Tree Physiology 21, 1015–1030

The ratio of NPP to GPP: evidence of change over the course of stand development

ANNIKKI MÄKELÄ[1] and HARRY T. VALENTINE[2]

[1] *Department of Forest Ecology, P.O. Box 27, FIN-00014 University of Helsinki, Finland*

[2] *USDA Forest Service, Northeastern Research Station, P.O. Box 640, Durham, NH 03824-0640, USA*

Received October 1, 2000

Summary Using Scots pine (*Pinus sylvestris* L.) in Fenno-Scandia as a case study, we investigate whether net primary production (NPP) and maintenance respiration are constant fractions of gross primary production (GPP) as even-aged mono-specific stands progress from initiation to old age. A model of the ratio of NPP to GPP is developed based on (1) the classical model of respiration, which divides total respiration into construction and maintenance components, and (2) a process-based model, which derives respiration from processes including construction, nitrate uptake and reduction, ion uptake, phloem loading and maintenance. Published estimates of specific respiration and production rates, and some recent measurements of components of dry matter in stands of different ages, are used to quantify the two approaches over the course of stand development in an average environment. Both approaches give similar results, showing a decrease in the NPP/GPP ratio with increasing tree height. In addition, we show that stand-growth models fitted under three different sets of assumptions—(*i*) annual specific rates of maintenance respiration of sapwood (m_W) and photosynthesis (s_C) are constant; (*ii*) m_W is constant, but s_C decreases with increasing tree height; and (*iii*) total maintenance respiration is a constant fraction of GPP and s_C decreases with increasing tree height—can lead to nearly identical model projections that agree with empirical observations of NPP and stand-growth variables. Remeasurements of GPP and respiration over time in chronosequences of stands may be needed to discern which set of assumptions is correct. Total (construction + maintenance) sapwood respiration per unit mass of sapwood (kg C (kg C year)$^{-1}$) decreased with increasing stand age, sapwood stock, and average tree height under all three assumptions. However, total sapwood respiration (kg C (ha year)$^{-1}$) increased over the course of stand development under (*i*) and (*ii*), contributing to a downward trend in the time course of the NPP/GPP ratio after closure. A moderate decrease in m_W with increasing tree height or sapwood cross-sectional area had little effect on the downward trend. On the basis of this evidence, we argue that a significant decline in the NPP/GPP ratio with tree size or age seems highly probable, although the decline may appear insignificant over some segments of stand development. We also argue that, because stand-growth models can give correct answers for the wrong reasons, statistical calibration of such models should be avoided whenever possible; instead, values of physiological parameters should come from measurements of the physiological processes themselves.

Keywords: carbon balance, photosynthesis, pipe-model theory, modeling, respiration, Scots pine.

Introduction

Stand-level measurement of gross primary production is extremely difficult and subject to many uncertainties (e.g., Lavigne et al. 1997). An adequate quantitative theory of ecosystem respiration is therefore crucial for the understanding and prediction of net (NPP) and gross (GPP) primary production over the course of stand development. Most model predictions of plant productivity are based on the theory of respiration originally developed by Penning de Vries (1974, 1975), which divides consumption processes into maintenance and growth components. Maintenance respiration has been explained by the amount of live biomass and its temperature, whereas growth respiration has been defined as the unit cost of constructing new plant tissue (e.g., Penning de Vries 1975, Waring and Schlesinger 1985, Ryan 1990, Sprugel 1990, Ryan et al. 1994). The theory has given rise to two widely held views in tree physiology. First, maintenance respiration has been thought to cause a decline in net primary productivity (NPP) over the course of an even-aged stand's development as the ratio of productive to consuming tissue decreases (Kira and Shidei 1967, Shidei and Kira 1977, Cannell 1989). Second, stands in warmer climates have been thought to have relatively higher respiration costs; this is because the rate of respiration increases exponentially with temperature (e.g., Ryan et al. 1994, 1995), whereas the rate of photosynthesis tends to stabilize over a wide range of temperatures, i.e., 20 to 35 °C (e.g., Küppers and Schulze 1985, Teskey et al. 1995). However, recent findings cast doubt on the correctness of both views.

Several studies have shown that the fraction of GPP allocated to respiration differs little among stands of herbaceous plants (Monteith 1977, Gifford 1994, Monje and Bugbee

1998) and trees (Linder 1985, Keith et al. 1997, Malhi et al. 1999). Each of these studies considered plants of comparable size across different environments, which suggests that the respiration process is acclimated to the local conditions and, therefore, the relationship between respiration and temperature cannot be generalized from one place to another.

In a study involving lodgepole pine (*Pinus contorta* Dougl.) in Oregon, Ryan and Waring (1992) found that the NPP of a 245-year-old stand was less than that of a 40-year-old stand. The estimated rate of sapwood maintenance respiration was slightly, but not significantly, higher in the older stand, so the difference in NPP could not be explained by respiration only. Their alternative explanation—that the older, taller trees had lower specific rates of photosynthesis and, hence, lower productivity because of higher hydraulic resistance in their stems and branches—was supported by subsequent measurements (Yoder et al. 1994, Hubbard et al. 1999).

These and other findings have given rise to new theories and hypotheses about the influence of respiration on stand development. Waring et al. (1998) suggested that NPP may be a constant fraction (approximately 1/2) of GPP in even-aged stands. If this were true, total respiration would also be a constant fraction of GPP. Consequently, respiration would not contribute to the decline in NPP generally seen in an even-aged stand following closure. However, Medlyn and Dewar (1999) pointed out that the evidence presented by Waring et al. (1998) was derived from the assumption that respiration of live wood was a constant fraction of aboveground production, so the question of whether the ratio of NPP to GPP is constant remains unanswered. Nevertheless, the assumption of a constant NPP/GPP ratio has been applied in stand-growth models with promising results (e.g., Battaglia and Sands 1997, Landsberg and Waring 1997).

An argument for a declining NPP/GPP ratio after stand closure can be developed from two assumptions: (1) the ratio of respiring wood to foliage should increase with plant size; and (2) the specific rate of respiration of live wood should remain fairly constant from year to year. Support of the first assumption exists in the form of a high linear correlation between cross-sectional area of sapwood and foliage mass (Shinozaki et al. 1964*a*, 1964*b*); hence, the ratio of sapwood volume to foliage mass in a closed stand tends to increase linearly with average tree height (e.g., Valentine 1988). In concert with the second assumption, Ryan (1990) and Sprugel (1990) demonstrated that, at any given temperature, maintenance respiration of sapwood is highly correlated with sapwood volume.

In contrast, Lavigne and Ryan (1997) found that maintenance respiration, measured by the mature tissue method, had a large growth-dependent component in three different tree species in two locations, whereas the component related to sapwood volume seemed smaller than expected. Pruyn et al. (2000) found that the amount of carbon dioxide released from excised sapwood varied with ring age in stems of ponderosa pine (*Pinus ponderosa* Laws.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees. Outer rings released more CO_2 than middle or inner rings of sapwood. Cannell and Thornley (2000) and Thornley and Cannell (2000) presented a new framework for analyzing total respiration that is based on substrate transport and utilization. Under this new framework, maintenance and growth respiration share some components that are inseparable. Furthermore, the framework allows for futile cycles, which could consume excess carbon substrate during highly active periods of plant life. However, Thornley and Cannell (2000) conclude, from a model analysis, that futile consumption may not be of great significance quantitatively. Their models suggest that the NPP/GPP ratio is not constant but it is confined to a narrow range. The model by Dewar et al. (1998) is similar, though it does not consider multiyear time periods.

Although it seems that the model employed by Thornley and Cannell (2000) could explain many of the recent controversies regarding maintenance respiration, the model has many parameters related to substrate transport and utilization rates that cannot be measured; instead, the parameters must be fitted to provide reasonable outputs (Thornley and Cannell 2000). Therefore, even if the model is qualitatively adequate, comparisons with conventional measurements of respiration and growth are problematic. Moreover, the degree to which the NPP/GPP ratio varies over the course of stand development remains an open question.

The objective of this study was to investigate the development of the NPP/GPP ratio in a simpler quantifiable modeling framework using Scots pine (*P. sylvestris* L.) in southern Fenno-Scandia as a case study. In our analysis, we ignore temperature effects, considering an average season, and focus on the influence of tree size over the course of stand development. We utilize previous estimates of specific respiration and production rates and some recent measurements of biomass fractions, including sapwood and fine roots, in Scots pine trees of different ages (Vanninen et al. 1996, Mäkelä and Vanninen 1998, Vanninen and Mäkelä 1999). We then insert the empirical findings into a dynamic stand-growth model to explore the implications of different assumptions concerning respiration and production rates on stand dynamics.

Ratio of net to gross primary productivity: the classic model

Let B denote live dry matter per unit land area (kg C ha^{-1}) in an even-aged, mono-specific stand of trees (see Table 1 for definitions of all symbols). Variable B, is partitioned into foliar (F), feeder-root (R), and live woody (W) dry matter, so that:

$$B = F + R + W. \quad (1)$$

The live woody dry matter includes the live portions of boles, the live branches, and the transport roots. The dry matter of reproductive organs is included with the foliar dry matter. Feeder roots consist of fine roots and mycorrhizae. The rate of production of dry matter per unit land area is G_B. This rate partitions into rates for the three components of dry matter, i.e.:

Table 1. Parameters and variables.

Symbol	Definition	Units
c_B	Respiratory cost of production of dry matter	kg C (kg C)$^{-1}$
c_F	Respiratory cost of production of foliar dry matter	kg C (kg C)$^{-1}$
c_N	Respiratory cost of nitrogen uptake	kg C (kg N)$^{-1}$
c_P	Respiratory cost of phloem loading	kg C (kg C)$^{-1}$
c_R	Respiratory cost of production of feeder-root dry matter	kg C (kg C)$^{-1}$
c_W	Respiratory cost of production of sapwood dry matter	kg C (kg C)$^{-1}$
c_{MB}	Cost of mineral uptake per unit production of dry matter	kg C (kg C)$^{-1}$
c_{NB}	Cost of N uptake and reduction per unit production of dry matter	kg C (kg C)$^{-1}$
f_{NF}	Nitrogen concentration in foliage	kg N (kg C)$^{-1}$
f_{NR}	Nitrogen concentration in feeder roots	kg N (kg C)$^{-1}$
f_{NW}	Nitrogen concentration in sapwood	kg N (kg C)$^{-1}$
m_F	Specific rate of maintenance respiration of foliage	kg C (kg C year)$^{-1}$
m_R	Specific rate of maintenance respiration of feeder roots	kg C (kg C year)$^{-1}$
m_R'	Specific rate of maintenance respiration of feeder roots times ratio of foliar to feeder-root mass	kg C (kg C year)$^{-1}$
m_W	Specific rate of maintenance respiration of live woody tissues	kg C (kg C year)$^{-1}$
m_W'	Specific rate of maintenance respiration of live woody tissues times ratio of foliar to sapwood mass	kg C (kg C year)$^{-1}$
r_{NF}	Rate of recycling of nitrogen in foliage	kg N (ha year)$^{-1}$
r_{NR}	Rate of recycling of nitrogen in feeder roots	kg N (ha year)$^{-1}$
r_{NW}	Rate of recycling of nitrogen in sapwood	kg N (ha year)$^{-1}$
s, s_0	Specific rate of production of photosynthate of unshaded foliage	kg C (kg C year)$^{-1}$
s_1	Decrease in the specific rate of production of photosynthate per unit tree height	kg C (kg C year m)$^{-1}$
s_1'	Decrease in the specific rate of production of photosynthate per unit length of sapwood pipe	kg C (kg C year m)$^{-1}$
s_C	Average specific rate of production of photosynthate of all foliage	kg C (kg C year)$^{-1}$
t	Time	year
z_F	Foliar dry matter per unit cross-sectional area of sapwood	kg C m^{-2}
z_R	Feeder-root dry matter per unit cross-sectional area of sapwood	kg C m^{-2}
z_W	Woody dry matter per unit wet volume	kg C m^{-3}
A	Cross-sectional area of sapwood per unit land area	m^2 ha^{-1}
B	Total live dry matter per unit land area	kg C ha^{-1}
E_1, E_2	Efficiency of conversion of photosynthate to dry matter (ratio of NPP to GPP)	–
F	Foliar dry matter per unit land area	kg C ha^{-1}
H	Average tree height	m
I	Ratio of the rate of photosynthesis of unshaded to all foliage	–
L	Average length of sapwood pipes	m
R	Feeder-root dry matter per unit land area	kg C ha^{-1}
W	Live woody dry matter per unit land area	kg C ha^{-1}
Y_G	Growth yield (production per unit substrate consumed)	kg C (kg C)$^{-1}$
P	Rate of production of photosynthate	kg C (ha year)$^{-1}$
G_B	Rate of production of dry matter	kg C (ha year)$^{-1}$
G_F	Rate of production of foliar dry matter	kg C (ha year)$^{-1}$
G_R	Rate of production of feeder-root dry matter	kg C (ha year)$^{-1}$
G_W	Rate of production of sapwood dry matter	kg C (ha year)$^{-1}$
R_T	Rate of total respiration	kg C (ha year)$^{-1}$
R_C	Rate of constructive respiration	kg C (ha year)$^{-1}$
R_M	Rate of maintenance respiration of live dry matter	kg C (ha year)$^{-1}$
R_{MW}	Rate of maintenance respiration of sapwood	kg C (ha year)$^{-1}$
R_N	Rate of respiration for nitrogen uptake	kg C (ha year)$^{-1}$
R_P	Rate of respiration for phloem loading	kg C (ha year)$^{-1}$
U_N	Rate of nitrogen uptake	kg N (ha year)$^{-1}$
λ	Fraction of photosynthate loaded into phloem	–

$$G_B = G_F + G_R + G_W, \quad (2)$$

where G_B is, by definition, NPP. Net primary production equates to the rate of gross photosynthesis (P) less the rate of respiration per unit land area. Respiration is divided into two components, maintenance (R_M) and construction (R_C), therefore:

$$G_B = P - R_M - R_C, \quad (3)$$

where all four rates have dimensions kg C (ha year)$^{-1}$. Variable P is synonymous with GPP. Division of Equation 3 by P gives the efficiency (E_1) of conversion of photosynthate to dry matter (i.e., the ratio of NPP to GPP):

$$E_1 = 1 - \frac{R_M + R_C}{P}. \quad (4)$$

The rate of construction respiration has been assumed proportional to the rate of production of dry matter (McCree 1970, Thornley and Johnson 1990), i.e.:

$$R_C = c_B G_B, \quad (5)$$

where c_B is the "overhead cost of construction," the amount of photosynthate consumed in respiration per unit of production of dry matter (kg C (kg C)$^{-1}$). If the three components of dry matter have differing costs, then:

$$c_B = \frac{c_F G_F + c_R G_R + c_W G_W}{G_B}. \quad (6)$$

Substitution into Equations 3 and 4 yields:

$$E_1 = \frac{1}{1 + c_B}\left(1 - \frac{R_M}{P}\right). \quad (7)$$

The quantity $(1 + c_B)^{-1}$ is often denoted by Y_G in plant models and called the "growth efficiency" or "yield." In the absence of maintenance respiration, $(1 + c_B)^{-1}$ would be the upper bound of E_1. Empirical data (Kira 1975) and stoichiometric analyses (e.g., Chung and Barnes 1977) suggest that the upper bound of $(1 + c_B)^{-1}$ is approximately 0.8. At the other extreme, $E_1 = 0$ when $P = R_M$. Kira (1975) listed estimates of E_1 for natural forests and plantations ranging from 0.23 to 0.68.

Maintenance respiration has been assumed proportional to live dry matter, although the coefficient of proportionality, i.e., the specific rate of maintenance respiration, can change with changing environmental conditions. The rate of maintenance respiration, expressed in terms of the three components of dry matter, is:

$$R_M = m_F F + m_R R + m_W W, \quad (8)$$

where m_i (i = F, R, W) is the specific rate of maintenance respiration (kg C (kg C year)$^{-1}$). Substitution of Equation 8 into Equation 7 and dividing maintenance respiration and photosynthesis by foliar dry matter, F, yields:

$$E_1 = \frac{1}{1 + c_B}\left(1 - \frac{m_F + m_R(R/F) + m_W(W/F)}{s_C}\right), \quad (9)$$

where s_C denotes the specific rate of photosynthesis (kg C (kg C year)$^{-1}$), i.e., photosynthesis per unit foliar mass per year, such that $P = s_C F$.

Ratio of net to gross primary productivity: a new model

Cannell and Thornley (2000) recently presented a reexamination of respiration based on recently gained knowledge about energy consumption in different physiological processes. Construction respiration was divided into a direct construction cost related to the biosynthesis of glucose into structural matter, and an indirect construction cost related to processes required in biosynthesis but not directly linked to it. These processes include nutrient uptake and translocation, phloem loading, and chemical reactions required to transform nutrients, especially nitrogen (N), to the forms utilized in structure. Processes giving rise to maintenance respiration include resynthesis of proteins, maintenance of cell ion concentrations and gradients, and respiration related to futile cycles. Cannell and Thornley (2000) pointed out that some of these processes can be involved in both construction and maintenance of the *status quo*; hence, it may be incorrect to define maintenance and construction respiration as independent processes. They proposed that a process-based description should provide a better understanding of total plant respiration, though the concepts of construction and maintenance respiration may be a useful approximation in many cases. In a companion paper, Thornley and Cannell (2000) proposed a way of incorporating the various respiratory processes into Thornley's (1991) model of substrate assimilation, translocation and utilization. In this section, we consider how these processes are related to the carbon balance in a less detailed framework.

A direct construction cost is proportional to the rate of production of dry matter (McCree 1970, Thornley and Johnson 1990, Cannell and Thornley 2000), as in the classic model, i.e., Equation 5.

The rate of respiration related to N, R_N (kg C (ha year)$^{-1}$), is due to N uptake and reduction (N fixation is not considered here). Assuming that a constant proportion of N is taken up as nitrate and reduced, the rest being taken up as ammonium, then the combined respiration is generally proportional to the rate of N uptake, U_N (kg N (ha year)$^{-1}$):

$$R_N = c_N U_N, \quad (10)$$

where c_N (kg C (kg N)$^{-1}$) is the amount of photosynthate consumed in respiration per unit amount of N taken up and reduced. On the other hand, the rate of N uptake and reduction is roughly proportional to the demand for N in structural growth. This can be expressed as the concentration of N in new tissue, f_{Ni} (kg N (kg C)$^{-1}$), multiplied by the rate of production of new tissue, G_i, minus the rate of recycling of N from senescent tissue, r_{Ni} (kg N (ha year)$^{-1}$):

$$U_N = \sum_{i = F, R, W}(f_{Ni} G_i - r_{Ni}), \quad (11)$$

where i (i = F, R, W) indexes the different types of tissue. If a respiration coefficient related to N is defined as the carbon utilized in N uptake and reduction per unit structural growth (c_{NB}), then:

$$c_{NB} = c_N \sum_i \frac{f_{Ni} G_i - r_{Ni}}{G_B}, \quad (12)$$

where c_{NB} has dimensions kg C (kg C)$^{-1}$. Quantifying the parameters and variables in the above equation allows us to analyze the possible time dependence of c_{NB}.

Other labile nutrients (e.g., minerals) can be treated in the same way (excluding the reduction term), whereas immobile nutrients will not have a significant recycling term affecting the overall demand and uptake. Let us denote the nutrient-related specific respiration rate analogous to c_{NB} by c_{MB}.

The respiration term due to phloem loading (R_P) proposed by Cannell and Thornley (2000) is proportional to the amount of carbon loaded from the foliage to the phloem, which includes the carbon utilized in sapwood and fine-root growth and respiration. In other words, the rate of phloem loading is proportional to total photosynthesis less the carbon utilized in the foliage for growth and respiration. Denoting the (time-dependent) proportion of carbon transported to tissues other than foliage by λ, we may write:

$$R_P = c_P \lambda P, \tag{13}$$

where c_P (kg C (kg C)$^{-1}$) is the respiratory cost of phloem loading. To summarize, respiration due to direct construction and the above processes related to construction (and partly maintenance) can be expressed as:

$$R_C = (c_B + c_{NB} + c_{MB})G_B + c_P \lambda P, \tag{14}$$

where c_B is constant but c_{NB}, c_{MB} and λ may vary with plant structure, and hence, time.

The residual respiration processes are related to the maintenance of live biomass. The open question here is whether the rate of maintenance respiration should be substrate limited. In a coarse approximation, the carbon substrate available to the plant per unit biomass per unit time is P/B. If the specific rate of maintenance respiration were proportional to the available carbon, then the total respiration rate would be proportional to $(P/B) \times B$ or, simply, P, the rate of gross photosynthesis. Thornley and Cannell (2000) assumed a saturating dependence of maintenance respiration on available carbon, but in model simulations, the concentration of carbon substrate in different tissues is rather stable and, in foliage, it increases with time (Thornley 1991), such that the substrate limitation does not appear to become operative. We shall, therefore, assume no direct dependence on substrate.

Substitution of Equation 14 into Equation 4 yields:

$$E_2 = \frac{1}{1+\sum c_i}\left(1 - c_P\lambda - \frac{R_M}{P}\right), \tag{15}$$

where $\sum c_i = c_B + c_{NB} + c_{MB}$. In the absence of maintenance respiration, $1 - c_P\lambda/(1 + c_B + c_{NB} + c_{MB})$ would be the upper bound of E_2. At the other extreme, $E_2 = 0$ when $P(1-c_P\lambda) = R_M$. The value of c_P is about 0.06 kg C (kg C)$^{-1}$ (Cannell and Thornley 2000). There are few data suited for the estimation of λ, but data presented by Ryan et al. (1997) infer values of λ in the range from 0.55 to 0.65 for six middle- and old-aged stands. Even if the variation in λ were larger, the small value of c_P implies a narrow range of variation for the term $(1-c_P\lambda)$, leaving it approximately 0.97–0.96. We shall assume it is 0.96.

Substitution of Equation 8 and $P = s_C F$ into Equation 15 and dividing maintenance respiration and photosynthesis by foliar dry matter, F, yields:

$$E_2 = \frac{1}{1+\sum c_i}\left(0.96 - \frac{m_F + m_R\left(\frac{R}{F}\right) + m_W\left(\frac{W}{F}\right)}{s_C}\right). \tag{16}$$

It is apparent from Equations 9 and 16 that the development of E_1 and E_2 with time depends on the ratios of (*i*) feeder root mass to foliar mass and (*ii*) sapwood mass to foliar mass, and on the specific rates of (*iii*) photosynthesis (s_C), (*iv*) maintenance respiration (m_F, m_R and m_W) and (*v*) construction respiration (c_B, c_{NB}, c_{MB}). Thus, the possible trends in E_1 and E_2 are derivable from trends in these parameters and variables.

Empirical bounds for the evolution of NPP/GPP

Trends in the root/foliage ratio

The ratio of fine roots to foliage has been found to be relatively stable within stands of conifers, although large differences have been observed among stands (Santantonio 1989, Vanninen and Mäkelä 1999). Vanninen and Mäkelä studied seven stands in Finland that ranged in age from 20 to 250 years; they found that the ratio of fine root mass (< 2 mm diameter) to foliar mass ranged from about 0.4 in Scots pine stands on fairly fertile sites to almost 0.7 in stands on poor sites.

Observations with individual plants indicate that the root/shoot ratio is dependent on the availability of nutrients and, therefore, it has been hypothesized that this ratio would increase in older stands because of depletion of resources (McMurtrie et al. 1995, Vanninen et al. 1996). In contrast to Vanninen and Mäkelä (1999), some stand-level studies have found evidence of an age-related increase in the ratio of feeder root mass to foliage mass (Ovington 1957, Usol'tsev and Vanclay 1995). However, studies of nutrient cycling indicate that older stands are less dependent on the soil and precipitation in their nutrient supply because of efficient retranslocation and utilization of leaf litter (Helmisaari 1992, 1995). Model calculations based on these premises have suggested that, because growth of N-rich tissues is not increasing, the role of feeder roots as N suppliers becomes less significant so the root/foliage ratio could decrease in older stands (Nikinmaa 1992). That fairly constant root/foliage ratios have been observed suggests that other factors such as water and nutrients less labile than N may be more important in determining this ratio.

Trends in the sapwood/foliage ratio

We know of few data that can be used to estimate the time

course or developmental course of the ratio of sapwood mass to foliar mass within a stand. Vanninen et al. (1996) measured the mass of foliage and sapwood—including stems, branches and coarse roots—of 18 dominant Scots pine trees in the same stands in which the previously noted fine-root measurements were taken. The sapwood/foliage ratio increased almost linearly with tree height, although the three largest trees suggest a faster than linear increase in the ratio with increasing height. No differences in this relationship could be detected between poor and fertile sites (Figure 1). Furthermore, the below- and aboveground sapwood masses were linearly correlated. It is remarkable that estimates reported by Ryan and Waring (1992) for subalpine lodgepole pine stands, ranging from 40 to 240 years of age, seem to fall on the same line, though the range of variation is narrower (Figure 1). In subsequent studies, foliage and aboveground sapwood were measured on suppressed, co-dominant, and dominant trees on sparsely and densely stocked plots within four Scots pine stands of different ages (Mäkelä and Vanninen 1998, Vanninen and Mäkelä 2000). The resultant relationship between height and the ratio of sapwood mass to foliar mass was less clear because of the variation in density dependent factors like crown ratio, but the increasing trend with height was still evident (Figure 2).

Trends in specific photosynthetic production

To separate the different possible causes of change in the specific photosynthetic production, s_C, we divide it into two factors:

$$s_C = sI, \tag{17}$$

where s is the specific rate of photosynthesis of unshaded foliage (kg C (kg C year)$^{-1}$) and I is a variable (dimensionless) that converts the rate for unshaded foliage to the average rate for all foliage.

The relative reduction of photosynthesis caused by shading generally depends on the amount of shading leaf area (Monsi and Saeki 1953). Hence, if older stands had less leaf area than young stands, their photosynthetic production per unit foliage area would increase. However, this is only strictly true if stand structure remains the same, e.g., if a homogeneous canopy can be assumed in both old and young stands. Calculations and measurements of light interception in different canopies have shown that the component of self-shading is greater in larger crowns (Pukkala and Kuuluvainen 1987, Oker-Blom et al. 1989). This is probably because larger crowns tend to have more foliage per unit crown surface area than smaller crowns (Mäkelä and Vanninen 1998), and crown surface area has been found to be a key variable in determining the relationship between productivity and shading (Kuuluvainen 1988, Grace 1990). Clustering in a Scots pine stand—with all-sided leaf area index (LAI) = 10 and assuming ellipsoidal crowns—could cause about a 5 to 10% reduction in photosynthetic production compared with a stand of the same LAI but smaller trees and full crown coverage (Figure 3, redrawn from Mäkelä 1990).

Yoder et al. (1994) presented evidence that the specific rate of assimilation (i.e., net carbon exchange per unit of foliar dry matter) declines in some coniferous trees as they increase in stature. The decline is thought to result from a decrease in hy-

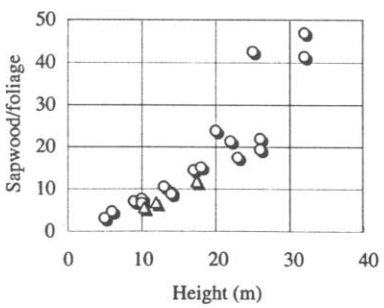

Figure 1. The ratio of sapwood mass to foliage mass as a function of tree height. Symbols: ○ represents 18 dominant Scots pine trees from different stands in southern Finland (data from Vanninen et al. 1996); sapwood includes stem, branch and coarse root components; △ represents the ratio calculated from stand average values of sapwood and foliage mass in three stands of subalpine lodgepole pine, plotted against stand average height (data from Ryan and Waring 1992).

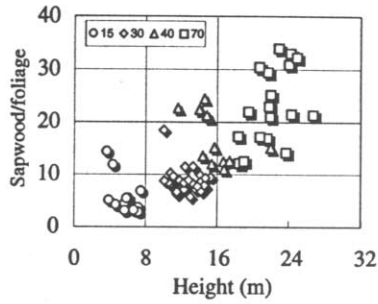

Figure 2. The ratio of sapwood mass to foliage mass as a function of tree height in four stands of Scots pine in southern Finland (data described in Mäkelä and Vanninen 1998, and Vanninen and Mäkelä 1999). Sapwood includes aboveground components only. Stands consist of sparse and dense plots and trees represent different dominance classes. Stand age is 15 years (○), 30 years (◇), 40 years (△) and 70 years (□).

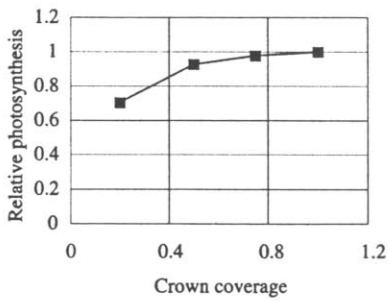

Figure 3. Dependence of annual stand photosynthesis on crown coverage in stands where (all-sided) LAI = 10 and crowns are assumed to be ellipsoidal with the ratio of crown width to length = 0.5 (data from Mäkelä 1990).

draulic conductance within stems and branches as they age and elongate, probably due to the increased chance of cavitation and number of branching internodes (Hubbard et al. 1999). Compared with younger trees, the lower hydraulic conductance of older trees may cause greater stomatal closure, which suppresses photosynthesis. In the ponderosa pines measured by Yoder et al. (1994), this effect could result in a difference of as much as 30% in daily net carbon exchange between trees of height 10 and 32 m.

Trends in specific rates of maintenance respiration

The specific rates of maintenance respiration have usually been assumed constant in a given environment for each type of tissue (Penning de Vries 1975). However, the tissue significant for wood respiration is difficult to isolate and measure. Ryan (1990) and Sprugel (1990) presented evidence that sapwood volume or mass should be taken as the basis for wood respiration, whereas cambial maintenance respiration, which tended toward proportionality to stem surface area, was of minor importance (cf. Stockfors and Linder 1998). Ryan (1990) measured respiration in trees of variable size (4–40 cm diameter at breast height) and age (40–240 years), with the conclusion that sapwood volume was the most significant determinant of maintenance respiration of the wood samples. Sprugel (1990) found that the respiration rate of branch sapwood was positively correlated with branch height, but this was thought to be associated with carbohydrate mobilization and CO_2 efflux from the transpiration stream.

Contrary to the findings of Ryan (1990) and Sprugel (1990), some recent evidence suggests that the specific rates of maintenance respiration may decrease with a general lowering of physiological activity as trees age. Lavigne and Ryan (1997) found that maintenance respiration, which they measured by the mature tissue method, was dependent not only on sapwood volume but also on the rate of production of sapwood. Lavigne et al. (1996) showed that maintenance respiration in balsam fir (*Abies balsamia* (L.) Mill.) was clearly related to sapwood volume, but there was also some indication that the relative thickness of sapwood affects the specific rate; stands with thicker sapwood generally had higher specific respiration rates. Linder and Troeng (1981) and Pruyn et al. (2000) reported that maintenance respiration was most active in the outer sapwood and also in sapwood cut from the upper portion of the stem, although the latter results were inconclusive.

These findings may indicate that part of maintenance respiration is substrate-driven, as interpreted by Thornley and Cannell (2000). Trees with higher rates of production would have more substrate available that could be used in futile respiration. As was noted, the model by Thornley (1991) provides for futile respiration because maintenance respiration is a saturating function of substrate carbon. It should be pointed out, however, that this structure is necessary for a substrate-based model to make sense; the absence of substrate-dependence would make respiration possible when there is no carbon.

Another explanation for the perceived size-dependence in specific rates of maintenance respiration could be related to the difficulties of measuring respiration. Sprugel (1990) pointed out that, especially in trees with thick bark, a large proportion of the carbon released in respiration may be caught by the transpiration stream and released higher up the stem or in branches where the bark is thinner and resistance to the diffusion of carbon dioxide is lower. If this were the case, species developing thick bark would show an age-related decline in the respiration measured over bark. In addition, it is not clear at which point in time (if ever) all respiration can be attributed to maintenance only. Linder and Troeng (1981) found that stem respiration in Scots pine reached its maximum about 1 month after the peak in stem growth. If processes other than growth are involved in construction respiration (e.g., nutrient uptake and phloem loading), as pointed out by Cannell and Thornley (2000), then it may be impossible to separate construction and maintenance respiration completely.

Because a significant proportion of maintenance respiration is thought to be driven by protein turnover (Penning de Vries 1975), the relative rates of maintenance respiration of different tissues should be proportional to the N concentrations of the tissues. Ryan (1995) and others have successfully tested the hypothesis that N concentrations of different tissues explain differences in their respiration rates in a given environment. Helmisaari (1990) looked for age- and size-related trends in the N concentrations of specific tissues of Scots pine, but found none.

Trends in specific rates of construction respiration

The direct construction cost of new growth (c_B in Equation 14) is tissue-specific, primarily depending on its concentration of proteins and lipids (Penning de Vries 1974). Although we have found little published evidence, it is conceivable that the average specific rate of construction respiration could change over the course of stand development. For example, a modeling study involving loblolly pine (*P. taeda* L.) suggests that the fraction of labile carbon allocated to wood production declines, whereas the fractions allocated to foliar and feeder-root production increase after stand closure (Valentine 1999). Much of the foliar and feeder-root production after closure is for turnover, i.e., the replacement of senescent tissue. Thus, it may be that, in a mature stand, the average new growth comprises a larger fraction of compounds that cost more to make, e.g., more lipids and proteins relative to cellulose.

The unit costs related indirectly to the construction of new biomass, such as the costs of nutrient uptake and phloem loading (Cannell and Thornley 2000, Thornley and Cannell 2000), may change more than the direct construction cost over time. These changes may be quantified by analyzing the development of the coefficients c_{NB}, c_{MB}, and λ in Equation 14. As was noted, the value of λ seems to vary little between stands of different structure, and the effect of the cost of phloem loading on E_2 is quite small.

The results of Helmisaari (1990) provide information about structural growth, nutrient uptake, and retranslocation in sapling, pole-stage, and mature Scots pine stands. The total N utilized per unit structural growth was about 0.009 kg N (kg C)$^{-1}$

in all stands, but retranslocation of N was about 30% in the young sapling stand compared with about 60% in the pole-stage and mature stands. This leaves an N demand of about 0.0063 kg N (kg C)$^{-1}$ in the sapling stand and about 0.0036 kg N (kg C)$^{-1}$ in the other stands. If all of this N were taken up as nitrate and reduced, the cost would be about 0.012 kg C (kg C structure)$^{-1}$ in the sapling stand and about 0.0072 kg C (kg C structure)$^{-1}$ in the pole-stage and mature stands. The costs would be only one-tenth of these values if all N were taken up as ammonium, using conversion factors provided by Cannell and Thornley (2000). In the boreal forest ecosystem, nitrate availability is low and, therefore, Scots pine acquires almost all of its N in the form of ammonium. A likely time dependence induced in c_B is on the order of 0.001, which represents less than 1% of total c_B.

The combined uptake of nine mineral nutrients in these same Scots pine stands was about 0.02 kg mineral (kg C)$^{-1}$ in structural growth in the sapling and mature stands and 0.01 kg mineral (kg C)$^{-1}$ in the pole-stage stand. Assuming a 50% recycling rate and the cost of uptake reported by Cannell and Thornley (2000), the corresponding c_{MB} would vary in the range 0.0003–0.0006 kg C (kg C)$^{-1}$.

Summary: evolution of NPP/GPP

We have cited published evidence that gives rise to the following postulates:

(1) the ratio of sapwood weight to foliage weight increases linearly, or faster than linearly, with tree height;

(2) the ratio of fine roots to foliage remains constant or increases with tree age or size;

(3) for any given LAI, shading caused by clustering of foliage decreases photosynthetic efficiency in larger trees;

(4) decreased hydraulic conductivity suppresses the photosynthetic production of foliage in larger trees;

(5) the (seasonal mean) specific rates of maintenance respiration are related to tissue N concentrations, which do not appear to have a pronounced age-related trend. However, the specific maintenance respiration of wood may be related to ring age or distance of the ring from meristematic tissue; and

(6) the overhead cost of construction of new tissue varies by tissue type and its chemical constituency, but possible trends in the average overhead cost over the course of stand development remain to be examined. The indirect cost of construction, including nutrient uptake and phloem loading, seems to vary little with age in Scots pine.

As already mentioned, we have not considered the dependence of respiration on temperature because we intend to compare the seasonal cumulative respiration and production rates over similar (average) seasons.

We can use the above conclusions to evaluate the development of E_1 and E_2 with stand age. To illustrate the phenomenon, we shall further assume that (1) the ratio of sapwood mass to foliage mass is linear with height, (2) the ratio of fine root mass to foliage mass is constant over time, and (3) the stand-level LAI is constant over time. We demonstrate that these simplifications do not affect the qualitative nature of the calculations. Further, we shall assume, *pro tem*, that the specific construction respiration is constant, but the sensitivity of the result to this assumption will be examined.

In accordance with the above assumptions, we fitted the data in Figure 1 (i.e., sapwood/foliage ratio versus tree height) with a straight line through the origin, and we fixed the fine root/foliage ratio, R/F, at 0.4. We assumed a linear decrease with tree height of the specific unshaded photosynthetic rate, s, such that:

$$s = s_0 - s_1 H. \tag{18}$$

We assumed that s is 30% less than the maximum value when H = 30 m. This decrease was assumed to incorporate both the impacts of clustering and decreased hydraulic conductivity, although clustering actually decreases in the early phase before canopy closure. The hydraulic conductivity is causally more closely related to the size of the crown than tree height (Hellkvist et al. 1974, Tyree 1988), but these variables are usually correlated with each other. For simplicity, we used the method suggested by Ryan (1990) to estimate the specific rate of maintenance respiration on the basis of tissue N concentrations (Helmisaari 1990) and mean annual temperature, giving 0.5 g C (g C year)$^{-1}$ for foliage and m_W = 0.03 g C (g C year)$^{-1}$ for sapwood. The foliage parameter was also used for fine roots. Korpilahti (1988) estimated from extensive measurements combined with model calculations that the annual photosynthetic production of unshaded foliage of Scots pine seedlings in southern Finland is about 5 kg C (kg C year)$^{-1}$; thus, we fixed s_0 = 5. Assuming an all-sided LAI of 6, which corresponds to 2500–3000 kg C ha^{-1} (Hari et al. 1982), the light interception model by Oker-Blom et al. (1989) yields a 35% reduction of photosynthesis from the maximum value, i.e., I = 0.65 (Mäkelä 1990).

We assumed a direct construction cost of c_B = 0.25, which corresponds to Y_G = 0.8 (Cannell and Thornley 2000), for the calculation of E_2. For calculating E_1, we used c_B = 0.30, the higher value covering for indirect costs (e.g., phloem loading, N and mineral uptake). These assumptions yield a clearly decreasing trend in the NPP/GPP ratio as a function of tree height and, hence, time (Figure 4a). The time courses of E_1 and E_2 are almost identical for the given parameter values.

To get an idea of the robustness of the decreasing trend, we also evaluated E_1 and E_2 under two additional assumptions: (1) s is constant over time, i.e., photosynthesis is not slowed by hydraulic constraints; and (2) the specific rate or respiration of sapwood decreases substantially with increasing tree height. The first assumption was quantified by setting s_1 = 0 in Equation 18, and for the second we assumed:

$$m_W = 0.04 - 0.0008H. \tag{19}$$

To make our results comparable with those presented by Thornley and Cannell (2000), we graphed R_T/P versus time (where $R_T = R_C + R_M$) using a measured time-dependence of H (Figures 4b and 4c). The two assumptions yield narrow ranges (0.4–0.65) and similar time-dependences for R_T/P. If both as-

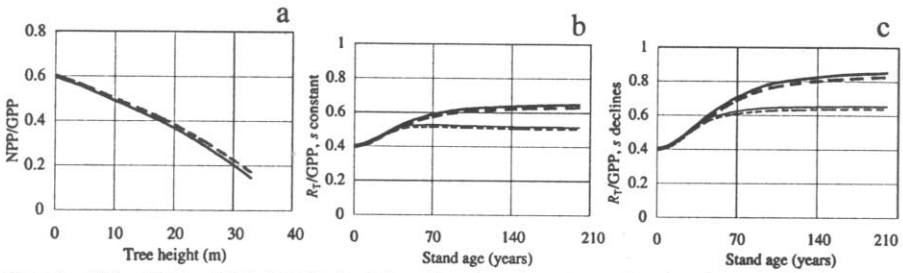

Figure 4. Development of NPP/GPP and R_T/GPP with stand age and height under different assumptions. (a) The NPP/GPP ratio as a function of mean tree height using the basic assumptions and parameter values (see text): E_1 (Equation 9), broken line; E_2 (Equation 16) solid line; (b) R_T/GPP (= $1 - E_i$) as a function of stand age when there is no decline in the specific photosynthetic rate with stand age: $1 - E_1$, dashed line; $1 - E_2$, solid line. Thick lines indicate a constant specific rate of sapwood maintenance respiration, m_W ; thin lines indicate a decline in m_W as hypothesized in Equation 19; (c) as in (b) but the specific photosynthetic rate, s, declines as hypothesized in Equation 18.

sumptions are applied simultaneously, the range of variation is only 0.4–0.55.

It is noteworthy that no stand dynamics other than height growth entered these calculations. The estimated photosynthetic productivity therefore corresponds to the same amount of LAI throughout. Changes in stand LAI with tree height will change the picture to some extent through changes in I. If I was larger during early stand development, because of a smaller LAI, the early values of R_T/P would be somewhat smaller (E_1 and E_2 would be larger).

A dynamic model of NPP/GPP

The above analysis demonstrated the dependence of E_1 and E_2 on tree height through the empirical correlation between W/F and height. Because there seems to be little quantitative difference between E_1 and E_2, we will concentrate on the former. As already pointed out, factors affecting E_1 at the stand level include LAI, canopy structure, specific leaf area, and the ratio of fine roots to foliage, R/F. Of these, LAI, in particular, changes dynamically during stand development, especially between stand initiation and closure. To analyze further the dynamics of E_1, we use the stand-growth model *Pipestem* (Valentine et al. 1997), which is based on pipe-model theory (Shinozaki et al. 1964*a*, 1964*b*) and the concept of functional balance.

The essence of these theories from the point of view of stand simulation is that they allow us to express R and W as functions of F. Let A (m^2 ha^{-1}) denote the cross-sectional area of sapwood beneath the canopy of the stand and let L (m) denote the average length of the sapwood pipes that run from feeder roots to foliage. Parameterizing the components of live dry matter in terms of A and L:

$$F = z_F A, \tag{20a}$$

$$R = z_R A, \tag{20b}$$

$$W = z_W AL, \tag{20c}$$

where z_F and z_R are foliar and feeder-root dry matter per unit cross-sectional area of sapwood (kg C m^{-2}), respectively, and z_W is woody dry matter per unit wet volume (kg C m^{-3}). Equation 20a is derived directly from pipe-model theory. Solving this equation for A and substituting into Equations 20b and 20c:

$$R = \frac{z_R}{z_F} F, \tag{21a}$$

$$W = \frac{z_W}{z_F} FL. \tag{21b}$$

Equation 21a indicates that the ratio of feeder-root to foliar dry matter is constant, which is consistent with (a) the empirical results for Scots pine stands presented above and (b) the concept of functional balance (e.g., Mäkelä 1986, 1997). Furthermore, Equation 21b provides for proportionality between the sapwood/foliage ratio and the average length of sapwood pipes, L. Because L tends toward proportionality with tree height, Equation 21b is consistent with the data presented in Figure 1. Exact proportionality between L and tree height is never strictly true because the former varies with crown ratio and stem/root ratio (i.e., the same factors that contribute to the scatter among plots within stands in Figure 2).

Under the assumptions of Equation 21, the ratio of NPP to GPP, i.e., E_1, can now be expressed in terms of the variables I and L:

$$E_1 = \frac{1}{1+c_B}\left(1 - \frac{m_F + m_R' + m_W' L}{(s_0 - s_1' L)I}\right), \tag{22}$$

where $s_1' = s_1 H/L, m_R' = (z_R/z_F)m_R$, and $m_W' = (z_W/z_F)m_W$. Similarly, NPP, which is codified as G_B, can be expressed in terms of I, L and F:

$$G_B = \frac{F}{1+c_B}\left((s_0 - s_1' L)I - m_F - \frac{z_R}{z_F} m_R - \frac{z_W}{z_F} m_W L\right),$$

$$= \frac{F}{1+c_B}(s_0 I - m_F - m_R' - (s_1' I + m_W')L). \tag{23}$$

These models of E_1 and NPP are consistent with *Pipestem*, so we can use the latter model to predict time courses for E_1, NPP, and other stand-level variables under different assumptions. First, however, let us examine Equation 23.

The time course of NPP is provided by a graph of G_B versus t. It is apparent from the right-hand side of Equation 23 that different sets of parameter values can produce essentially the same time course for NPP. Leaf area index may decrease after stand closure (Ryan et al. 1997), but simultaneously, clumping increases and specific leaf area decreases (van Hees and Bartelink 1993), so let us assume, for simplicity, that I takes a constant value I^*. Under this restriction, the time course of NPP should be affected little if the values of s_l' and m_W' are altered, so long as the values are nonnegative and constrained by:

$$s_l' I^* + m_W' = \text{constant}. \quad (24)$$

Similarly, there is no effect on the time course of NPP if $1 + c_B$ and the values of the other parameters are varied in proportion. A graphic demonstration of these claims is provided by runs of *Pipestem*.

Alternative assumptions

We used *Pipestem* to predict time courses of NPP, GPP, R_M, and E_l under each of three assumptions with parameter values appropriate for Scots pine. *Pipestem* also provided predicted time courses of readily observable, stand-level response variables, including average tree height, quadratic mean diameter, stem density and total dry matter. Because *Pipestem* is a deterministic carbon-allocation model, the time courses of the "observable response variables" are determined, in large part, by the time course of NPP.

(*i*) Under an *increasing-respiration assumption*, the specific rate of photosynthesis is unrelated to the length of the sapwood pipes that connect leaves to feeder roots ($s_l = 0$). However, $m_W > 0$, so the rate of consumption of carbon substrate for maintenance of sapwood pipes increases with the average length of the sapwood pipes, L. This assumption was implemented with $s_0 = 5$, $s_l' = 0$, $z_F = 250.0$, $z_W = 200.0$, and $m_W = 0.06$, which gave $s_l' I^* + m_W' = 0.048$.

(*ii*) Under a *decreasing-photosynthesis assumption* (based on the hydraulic limitation hypothesis of Ryan and Yoder (1997)), the specific rate of photosynthesis decreases with the elongation of the average length of the sapwood pipes ($s_l' > 0$). We implemented this hypothesis with $s_l' = 0.037$ and $m_W = 0.03$; the other parameter values were unchanged. These values gave $s_l' I^* + m_W' = 0.048$, where $I^* = 0.65$.

(*iii*) Under a *constant-ratio assumption* (based on the analysis of Waring et al. 1998), NPP is a constant fraction of GPP. We assumed that $E_l = 0.5$, which implies $R_C + R_M = 0.5P$. This hypothesis cannot be simulated with constant values for the specific maintenance respiration parameters. If maintenance respiration and GPP are expressed as in the model, then this requires:

$$(m_F + m_R' + m_W' L) F = (1 - E_l (1 + c_B)) \times \quad (25)$$

$$(s_0 - s_l' L) IF,$$

where the left-hand side is R_M, $(1 - E_l (1 + c_B))$ is the constant of proportionality and the remainder of the right-hand side is GPP. Because L increases with time, no positive constant values of the parameters can satisfy this equation, except in the unlikely event that an increase in I would more than counteract the effect of the increase in L on GPP. Thus, one or more of the specific rates of respiration must be variable, decreasing in value with increasing L (and tree height).

The constant-ratio assumption can be forced with no lack of generality by setting $m_F = m_R = m_W = 0$ and $c_B = 1$. This will lead to $E_l = 0.5$, but the parameter c_B is now interpreted as the combined effect of both maintenance and construction respiration, which must be proportional to the rate of production of dry matter, G_B, for E_l to be constant. Because the components of respiration are not differentiated, we can assume, e.g., that $R_C = 0.15P$ and $R_M = 0.35P$. To bring the time course of NPP approximately in line with those generated under the other two assumptions, we used $s_0 = 6.2$ and $s_l' = 0.12$. The value of s_0 was elevated because the high rate of respiration, $R = 0.5P$, depressed NPP at the outset of stand development compared to the two other assumptions. Because the value of s_0 was elevated, the value of s_l' also had to be elevated to depress NPP in the later stages of stand development.

In all solutions of the model, the value of I decreased from nearly 1 to 0.65 as the model stand progressed from planting, at a density of 2500 trees ha^{-1}, to closure.

Solutions

Considerable differences corresponding to the three different assumptions are seen in the time courses of GPP, maintenance respiration, and the ratio of NPP to GPP (Figure 5). Yet the time courses of NPP, as well as the development of some standard forestry variables (Figure 6), are remarkably similar,

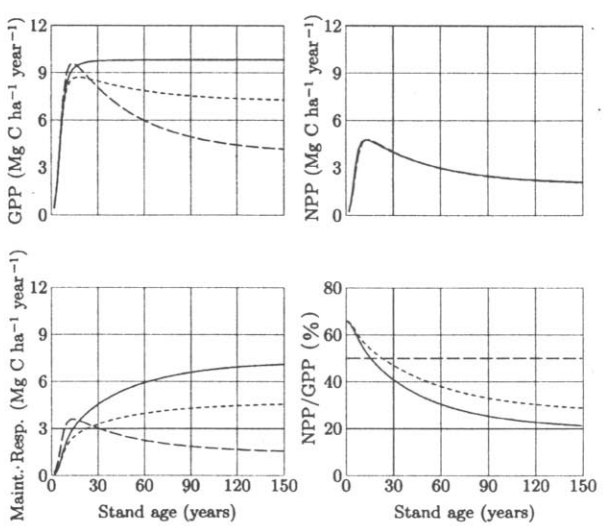

Figure 5. Time courses of carbon-balance components: increasing-respiration assumption, solid line; decreasing-photosynthesis assumption, short dashed line; and the constant-ratio assumption, long dashed line.

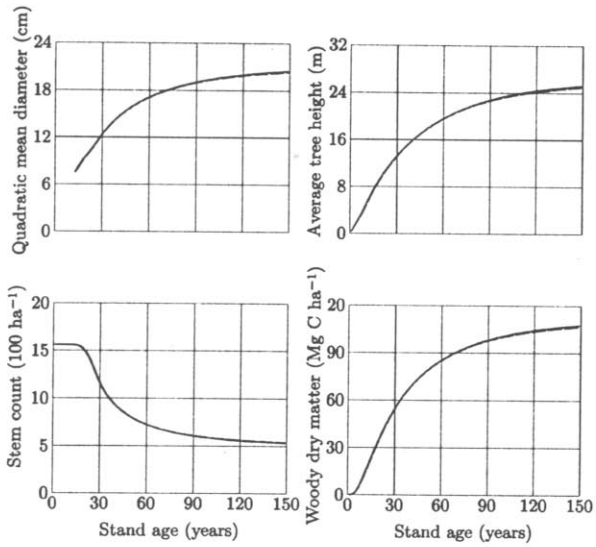

Figure 6. Time courses of stand-level response variables: increasing-respiration assumption, solid line; decreasing-photosynthesis assumption, short dashed line; and the constant-ratio assumption, long dashed line. Note: the dashed lines are virtually indistinguishable from the solid lines.

demonstrating that models based on different assumptions can yield essentially the same solutions.

Projected values of GPP, NPP, the ratio of NPP to GPP, and maintenance respiration are plotted against mean tree height in Figure 7. Also plotted against mean tree height are two other ratios: (1) NPP per unit foliage mass and (2) units of sapwood mass per unit foliage mass. The projections of units of sapwood per unit foliage agree quite well with the observations of Vanninen et al. (1996) for Scots pine (see Figure 1). The linear decrease in the ratio of NPP to foliage mass (after closure) also agrees with observation (Albrektson 1980).

The projected rate of sapwood respiration (maintenance + construction) per unit mass of sapwood (kg C year^{-1} (kg C)$^{-1}$) is plotted against mean tree height in Figure 8. This rate decreases with increasing age, stock of sapwood, and mean tree height under both the increasing respiration and decreasing photosynthesis assumptions. This decrease occurs even though the two specific rates of respiration, c_W and m_W, are fixed constants. Projected rates of total sapwood respiration per unit mass of sapwood also decrease with increasing mean tree height under the constant-ratio assumption with additional assumptions about carbon allocation. Because sapwood respiration is not differentiated under the constant-ratio assumption, we specified:

$$c_W G_W + m_W W = 0.5P - c_F G_F - c_R G_R - m_F F - m_R R, \quad (26)$$

where $c_F = c_R = 0.3$ and $m_F = m_R = 0.5$. Under the additional assumption of a fixed construction cost for sapwood ($c_W = 0.3$), the specific rate of maintenance respiration of sapwood varies as a function of P, G_B, F and R, i.e.:

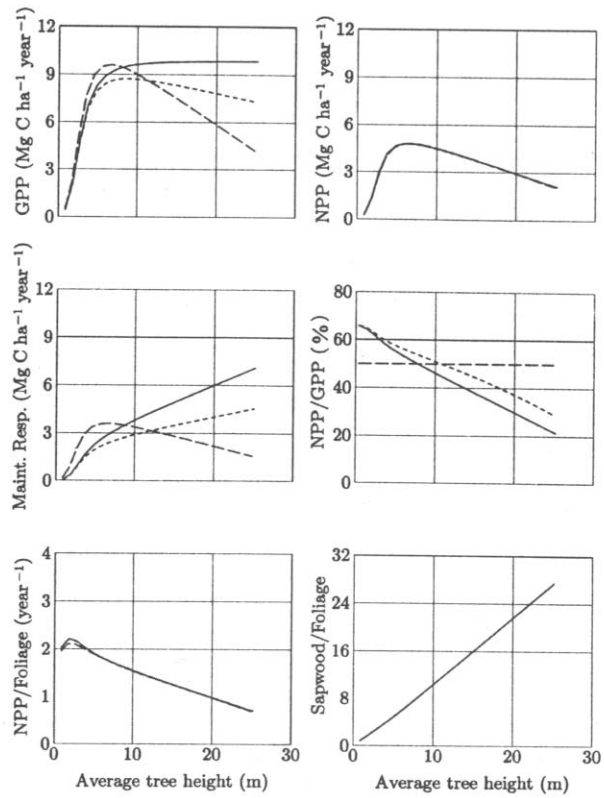

Figure 7. Carbon-balance and dry-matter components versus average tree height: increasing-respiration assumption, solid line; decreasing-photosynthesis assumption, short dashed line; and the constant-ratio assumption, long dashed line.

$$m_W(\cdot) = \frac{0.5P - c_B G_B - m_F F - m_R R}{W}. \quad (27)$$

For our particular set of parameter values, $m_W(\cdot)$ decreases rapidly from a high value before closure to a low value afterwards, eventually becoming negative as the model stand ma-

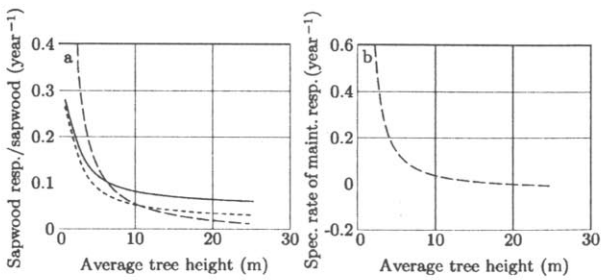

Figure 8. (a) Total (construction + maintenance) sapwood respiration per unit mass of sapwood versus average tree height for: increasing-respiration assumption, solid line; decreasing-photosynthesis assumption, short dashed line; constant-ratio assumption, long dashed line. (b) Specific rate of maintenance respiration of sapwood for the constant-ratio hypothesis, assuming all other rates of respiration are fixed (see text).

tures (Figure 8b). Nonnegativity can be forced by reducing one or more of the values of the fixed parameters. Nevertheless, our result shows graphically that the constant-ratio assumption is not consistent with fixed specific rates of respiration.

It has been suggested that the specific rate of maintenance respiration of sapwood may decrease over the course of stand development, as trees grow taller. The effects of a fixed rate, $m_W = 0.03$, are compared with the effects of the variable rate provided by Equation 19 in Figure 9. Use of Equation 19, in connection with the decreasing-photosynthesis assumption, effected a fairly constant NPP/GPP ratio after Age 60 and a slight decreasing trend in the total maintenance respiration of the stand after Age 90. The effects of an alternative variable rate, i.e., $m_W = 0.04 - 0.0004H$, differ little from the effects of the fixed rate. The effects of a pattern of respiration suggested by the measurements of Pruyn et al. (2000), that outer sapwood respires at twice the rate of middle or inner sapwood, is also demonstrated in Figure 9. Trees produce outer sapwood that gradually converts to middle and then inner sapwood. Projected sapwood cross-sectional area reaches a maximum (A_{max}) at stand closure, coincident with the foliar maximum. We assumed that the total rate of maintenance respiration of sapwood (R_{MW}) was provided by:

$$R_{MW} = m_W z_W L \left(\begin{array}{l} \min\left(A, \frac{A_{max}}{3}\right) + \\ \frac{1}{2}\max\left(0, A - \frac{A_{max}}{3}\right) \end{array} \right). \quad (28)$$

We used m_W(outer) = 0.045, so if $A \leq A_{max}/3$, then R_{MW} = 0.045 W. If $A = A_{max}$, then 1/3 of the sapwood respires with a specific rate of m_W(outer) = 0.045 and the remainder, the middle and inner sapwood, respires with a specific rate of m_W (mid-inner) = 0.0225, which provides $R_{MW} = 0.03W$. Thus, as A increases from $A_{max}/3$ to A_{max}, the rate of sapwood maintenance respiration decreases from $R_{MW} = 0.045W$ to $R_{MW} = 0.03W$. The effects of this varying specific rate of maintenance respiration (i.e.,"inner–outer assumption") are indistinguishable in Figure 9 from the effects of a constant specific rate of $m_W = 0.03$.

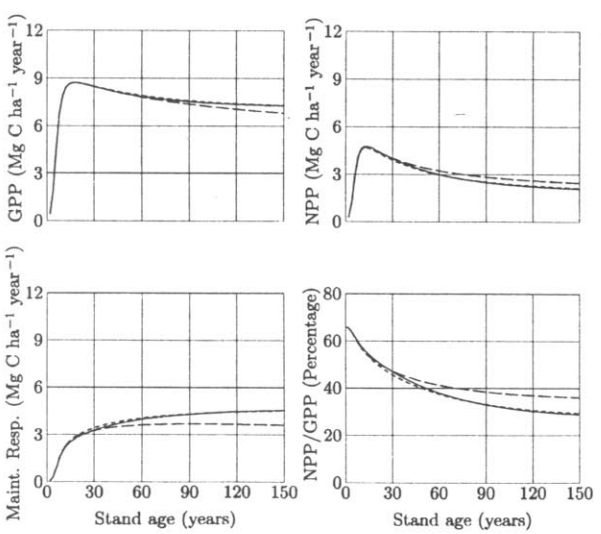

Figure 9. Decreasing-photosynthesis assumption ($s_1 = 0.037$) with variable specific rate of sapwood respiration: $m_W = 0.03$, solid line; $m_W = 0.04 - 0.0004H$, short dashed line; $m_W = 0.04 - 0.0008H$, long dashed line; inner–outer assumption (see text), which is indistinguishable from the solid lines.

Parameter identification

The modeling exercise demonstrates that the assumption E_1 = 0.5 may produce accurate predicted time courses for response variables of interest, but so do other assumptions. The modeling exercise also shows that parameter values are not identifiable from the time course of NPP. In other words, if one were to fit the model to produce agreement between the predicted time course of NPP and a data stream for NPP, the resultant parameter values most likely would be in error because different sets of parameter values could provide equally good fits to the data.

Measurements of mean or dominant height, basal area, and stand volume are easily obtained and, therefore, are commonly used to judge the accuracy of stand-growth models (Korol et al. 1996, Landsberg and Waring 1997, Bartelink 1998). However, if the time courses of these variables really are determined by the time course of NPP, then data streams for these variables will be of no help in estimating the values of the physiological parameters.

Needed are data streams of both NPP and GPP or both GPP and autotrophic respiration. However, measurements of total (above- and belowground) NPP, and stand-level GPP and respiration are generally unavailable, at least for prolonged periods. Eddy covariance methods yield long streams of net ecosystem exchange, but E_1 can not be calculated from these streams unless both ecosystem and autotrophic respiration are measured or estimated accurately.

Discussion

We have cited evidence from published studies and presented data for Scots pine in Fenno-Scandia, which, in combination, suggest that maintenance respiration of an increasing amount of sapwood is one contributing cause of the downward trend in NPP following closure in even-aged stands. Hunt et al. (1999) recently concluded that increasing respiration was the primary mechanism responsible for the age-related decline in NPP in 25 balsam fir stands. Their conclusion was based on extensive measurements of stem respiration in dissimilar stands (Lavigne et al. 1996) and a modeling analysis. A line of research initiated by Ryan and Waring (1992) indicates that a downward trend in the rate of photosynthesis may exacerbate the decline of NPP as stands increase in height. Decreasing photosynthesis appears to be the primary mechanism for the decline in NPP in stands of some coniferous species in western North America. If both mechanisms are operative, then E_1, the

ratio of NPP to GPP, cannot be constant. The constant ratio is possible only if respiration has a downward trend proportional to that of photosynthesis.

Our conclusion that increasing respiration—most likely in combination with decreasing photosynthesis—contributes to a downward trend in NPP is based largely on data that indicate an increase in the ratio of sapwood mass to foliar mass with increasing tree height in Scots pine. Consistent with pipe-model theory, we assumed, in our calculations and model analysis, that this relationship was linear, although the empirical evidence indicated the possibility of a slightly faster than linear increase in this ratio with increasing height. However, if the amount of sapwood increased faster than theorized, the respiratory cost of sapwood would increase proportionately, and would thus reinforce our conclusions. The same argument applies to the ratio of fine roots to foliage. If more fine roots per unit foliage are maintained in older than in younger stands, as indicated by some studies (Ovington 1957, Usol'tsev and Vanclay 1995), then the amount of respiring tissue relative to photosynthesizing tissue increases as trees grow and age.

Our analysis suggests that, over long periods and in a stable environment, the time courses of respiration are similar under the classic model (Penning de Vries 1974, 1975) and under the new process-based formulation presented by Cannell and Thornley (2000) and Thornley and Cannell (2000). These results do not preclude the possibility that the two models may differ significantly over shorter time periods and under environmental variation (Dewar et al. 1998). Our results may also be considered conditional on our choice to ignore futile respiration in the derivation of E_2. However, the model of Thornley and Cannell (2000) provides little justification for such a futile component. Although their model provides for substrate limitation, the specific rates of maintenance respiration saturate under increasing substrate concentrations, so excessive waste of carbon in futile respiration does not occur. Depending on the parameter values, the model could allow for some change in the specific maintenance rates, but because substrate concentrations do not necessarily decrease with age, unequivocal conclusions are difficult to draw.

Our calculations and model analysis also assumed, for simplicity, that the foliar biomass in a stand remains constant after canopy closure. There is conflicting evidence as to whether the foliar mass stays level or decreases in older stands (Kira and Shidei 1967, Forrest and Ovington 1970, Marks 1974, Albrektson 1980, Sprugel 1984). Studies of chronosequences suggest that LAI decreases after closure (e.g., Ryan et al. 1997, Smith and Resh 1999), but the time courses of LAI and foliar biomass are not necessarily coincident. Decreasing LAI may be accompanied by counteracting processes, such as increased clumping of foliage and a reduction in average specific leaf area (van Hees and Bartelink 1993). Each of these factors affects the specific rate of photosynthesis, which, in our model, is modified by I. It is not clear what the time course of I would be under the assumption that foliar mass decreases as stands age. In test simulations with *Pipestem*, a decreasing trend in foliar mass had little effect on the time course of E_1.

A further assumption was that the average specific construction cost, c_B, does not change over the lifetime of the stand. However, the cost is compound-specific, such that protein- or lipid-rich tissue is more costly to construct than, say, cellulose (Penning de Vries 1974). If the proportions of different tissues change over the course of stand development, it might also cause the average value of c_B to change. However, in a test run of the model, tissue-specific construction costs had little effect on the time course of NPP.

Because futile respiration was not included in the model, we analyzed the possibility of variable maintenance rates separately. The results were not sensitive to a moderate decrease of the woody maintenance rate with tree height. On the other hand, a stronger decrease led to decreasing absolute maintenance respiration with an increasing amount of sapwood. Because such a decrease seems hardly plausible, we believe that our results are robust even if allowing for the possibility of maintenance rates decreasing within a measured range. Pruyn et al. (2000) measured rates of CO_2 release from the outer sapwood growth rings that were twice the rates of release in middle or inner rings. However, if sapwood cross-sectional area reaches a maximum at closure, then the two rates should have a fairly stable average after closure.

By contrast, the constant-ratio hypothesis implied considerable temporal changes in the specific rates of maintenance respiration. On the one hand, there would be notable excess respiration in young plants, with specific rates of maintenance respiration nearly 100-fold greater than theoretical values computed either from stoichiometry or from the process rates suggested by Cannell and Thornley (2000). On the other hand, the constant-ratio hypothesis seems to imply low maintenance rates in older stands.

That the specific rate of maintenance respiration of live woody tissue should decrease as the amount of tissue increases suggests that a tree wastes substrate when respiration is proceeding at greater than some minimal rate that maintains normal function. From a Darwinian perspective, such waste of substrate seems improbable. We suppose that normal function could be defined to include the consumption of "excess substrate," in which case maintenance respiration should not be characterized as substrate limited, but rather as "substrate driven," such as in the implications of the constant-ratio hypothesis. Whether substrate is ever produced in amounts that exceed the capacities of "non-maintenance sinks" is an open question.

Our model suggests that the specific rate of total sapwood respiration strongly decreases with increasing tree height (as demonstrated in Figure 8), stand age and sapwood mass. Because the separation of maintenance and construction respiration by *in situ* measurements is difficult, any confusion of maintenance and construction respiration would easily lead to the observation of a growth-dependent component in maintenance respiration, which would lead to the conclusion that specific maintenance respiration decreases with tree size. In principle, maintenance respiration should be measured in detached wood where no growth can occur, but this may lead to a disturbance of the system as a result of injury.

The studies of the correlation between respiration rates and

N concentrations in sapwood, and the separate studies that indicate that N concentrations do not change significantly with tree age, suggest that the annual specific rate of maintenance respiration of sapwood is more or less constant over the course of stand development. A constant specific rate does not accord with maintenance respiration being substrate-limited or substrate-driven. However, because results of separate studies must be combined to achieve a conclusion, its validity is uncertain. More comprehensive, combined studies of both the correlation between respiration and N concentration and the long-term dynamics of N concentrations would help eliminate this uncertainty.

We have demonstrated that agreement of our model's response with observable stand-level data is no guarantee of accuracy at the physiological level. This result illustrates the problems related to the statistical calibration of physiologically based models in general. It is often the case that certain parameter values are not identifiable through model fitting (Luenberger 1979). We have shown, for example, that a high value of one parameter (m_W) may compensate for a low value of another (s_1) to produce accurate time courses for observed variables. Such effects are often discovered in a statistical fitting of a model with many parameters (Sievänen and Burk 1993). Apart from correlations among parameters, it currently seems that the most serious obstacle for statistical fitting of forest growth models is a lack of long-term data streams for GPP and respiration (Mäkelä et al. 2000). It is clear that any particular measurement of NPP and growth will be consistent with an infinite set of GPP and respiration values. Thus, unless direct measurements of GPP and respiration can be conducted at the stand level, the related parameters should be calibrated at the physiological level whenever possible.

In conclusion, our indirect evidence suggests that the ratio of NPP to GPP declines over the course of development of an even-aged forest stand, but the significance of this decline from the point of view of overall primary productivity depends on the relative importance of other growth limiting factors. It seems highly probable, at least for Scots pine in Fenno-Scandia, that the assumption of a constant E_1 is not justified over the entire rotation length of a stand. It is possible, however, that this assumption could be put to some good use in studies covering shorter periods of time, especially because it obviates the need for the, often problematic, explicit measurement of respiration (Waring et al. 1998). However, more direct evidence is required to confirm our conclusion, preferably in the form of remeasurements of E_1 over time in a chronosequence of stands.

References

Albrektsón, A. 1980. Biomass of Scots pine (*Pinus sylvestris* L.) amount, development, methods of mensuration. The Swedish University of Agricultural Sciences. Dept. of Silviculture. Report No. 2, Umeå, 189 p.

Bartelink, H.H. 1998. Simulation of growth and competition in mixed stands of Douglas fir and beech. Thesis Landbouwuniv., Wageningen, 222 p.

Battaglia, M. and P. Sands. 1997. Modelling site productivity of *Eucalyptus globulus* in response to climatic and site factors. Aust. J. Plant Physiol. 24:831–850.

Cannell, M.G.R. 1989. Physiological basis of wood production: a review. Scand. J. For. Res. 4:459–490.

Cannell, M.G.R. and J.H.M. Thornley. 2000. Modelling the components of plant respiration: some guiding principles. Ann. Bot. 85: 45–54.

Chung, H.-H. and R.L. Barnes. 1977. Photosynthate allocation in *Pinus taeda*. I. Substrate requirements for synthesis of shoot biomass. Can. J. For. Res. 7:106–111.

Dewar, R.C., B.E. Medlyn and R.E. McMurtrie. 1998. A mechanistic analysis of light and carbon use efficiencies. Plant Cell Environ. 21:573–588.

Forrest, W.G. and J.D. Ovington. 1970. Organic matter changes in an age series of *Pinus radiata* plantations. J. Appl. Ecol. 7:177–186.

Gifford, R.M. 1994. The global carbon cycle: a viewpoint on the missing sink. Aust. J. Plant Physiol. 21:1–15.

Grace, J.C. 1990. Modeling the interception of solar radiant energy and net photosynthesis. *In* Process Modeling of Forest Growth Responses to Environmental Stress. Eds. R.K. Dixon, R.S. Meldahl, G.A. Ruark and W.G. Warren. Timber Press, Portland, OR, pp 142–158.

Hari, P., S. Kellomäki, A. Mäkelä, P. Ilonen, M. Kanninen, E. Korpilahti and M. Nygren. 1982. Metsikön varhaiskehityksen dynamiikka. Summary: dynamics of early development of tree stand. Acta For. Fenn. 177:1–42. In Finnish.

Hellkvist, J., G.P. Richards and P.G. Jarvis. 1974. Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. J. Appl. Ecol. 7:637–667.

Helmisaari, H.-S. 1990. Nutrient retranslocation within *Pinus sylvestris*. Academic dissertation. Univ. Joensuu, Finland, 106 p.

Helmisaari, H.-S. 1992. Nutrient retranslocation in three *Pinus sylvestris* stands. For. Ecol. Manage. 51:347–367.

Helmisaari, H.-S. 1995. Nutrient cycling in *Pinus sylvestris* stands in eastern Finland. Plant Soil 168/169:327–336.

Hubbard, R.M., B.J. Bond and M.G. Ryan. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiol. 19:165–172.

Hunt, E.R., Jr., M.B. Lavigne and S.E. Franklin. 1999. Factors controlling the decline of net primary production with stand age for balsam fir in Newfoundland assessed using an ecosystem simulation model. Ecol. Model. 122:151–164.

Keith, H., R.J. Raison and K.L. Jacobsen. 1997. Allocation of carbon in a mature eucalypt forest and some effects of soil phosphorus availability. Plant Soil 196:81–99.

Kira, T. 1975. Primary production of forests. *In* Photosynthesis and Productivity in Different Environments. Ed. J.P. Cooper. Cambridge Univ. Press, Cambridge, pp 5–40.

Kira, T. and T. Shidei. 1967. Primary production and turnover of organic mater in different forest ecosystems of the Western Pacific. Jpn. J. Ecol. 17:70–87.

Korol, R.L., K.S. Milner and S.W. Running. 1996. Testing a mechanistic model for predicting stand and tree growth. For. Sci. 42: 139–153.

Korpilahti, E. 1988. Photosynthetic production of Scots pine in the natural environment. Acta For. Fenn. 202:1–71.

Küppers, M. and E.-D. Schulze. 1985. An empirical model of net photosynthesis and leaf conductance for the simulation of diurnal courses of CO_2 and H_2O exchange. Aust. J. Plant Physiol. 12: 13–21.

Kuuluvainen, T. 1988. Crown architecture and stemwood production in Norway spruce (*Picea abies* (L.) Karst.). Tree Physiol. 4: 337–346.

Landsberg, J.J. and R.H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manage. 95:209–228.

Lavigne, M.B. and M.G. Ryan. 1997. Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. Tree Physiol. 17:543–551.

Lavigne, M.B., S.E. Franklin and E.R. Hunt, Jr. 1996. Estimating stem maintenance respiration rates of dissimilar balsam fir stands. Tree Physiol. 16:687–695.

Lavigne, M.B., M.G. Ryan, D.E. Anderson, et al. 1997. Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites. J. Geophys. Res. 28:977–985.

Linder, S. 1985. Potential and actual production in Australian forest stands. *In* Research for Forest Management. Eds. J.J. Landsberg and W. Parsons. Proceedings of a conference organized by the Division of Forest Research, CSIRO, Melbourne, Australia, pp 11–35.

Linder, S. and E. Troeng. 1981. The seasonal variation in stem and coarse root respiration of a 20-year-old Scots pine (*Pinus sylvestris* L.). Mitt. Forstl. Bundes-Versuchsanst. Wien 142:125–139.

Luenberger, D.G. 1979. Introduction to dynamic systems. Theory, models, and applications. John Wiley, New York, 446 p.

Mäkelä, A. 1986. Implications of the pipe model theory on dry matter partitioning and height growth in trees. J. Theor. Biol. 123: 103–120.

Mäkelä, A. 1990. Adaptation of light interception computations to stand growth models. Silva Carelica 15:221–239.

Mäkelä, A. 1997. A carbon balance model of growth and self-pruning in trees based on structural relationships. For. Sci. 43:7–24.

Mäkelä, A. and P. Vanninen. 1998. Impacts of size and competition on tree form and distribution of above-ground biomass in Scots pine. Can. J. For. Res. 28:216–227.

Mäkelä, A., J. Landsberg, A.R. Ek, T.E. Burk, M. Ter-Mikaelian, G.I. Ågren, C.D. Oliver and P. Puttonen. 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. Tree Physiol. 20:289–298.

Malhi, Y., D.D. Baldocchi and P.G. Jarvis. 1999. The carbon balance of tropical, temperate and boreal forests. Plant Cell Environ. 22: 715–740.

Marks, P.L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecol. Monogr. 44:73–88.

McCree, K.J. 1970. An equation for the respiration of white clover plants grown under controlled conditions. *In* Prediction and Measurement of Photosynthetic Productivity. Ed. I. Setlik. Pudoc, Wageningen, pp 221–229.

McMurtrie, R.E., S.T. Gower and M.G. Ryan. 1995. Forest productivity: explaining its decline with stand age. Bull. Ecol. Soc. Am. 76:152–154.

Medlyn, B.E. and R.C. Dewar. 1999. Comment on the article by R.H. Waring, J.J. Landsberg and M. Williams relating net primary production to gross primary production. Tree Physiol. 19:137–138.

Monje, O. and B. Bugbee. 1998. Adaptation to high CO_2 concentration in an optimal environment: radiation capture, canopy quantum yield and carbon use efficiency. Plant Cell Environ. 21:315–324.

Monsi, M. and T. Saeki. 1953. Über den Lichtfactor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Jpn. J. Bot. 14:22–52.

Monteith, J.L. 1977. Climate and the efficiency of crop production in Britain. Phil. Trans. R. Soc. B. 281:277–294.

Nikinmaa, E. 1992. Analyses of the growth of Scots pine: Matching structure with function. Acta For. Fenn. 235:68.

Oker-Blom, P., T. Pukkala and T. Kuuluvainen. 1989. The relationship between radiation interception and photosynthesis in forest canopies: effect of stand structure and latitude. Ecol. Model. 49: 73–87.

Ovington, J.D. 1957. Dry-matter production by *Pinus sylvestris* L. Ann. Bot. 21:287–314.

Penning de Vries, F.W.T. 1974. Substrate utilization and respiration in relation to growth and maintenance in higher plants. Neth. J. Agric. Sci. 22:40–44.

Penning de Vries, F.W.T. 1975. The cost of maintenance processes in plant cells. Ann. Bot. 39:77–92.

Pruyn, M.L., B.L. Gartner and M.E. Harmon. 2000. Respiratory potential in sapwood of old versus young coniferous trees. *In* Abstracts of the Ecological Society of America 85th Annual Meeting. The Ecological Society of America, Washington, D.C., 180 p.

Pukkala, T. and T. Kuuluvainen. 1987. Effect of canopy structure on the diurnal interception of direct solar radiation and photosynthesis in a tree stand. Silva Fenn. 21:237–250.

Ryan, M.G. 1990. Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. Can. J. For. Res. 20:48–57.

Ryan, M.G. 1995. Foliar maintenance respiration of subalpine and boreal trees and shrubs in relation to nitrogen content. Plant Cell Environ. 18:765–772.

Ryan, M.G. and R.H. Waring. 1992. Maintenance respiration and stand development in a subalpine lodgepole pine forest. Ecology 73:2100-2108.

Ryan, M.G. and B.J. Yoder. 1997. Hydraulic limits to tree height growth. BioScience 47:235–242.

Ryan, M.G., S.T. Gower, R.M. Hubbard, R.H. Waring, H.L. Gholz, W.P. Cropper, Jr. and S.W. Running. 1995. Woody tissue maintenance respiration of four conifers in contrasting climates. Oecologia 101:133–140.

Ryan, M.G., M.B. Lavigne and S.T. Gower. 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. J. Geophys. Res. 102:28,871–28,883.

Ryan, M.G., S. Linder, J.M. Vose and R.M. Hubbard. 1994. Dark respiration in pines. Ecol. Bull. 43:50–63.

Santantonio, D. 1989. Dry-matter partitioning and fine-root production in forests-new approaches to a difficult problem. *In* Biomass Production by Fast Growing Trees. Eds. J.S. Pereira and J.J. Landsberg. NATO ASI Series, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 57–72.

Shidei, T. and T. Kira. 1977. Primary productivity of Japanese forests. Productivity of terrestrial communities. JIBP synthesis. Vol. 16. Japanese Committee for the International Biological Program. Univ. Tokyo Press. 289 p.

Shinozaki, K., K. Yoda, K. Hozumi and T. Kira. 1964*a*. A quantitative analysis of plant form—the pipe model theory. I. Basic analyses. Jpn. J. Ecol. 14:97–105.

Shinozaki, K., K. Yoda, K. Hozumi and T. Kira. 1964*b*. A quantitative analysis of plant form—the pipe model theory. II. Further evidence of the theory and its application in forest ecology. Jpn. J. Ecol. 14:133–139.

Sievänen, R. and T.E. Burk. 1993. A process-based model for the dimensional growth of even-aged stands. Scand. J. For. Res. 8: 28–48.

Smith, F.W. and S.C. Resh. 1999. Age-related changes in production and below-ground carbon allocation in *Pinus contorta* forests. For. Sci. 45:33–341.

Sprugel, D.G. 1984. Density, biomass, productivity, and nutrient-cycling changes during stand development in wave regenerated Balsam fir forests. Ecol. Monogr. 54:165–186.

Sprugel, D.G. 1990. Components of woody-tissue respiration in young *Abies amabilis* (Dougl.) Forbes trees. Trees 4:88–99.

Stockfors, J. and S. Linder. 1998. Effect of nitrogen on the seasonal course of growth and maintenance respiration in stems of Norway spruce trees. Tree Physiol. 18:155–166.

Teskey, R.O., D.W. Sherff, D.Y. Hollinger and R.B. Thomas. 1995. External and internal factors regulating photosynthesis. *In* Resource Physiology of Conifers. Eds. W.K. Smith and T.M. Hinckley. Academic Press, New York, pp 105–140.

Thornley, J.H.M. 1991. A transport-resistance model of forest growth and partitioning. Ann. Bot. 68:211–226.

Thornley, J.H.M. and M.G.R. Cannell. 2000. Modelling the components of plant respiration. Ann. Bot. 85:55–67.

Thornley, J.H.M. and I.R. Johnson. 1990. Plant and crop models. Clarendon Press, Oxford, 669 p.

Tyree, M.T. 1988. A dynamic model for water flow in a single tree: Evidence that models must account for hydraulic architecture. Tree Physiol. 4:195–217.

Usol'tsev, V.A. and J.K. Vanclay. 1995. Stand biomass dynamics of pine plantations and natural forests on dry steppe in Kazakhstan. Scand. J. For. Res. 10:305–312.

Valentine, H.T. 1988. A carbon-balance model of stand growth: a derivation employing pipe-model theory and the self-thinning rule. Ann. Bot. 62:389–396.

Valentine, H.T. 1999. Estimation of the net primary productivity of even-aged stands with a carbon-allocation model. Ecol. Model. 122:139–149.

Valentine, H.T., T.G. Gregoire, H.E. Burkhart and D.Y. Hollinger. 1997. A stand-level model of carbon allocation and growth, calibrated for loblolly pine. Can. J. For. Res. 27:817–830.

van Hees, A.F.M. and H.H. Bartelink. 1993. Needle area relationships of Scots pine in the Netherlands. For. Ecol. Manage. 58:19–31.

Vanninen, P. and A. Mäkelä. 1999. Fine root biomass of Scots pine stands differing in age and soil fertility in southern Finland. Tree Physiol. 19:823–830.

Vanninen, P. and A. Mäkelä. 2000. Allocation of growth between needle and stemwood production in Scots pine (*Pinus sylvestris* L.) trees of different age, size, and competitive status. Tree Physiol. 20:527–533.

Vanninen, P., H. Ylitalo, R. Sievänen and A. Mäkelä. 1996. Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L.). Trees 10:231–238.

Waring, R.H. and W.H. Schlesinger. 1985. Forest Ecosystems. Concepts and Management. Academic Press, Orlando, FL, 340 p.

Waring, R.H., J.J. Landsberg and M. Williams. 1998. Net primary production of forests: a constant fraction of gross primary production? Tree Physiol. 18:129–134.

Yoder, B.J., M.G. Ryan, R.H. Waring, A.W. Schoettle and M.R. Kaufmann. 1994. Evidence of reduced photosynthetic rates in old trees. For. Sci. 40:513–526.