth in stands occurs after these ages in these species, suggesting that maturation is not a factor — trees that are slowing in growth rate are already 'mature'.

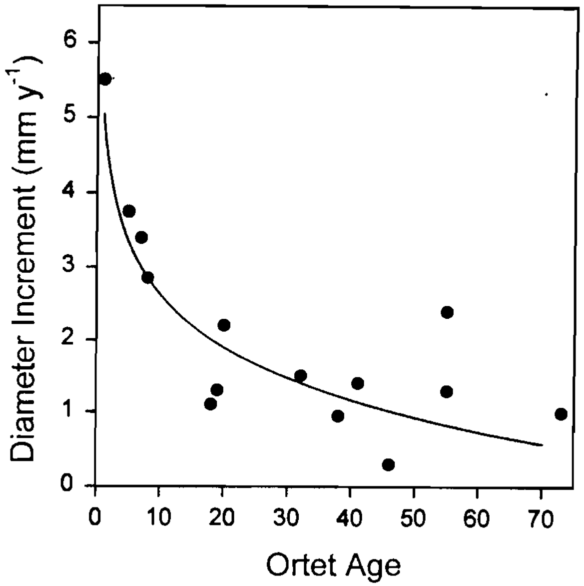

Fig. 7. One-year diameter growth of grafted scions from different-aged ortets (parent trees). Redrawn from Greenwood and Hutchinson (1993).

The living portion of a tree is quite young because the canopy and fine roots are replaced frequently, even in conifers. The oldest cells are ray parenchyma found in the sapwood, which rarely exceed 80 years even in very old trees (Connor and Lanner, 1990). Because of the young age of living tissue, it is unlikely that the individual's age is a factor in growth (Noodén, 1988). Animal cells have a mechanism that slows cell division as cells age and limits the total number of cell divisions that can occur. If plant cells have a similar mechanism, meristems would continuously decrease in activity with age (Greenwood, 1984). However, no direct evidence exists linking maturation and mitotic activity in the apical meristem.

B. Tree Mortality

Most of the data on age-related productivity decline focuses on stands, even though growth per unit of leaf area also declines in individual trees (see section IV). Mortality is a stand-level phenomenon that could alter net wood growth. An increase in mortality with stand age, if it occurred, would lower net wood production. Data on mortality are rare because large plots and long time spans are needed to obtain reliable estimates. However, the sparse existing data do not appear to support an increased mortality with stand age as a factor in age-related productivity decline.

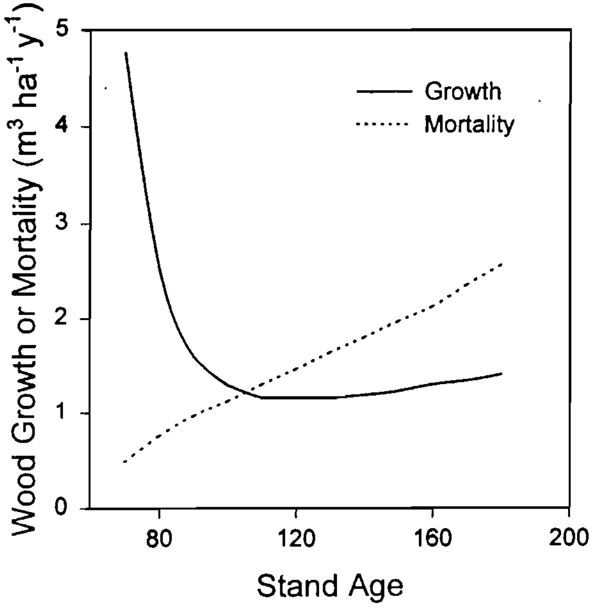

Fig. 8. Annual gross stem growth and mortality for black spruce, drawn from yield tables in Perala (1971).

Forestry yield tables rarely calculate mortality or the number of individuals, but an example from black spruce (Perala, 1971) shows a sharp decline in productivity accompanied by only a modest increase in mortality (Figure 8). An examination of inventory data from the U.S. Rocky Mountain region showed no trend of mortality with stand age (W. K. Olsen, personal communication, 1995): 79% of the stands had no mortality in the last 10 years, and mortality in the other 21% of the stands was variable.

Low net growth rates in old-growth stands apparently result from poor growth, not high mortality. Mortality probabilities for Douglas fir trees in even-aged stands are highest during the first century of stand development (Franklin and Hemstron, 1981), when growth is at its highest (Grier *et al.*, 1989). Long-term studies of tree mortality in old-growth stands (DeBell and Franklin, 1987; Franklin and DeBell, 1988; Hofgaard, 1993) have shown that mortality is roughly equal to production on the surviving trees, so biomass accumulation is near zero. However, growth rates of surviving trees were still low compared with those of younger stands. For example, annual growth of live trees in a mixed western hemlock and Douglas fir old-growth forest was 6.5 m^3 ha^{-1} (DeBell and Franklin, 1987), while peak productivity of a younger Douglas fir stand on a less productive site, was 15 m^3 ha^{-1} (Turner and Long, 1975). In lodgepole pine, growth of survivors in an old-growth forest was 0.74–0.94 Mg ha^{-1} yr^{-1}, while mortality ranged from 0.32 to 1.03 Mg ha^{-1} yr^{-1} (W. Moir, personal communication, 1996). The growth rate was comparable to that found for an old-growth stand in another study on the same site; however, an adjacent younger stand had a growth rate of 4.2 Mg ha^{+1} yr^{-1} (Ryan and Waring, 1992). Binkley and Greene (1983) examined patterns in above-ground NPP for 50 years in stands of red alder, conifers (mostly Douglas fir), and a mixture of red alder and conifers. Above-ground NPP declined in all three stands, whereas mortality was relatively constant after age 25. In 8- to 50-year-old stands of loblolly pine, mortality rate was a constant proportion of total tree number across a 20-fold range of initial stand density (Christensen and Peet, 1981).

In dense monocultures, total stand biomass and the number of individuals are strongly related, with population size decreasing as stand biomass and the size of the average individual increases. One formulation of this relationship (Westoby, 1984), in terms of stand biomass (*B*) and the number of individuals, (*N*) is:

$$B = CN^{0.5} \tag{2}$$

where *C* is a constant. This *self-thinning* rule defines an upper limit for the relationship between density and biomass that many even-aged stands follow (Westoby, 1984). While time is not explicit in the equation, we do know that older stands have fewer, larger individuals. Therefore, it may be instructive to examine the pattern of mortality that would occur if a stand were moving along a self-thinning trajectory. What we find is that with a unit increase in biomass, the percentage of stems dying decreases as stand biomass (or average size of individual) increases, but the biomass of the trees that die is constant as stand biomass increases. Because stands accumulate biomass faster earlier in their life, stands following a self-thinning trajectory should show lower mortality when trees are older and growing slowly. We note that the death of a single large tree leaves a bigger gap than the death of a small tree, and the time required to 'fill' the gap could be longer in older forests. Therefore, a constant rate of mortality of individuals could lower greater productivity in older forests.

C. Stand Structure

Stand structure changes dramatically with stand development (Bingham and Sawyer, 1991; Spies and Franklin, 1991). The height, diameter, and size of the average individual increase through time, together with stand biomass (Bingham and Sawyer, 1991; Spies and Franklin, 1991). Stand density declines (see section X.B) as the crowns of larger trees shade smaller competitors and the smaller trees die. Understory and herbaceous cover increase (Bingham and Sawyer, 1991; Spies and Franklin, 1991) as the stand leaf area declines (see section VI.A) and gaps form from dead trees (Spies *et al.*, 1990). Crown damage from windstorms can increase (Spies and Franklin, 1991), and the amount of woody debris may increase (Spies and Franklin, 1991) or decrease (Bingham and Sawyer, 1991), most likely reflecting the conditions under which stands were formed. Decreases in density and increases in tree size, woody debris, and gap fraction continue to occur even as old-growth stands age (Tyrrell and Crow, 1994).

Reduction in leaf area is the structural change most likely to affect wood production (see section VI.A) because of the loss in carbon assimilation. Tree height may also be a significant factor if photosynthesis is limited by hydraulic conductivity of the stem (section VI.C). However, if woody litter increases, nitrogen will be immobilized by the decaying wood (Murty *et al.*, 1996), lowering nitrogen availability for the overstory (see section VII). Low nutrient availability may lower the photosynthetic capacity of leaves and perhaps also the total leaf area. However, lower leaf area and a higher gap fraction will allow more solar radiation to the forest floor, perhaps warming it and increasing decomposition.

XI. CONCLUDING REMARKS

Declining growth after an even-aged stand reaches some limit appears to be universal, but the timing and magnitude of the decline vary. In our literature search, we found no support for the textbook explanation that growth decline results from increased respiration. Maintenance costs of woody-tissue respiration are low, and the amount of living cells in wood is small and changes little with biomass accumulation. There is also evidence that the balance of assimilation and respiration is conservative, so respiratory load declines as growth declines. The ultimate test of this hypothesis (which yet to be done) would be in the wet tropics, where high biomass and warm temperatures should yield the highest respiration rates.

In our search for mechanistic explanations, we identified two promising candidates:

(1) A decline in stand leaf area usually accompanies a decline in aboveground wood growth, and some of the growth decline is undoubtedly caused by decreased assimilation of a canopy with lower leaf area. Leaf area decline may be caused (a) by the loss of branches through abrasion or the formation of gaps too large for existing trees to exploit, (b) as a response to photosynthesis lowered by hydraulic limitation, (c) through a complex interaction with nutrition, or (d) through maturational changes. Branch abrasion and gap formation occur in even-aged forests, but it is not known whether these processes are common. Lower hydraulic conductance of older trees may reduce photosynthesis and ultimately leaf area. If nutrients become bound in living biomass or are immobilized in decaying wood, nutrient availability will be lower. Fertilization experiments show that improved nutrition will encourage more leaf area, so it may be reasonable that lowered nutrition will encourage shedding of foliage. However, the evidence for declines in nutrient availability that accompany stand development is mixed. The bulk of maturational changes appear to occur very early in the life of a tree, while growth decline generally occurs in mature trees.

(2) Limited evidence suggests that older trees have lower photosynthetic capacity and total diurnal assimilation than younger trees, which will lower canopy assimilation and provide less carbohydrate for wood production. Reductions in capacity may be caused by a feedback with the tree's hydraulic system, lower nutrient availability, or maturation changes. If stomatal behavior limits maximum transpiration and maximum transpiration declines as tree height and branch length increase, stomatal conductance and photosynthesis will be lower in taller trees. Consistently lower assimilation may lower photosynthetic capacity via a mechanism similar to that promoting lower capacity in older conifer needles.

The common patterns of a decline in stand leaf area and leaf photosynthetic capacity suggest a new model of carbon balance with stand development (Figure 9). In this model, photosynthesis and above-ground dry-matter production increase with canopy development. After the forest reaches a maximum leaf area, photosynthesis and dry-matter production decline as leaf area, photosynthetic capacity, and photosynthesis decline. The model assumes that allocation to respiration and below ground to roots and symbionts is a constant fraction of assimilation over the life of a forest stand.

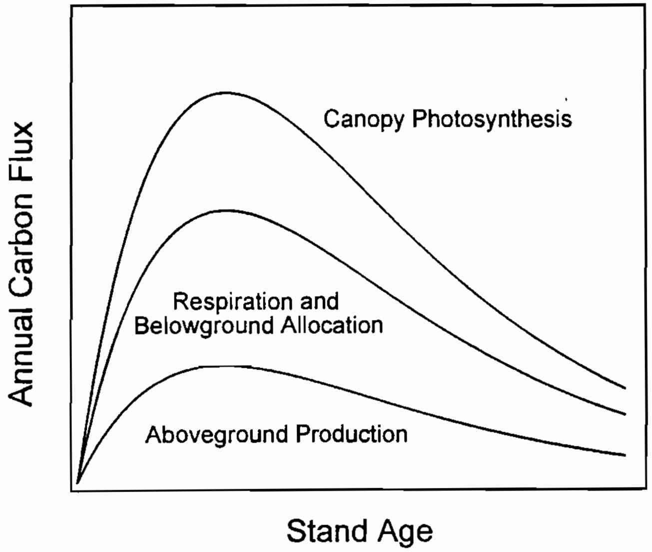

Fig. 9. Proposed model of carbon flux during forest stand development. Canopy photosynthesis increases as leaf area develops and decreases after maximum as leaf area and photosynthetic rates decline.

Other potential mechanisms appeared less promising as general explanations for growth decline. These mechanisms can affect forest carbon balance and may reduce the productivity of older forests in some cases. Experimental tests of these hypotheses are rare:

(1) Below-ground carbon allocation (fine root production or allocation to symbionts) may increase with stand age, but the evidence is mixed. Increased fine-root production or allocation to symbionts could result from lower nutrient availability and decrease the carbohydrate available for wood production. Because our literature review showed that there was no consistent pattern of nutrition with stand age, we suspect that belowground allocation will not universally increase with stand age, although it may feature in the development of some forests.

(2) Mortality of individual trees (as per cent of the current population) decreases as stands accumulate biomass. If stands follow a self-thinning curve, the biomass lost to mortality is constant as biomass accumulates. Therefore, it is unlikely that increased mortality contributes to growth decline unless larger gaps formed in older stand require substantially more time for in-filling.

(3) Reproductive costs can reduce stem growth. However, annual reproductive costs vary dramatically while growth declines continuously with stand age.

As forests age, then, they develop a syndrome of changes (lower leaf area, lower photosynthetic capacity, perhaps changes in allocation) that acts to lower primary production. If hydraulic resistance does constrain stomatal conductance and assimilation (a very active area of research), then all trees will suffer this limitation as they grow. However, nutrient limitations and shifts in allocation may also be important.

Experiments are needed to better understand how and why forests function differently as they age. We believe that the most critical questions are:

(1) Why does leaf area decline with stand age?
(2) Does nutrition change with stand development? What is the role of nutrition in forcing changes in below-ground allocation, leaf area, and photosynthesis?
(3) Do hydraulic limitations always lead to reduced photosynthesis as trees grow in height and branches lengthen?
(4) Does below-ground allocation (fine-roots and symbionts) change with stand development? If so, why? Are any changes in below-ground allocation substantial enough to account for changes in above-ground wood growth?

Guying trees (to prevent crown interaction) and fertilization of old forests can discriminate between some of the causes of leaf area decline. Fertilization studies in old, slow-growing forests can determine the role of nutrition in growth decline, allocation to foliage and roots, and photosynthesis; studies in aggrading forests can determine whether nutrition will alter the timing or presence of a growth decline. Leaf and stand measurements of CO_2 and water, together with experimental manipulations of leaf-specific hydraulic conductivity, can determine the role of hydraulic limitation. To determine whether below-ground allocation changes with stand development, we suggest that it be examined (perhaps using the carbon-balance approach) for a wide variety of chronosequences, and over time for rapidly growing stands. While not a critical issue, the respiration hypothesis should be examined in a tropical ecosystem, where respiration costs are expected to be high.

Given the evidence for differences in structure and function between young, mature, and old forests, it is surprising how little information is available. We hope this review will stimulate further efforts to understand growth decline and the changes that occur as a forest ages. Information on nutrition, carbon allocation, and physiological differences is sparse and much needed.

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