

Declining forest productivity in aging forest stands: a modeling analysis of alternative hypotheses

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Summary Several explanations have been advanced to account for the decline in forest net primary productivity (NPP) with age in closed-canopy stands including the hypotheses that: (1) sapwood maintenance respiration rate increases, reducing the availability of carbon to support new growth; (2) stomatal conductance and hence photosynthetic efficiency decline; and (3) soil nutrient availability declines. To evaluate these hypotheses we applied the ecosystem model G'DAY to a 40- and a 245-year-old stand of lodgepole pine (*Pinus contorta* Dougl. ex Loud.), growing on infertile soils. Net primary productivity estimated from biomass data was 0.47 and 0.25 kg C m⁻² year⁻¹ and foliar nitrogen/carbon ratio (N/C) was 0.0175 and 0.017 for the 40- and 245-year-old stands, respectively.

Productivities of the young and old stands were derived from a graphical analysis of the G'DAY model. The graphical analysis also indicated that the observed age-related decline in NPP can be explained in terms of interacting processes associated with Hypotheses 2 and 3. However, the relative importance of these two hypotheses differed depending on key model assumptions, in particular those relating to variation in soil N/C ratio. Thus, if we assumed that soil N/C ratio can vary significantly during stand development, then Hypotheses 2 and 3 jointly explain the decline in NPP, whereas if we assumed that soil N/C ratios are constant, then Hypothesis 3 alone explains the decline in NPP. The analysis revealed that only a small fraction of the decline of NPP can be explained in terms of increasing sapwood respiration.

Keywords: forest decline, net primary productivity, nitrogen availability, photosynthetic efficiency, *Pinus contorta*, respiration, stand age, woody litter.

Introduction

For closed-canopy forests, both net primary productivity (NPP) and wood yield decline as stands age (Turner and Long 1975, Attiwill 1979, Waring and Schlesinger 1985, Attiwill and Leeper 1987, Borman and Siddle 1990, Kozlowski et al. 1991, Ryan 1991, Long and Smith 1992, Ryan and Waring 1992). Although the age-related decline in forest NPP appears to be a universal phenomenon, its physiological mechanisms

are not well understood. The decline has been attributed to increasing amounts of respiring sapwood tissue (Peet 1980, Waring and Schlesinger 1985, Kozlowski et al. 1991, Yoder et al. 1994). However, Ryan (1991) and Ryan and Waring (1992) found that sapwood maintenance respiration was only 5% higher in a 245-year old lodgepole pine stand than in a 40-year old stand, and they concluded that this small increase in respiratory load could not account for a 40% decline in measured NPP. Ryan and Waring (1992) identified two other factors contributing to the lower NPP in the 245-year-old stand compared with the 40-year-old stand: (1) photosynthesis and stomatal conductance of 1-year-old needles were 16 to 22% lower in the older stand; and (2) foliar biomass was 37% lower in the older stand. An age-related decline in gas exchange rates has also been reported by Yoder et al. (1994) who proposed that the decline was associated with changes in canopy hydraulic resistance which affects canopy water potential and stomatal conductance. An age-related decline in foliar biomass is well documented (Gholz and Fisher 1982, Madgwick 1985, Waring and Schlesinger 1985, Ryan and Waring 1992, Binkley et al. 1995, Gower et al. 1995, Vose et al. 1995) and is associated with a reduction in NPP as a result of a decrease in the amount of photosynthetically active radiation (PAR) absorbed by the forest canopy.

Several other studies have questioned whether increasing sapwood respiration alone can explain the decline in NPP as stands age. Borman and Siddle (1990) concluded from studies of a *Picea sitchensis* chronosequence that the decline in NPP could not be explained by increased respiratory losses and attributed the decline to reduced nutrient availability (cf. Gholz et al. 1985, Binkley et al. 1995). Other investigators have concluded that large declines in NPP observed in aging forest stands are associated with reduced N availability (Grier et al. 1981, Gower et al. 1995, Schulze et al. 1995). Declining N availability may also affect allocation of NPP because below-ground allocation of NPP increases with declining N availability (Keyes and Grier 1981, Cannell 1985, Santantonio 1989, Lambers and Poorter 1992, Ågren and Wikström 1993, Kirschbaum et al. 1994) and stand age (Grier et al. 1981, Meier et al. 1985, Ryan and Waring 1992). Increased belowground

allocation has been associated with both reduced stem production and reduced NPP (Cannell 1985, Santantonio 1989).

Accumulation of woody litter may contribute to a decline in soil N availability. Because woody litter has a very low nitrogen/carbon (N/C) ratio, as it accumulates and decomposes, large amounts of N can be immobilized from throughfall, N-fixation and soil reserves (Turner 1977, Grier 1978, Foster and Lang 1982, Fahey 1983, Chapin et al. 1986, Stevenson 1986, Rayner and Boddy 1988). Zimmerman et al. (1995) concluded that woody debris immobilizes large amounts of N, resulting in decreased N availability and NPP (cf. Pastor et al. 1987, Polglase et al. 1992). The rate of N immobilization by woody litter depends on its rate of breakdown by microbial decomposers, which in turn varies with climate (Hunt 1977, Parton et al. 1987, Jenkinson 1990, O'Connell 1990, Bonan and Van Cleve 1992) and with litter quality and particle size (Adams and Attiwill 1986, Chapin et al. 1986, Rayner and Boddy 1988, Johnson 1993). There is considerable evidence that woody litter decay rates decline as stands age (Turner and Long 1975, Pearson et al. 1987, Polglase and Attiwill 1992).

Because both physiological and soil nutrition processes have been invoked to explain the decline in productivity with age, we have attempted to integrate and analyze these processes by applying the ecosystem model G'DAY (Generic Decomposition And Yield (Comins and McMurtrie 1993)) to the two lodgepole stands studied by Ryan (1991) and Ryan and Waring (1992). The model G'DAY simulates growth and decomposition processes in forest ecosystems (McMurtrie et al. 1992, Comins and McMurtrie 1993, Comins 1994, Kirschbaum et al. 1994, McMurtrie and Comins 1995). However, because the G'DAY model does not incorporate aging effects on maintenance respiration, photosynthetic efficiency and N availability, we modified the model to simulate age-dependent effects.

The objective of the study was to assess whether G'DAY can be used to test three hypotheses put forward to explain the decline in productivity over time. The hypotheses tested were that: (1) sapwood maintenance respiration rate increases, reducing C availability to support plant growth; (2) stomatal conductance declines, leading to reduced canopy photosynthetic efficiency; and (3) nitrogen immobilization in decomposing woody litter increases, reducing N availability to support tree growth. We parameterized the model with data obtained from the two stands studied by Ryan (1991) and Ryan and Waring (1992), and then used the parameterized model to predict the NPP of the same stands. Predictions were based on several assumptions about how the stands differ in amount of respiring sapwood, their photosynthetic efficiency, and rates of N immobilization in decaying woody litter.

Model description

The G'DAY model of Comins and McMurtrie (1993)

The G'DAY model (Comins and McMurtrie 1993), hereafter referred to as CM, consists of a set of 10 differential equations describing C and N dynamics of various tree and soil pools. The model's structure is illustrated schematically in Figure 1.

We assume that annual net primary production NPP ($\text{kg C m}^{-2} \text{ year}^{-1}$) is proportional to absorbed photosynthetically active radiation, APAR (Monteith 1977):

$$\text{NPP} = \varepsilon E(n_f) \text{APAR}, \quad (1)$$

where ε is maximum net PAR utilization efficiency, and $E(n_f)$ represents its dependence on the foliar N/C ratio (n_f) (Kirschbaum et al. 1994):

$$E(n_f) = \frac{1.84n_f - 0.01}{0.017 + n_f} / \frac{1.84n_{\text{crit}} - 0.01}{0.017 + n_{\text{crit}}} \quad \text{if } n_f < n_{\text{crit}} \quad (2a)$$

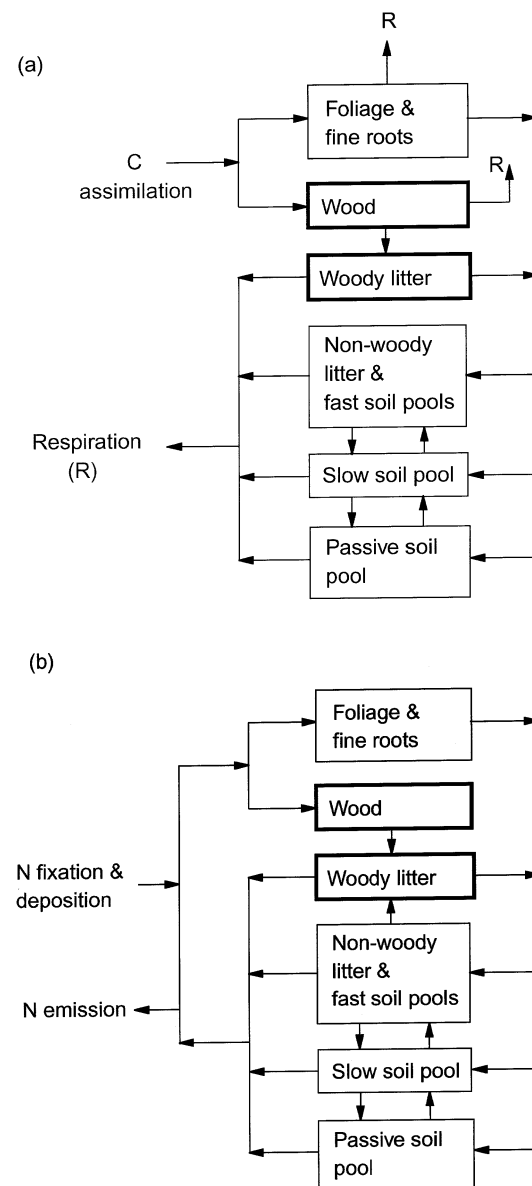


Figure 1. Carbon (a) and nitrogen (b) cycling in the G'DAY model, adapted to simulate aging. Fast pools and passive soil pools are indicated by thin boxes and the remaining slow pools by thick boxes.

$$E(n_f) = 1 \quad \text{if } n_f \geq n_{\text{crit}}, \quad (2b)$$

where n_{crit} represents the n_f ratio below which production is limited by N. The APAR is calculated from Beer's law (Jarvis and Leverenz 1983):

$$\text{APAR} = I_0(1 - \exp(-k\sigma C_f)), \quad (3)$$

where I_0 is incident PAR, k is the light extinction coefficient, σ is leaf area per unit carbon and C_f is foliar carbon mass.

Carbon acquired through photosynthesis is distributed to foliage, fine roots and woody tissue in fixed proportions, $a_f/a_r/a_w$, respectively. Senescence rates of the biomass components are fixed. Plant litter is subdivided into four pools: aboveground and belowground structural and metabolic fractions. Carbon from decomposing litter enters three soil pools: active, slow and passive, with decay time constants of order 1–5, 20–50 and 200–2000 years, respectively (Parton et al. 1987). Decomposition rates are functions of soil water and air temperature. The G'DAY model simulates fluxes of N corresponding to each C flux, and N fluxes associated with atmospheric deposition, biological fixation, soil mineralization, nutrient uptake, soil gaseous emission and leaching.

Fast and slow pools in the G'DAY model

Foliage, fine roots, the four litter pools and active soil organic matter (SOM) have turnover times of 1 to 5 years. The other pools (slow and passive SOM and woody biomass) have turnover times of much more than 5 years. In the G'DAY simulations, pools with short turnover times stabilize rapidly, leading to an effective equilibrium where foliage, fine roots, litter and active SOM are equilibrated, whereas slow and passive SOM and wood are not (Comins 1994, McMurtrie and Comins 1995). The equilibrated pools are designated fast variables and the nonequilibrated pools are designated slow variables. (The fast-variable equilibrium differs from the longer-term equilibrium considered by CM who treated the slow SOM as a fast variable.)

To predict forest growth response 50 to 100 years after an instantaneous doubling of atmospheric CO_2 , CM developed an equilibrium-based version of G'DAY based on an analytical method called two-timing. Two-timing consists in: (i) dividing variables into fast and slow relative to a chosen timescale; (ii) calculating the equilibrium of the fast variables with slow variables kept constant; and (iii) substituting this equilibrium into the original difference equations for the slow variables. This leads to a simplified model for the slow variables alone. In this paper, we consider only stages (i) and (ii) of the two-timing method. Once fast pools have reached equilibrium, fluxes of C and N into these pools match fluxes out. The productivity of young and old forest stands can be evaluated from considerations of C and N conservation at this effective equilibrium.

Photosynthetic and nitrogen cycling constraints to production

The equilibrium foliar C mass (C_f) can be evaluated by equating leaf production and leaf fall:

$$C_f = a_f \text{NPP} / s_f, \quad (4)$$

where parameters a_f and s_f represent the proportion of NPP allocated to foliage and the specific leaf senescence rate, respectively. (See Appendix 1 for definitions of all symbols.) By substituting Equation 4 into Equations 1 and 3, C_f can be eliminated to obtain:

$$\frac{\text{NPP}}{1 - \exp\left(-\frac{k\sigma a_f \text{NPP}}{s_f}\right)} = I_0 \varepsilon E(n_f). \quad (5)$$

Equation 5 can be solved to express NPP as a function of n_f ; this relationship is called the photosynthetic constraint to production. It is illustrated in Figure 2 for the parameter values specified in Appendix 1. The photosynthetic constraint has a positive slope reflecting the strong N dependence of PAR utilization efficiency, assumed in Equation 2.

The photosynthetic constraint (Equation 5) is derived from considerations of C conservation at the effective equilibrium; a second constraint to production is obtained by invoking N conservation. At the effective equilibrium, N fluxes into and out of the aggregated fast pools are equal:

$$N_A + N_F + N_{R_s} + N_{R_p} + N_{R_{wl}} = N_{S_s} + N_{S_p} + N_{S_w} + N_E, \quad (6)$$

where N_A and N_F are rates of N input from atmospheric deposition and N fixation, respectively. The variables N_{R_s} , N_{R_p} and $N_{R_{wl}}$ are net rates of N release through decomposition of slow and passive SOM and woody litter, respectively; N_E is the gaseous N emission rate from soil; and N_{S_s} , N_{S_p} and N_{S_w} are rates of N sequestration in the slow and passive soil pools and

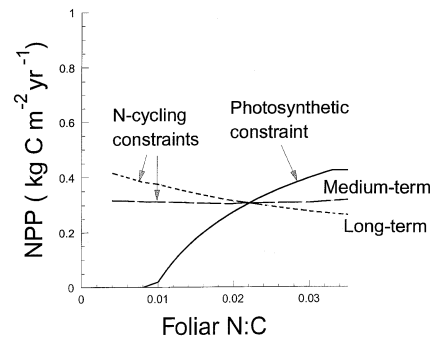


Figure 2. Photosynthetic (solid line) and long-term and medium-term N cycling constraints to production (dashed lines), derived from Equations 5, 13 and 11, respectively. Parameters for the 245-year-old lodgepole pine stand are given in Appendix 1. Here we ignore woody litter decay and changes in maintenance respiration and photosynthetic efficiency. The maximum net PAR utilization efficiency is $0.46 \text{ kg C GJ}^{-1}$. We assume constant soil N/C ratios.

in woody biomass, respectively. An expression for the rate of N sequestration in new wood (N_{sw}) is obtained by multiplying woody C production ($a_w NPP$) by the N/C ratio of new wood, n_w , and deducting the fraction (r_w) of N attained by new wood through retranslocation from old wood:

$$N_{sw} = a_w NPP n_w (1 - r_w). \quad (7a)$$

Analogous expressions for N fluxes into slow and passive SOM are derived by multiplying C sequestration rates, expressed as proportions of litterfall C subsequently entering soil storage, by N/C ratios of newly formed slow and passive SOM, n_{so} and n_{po} , respectively. Under the further assumption of equilibrated foliar and root carbon (cf. Equation 4), CM obtained:

$$N_{ss} = (a_f b_{sf} + a_r b_{sr}) NPP n_{so} \quad (7b)$$

and

$$N_{sp} = (a_f b_{pf} + a_r b_{pr}) NPP n_{po}, \quad (7c)$$

where b_{if} and b_{ir} represent the fractions of leaf and root litterfall C which subsequently enter the slow ($i = s$) and passive ($i = p$) soil pools, respectively. The sequestration coefficients b_{if} and b_{ir} are functions of litter lignin/N ratios (Parton et al. 1987).

Rates of N release from decomposing slow and passive SOM (N_{Rs} and N_{Rp} , respectively) depend on pool N contents and temperature- and moisture-dependent specific decomposition rates, but not directly on NPP. An equation for N_E is obtained by assuming soil gaseous N emissions are proportional to the rate of N mineralization (N_{min}) with proportionality constant x :

$$N_E = x N_{min}. \quad (8)$$

At the fast-variable equilibrium, N uptake by plants (U), given by

$$U = N_{min} (1 - x), \quad (9a)$$

is balanced by N export through leaf and root litterfall and wood growth:

$$U = (a_w n_w (1 - r_w) + a_f n_{fl} + a_r n_{rl}) NPP, \quad (9b)$$

where n_{fl} and n_{rl} are N/C ratios of senescing leaves and roots. We assume that N/C ratios of foliage and roots are proportional to those of live tissues ($n_{fl} = \lambda_f n_f$ and $n_{rl} = \lambda_r n_r$), where λ_f and λ_r are the ratios of litter N/C to live tissue N/C for leaf and root, respectively. Combining Equations 8 and 9 to eliminate N_{min} and U gives an expression for N_E :

$$N_E = \frac{x}{1 - x} (a_w n_w (1 - r_w) + a_f n_{fl} + a_r n_{rl}) NPP. \quad (10)$$

Finally, when the above expressions for N_{sw} , N_{ss} , N_{sp} and N_E are substituted into Equation 6, we obtain an equation relating NPP to n_f , which is called the N-cycling constraint to production:

$$\begin{aligned} NPP = & (N_A + N_F + N_{Rs} + N_{Rp} + N_{Rwl}) / (a_w n_w [1 - r_w] \\ & + a_f [b_{sf} n_{so} + b_{pf} n_{po}] + a_r [b_{sr} n_{so} + b_{pr} n_{po}] \\ & + \frac{x}{1 - x} [a_w n_w [1 - r_w] + a_f n_{fl} + a_r n_{rl}]). \end{aligned} \quad (11)$$

Equation 11 applies when all fast pools are in equilibrium. Simulations of G'DAY for *P. radiata* D. Don predict that this canopy closure condition is achieved by age approximately 20 years (McMurtrie and Comins 1995). We therefore call Equation 11 the medium-term N-cycling constraint to production. Once stands have achieved this closed state, the fast pools remain in effective equilibrium, whereas the other pools (slow and passive SOM and woody biomass) gradually change as trees age. As shown by McMurtrie and Comins (1995), slow SOM gradually approaches equilibrium (passive SOM and woody biomass remain unequilibrated). When its equilibrium condition, $N_{Rs} = N_{ss}$ is substituted into Equations 6, the N-cycling constraint is:

$$N_A + N_F + N_{Rp} + N_{Rwl} = N_{sp} + N_{sw} + N_E \quad (12)$$

or

$$\begin{aligned} NPP = & (N_A + N_F + N_{Rp} + N_{Rwl}) / (a_w n_w [1 - r_w] \\ & + a_f b_{pf} n_{po} + a_r b_{pr} n_{po} + \\ & \frac{x}{1 - x} [a_w n_w [1 - r_w] + a_f n_{fl} + a_r n_{rl}]). \end{aligned} \quad (13)$$

This is called the long-term N-cycling constraint to production. The relationships in Equations 11 and 13 are illustrated in Figure 2 as functions of n_f . The downward slope of the long-term N-cycling constraint with increasing n_f is due to the increased proportional loss of mineralized nitrogen through gaseous losses (N_E , given by Equation 10); as a result of these increased N losses, less N is available to support tree growth. The slight positive slope of the medium-term N-cycling constraint is due to the effect of increasing n_f on litter quality; if n_f increases, litter quality (defined by its lignin/N ratio, Aber et al. 1990) increases, leading to reduced C sequestration coefficients (b_{sf} , b_{sr} , b_{pf} and b_{pr} in Equation 11) and hence to increased availability of N to support plant growth. The gaseous emission effect, which gives the long-term N-cycling constraint its negative slope, is present in both Equations 11 and 13; however, in Equation 11 it is masked by the stronger litter quality effect on rates of soil C storage, particularly into slow SOM.

The photosynthetic constraint to production (Equation 5) and the N-cycling constraints (Equations 11 and 13) represent NPP derived from considerations of C and N conservation at the effective equilibrium, respectively. The intersection of the

photosynthetic constraint curve with the medium-term N-cycling constraint gives production and n_f achieved when all fast pools are equilibrated (i.e., at the medium-term equilibrium). The intersection with the long-term N-cycling constraint gives the long-term equilibrium when the slow soil pool is also equilibrated. Both constraint curves are shown in Figure 2. Because the medium-term N-cycling constraint shown in Figure 2 is actually evaluated with the slow soil pool at equilibrium, the medium- and long-term equilibria coincide. The advantage of the graphical analysis (Figure 2) over an analysis based on model simulations is the insight the graphical approach provides into how individual parameters affect NPP, and the qualitative understanding it offers into the model's dynamic behavior.

Plant respiration

Because CM's model does not explicitly represent plant respiration (Hypothesis 1) or effects of age on stomatal conductance and photosynthetic efficiency (Hypothesis 2), and woody litter decay is ignored (i.e., $N_{Rwl} = 0$ in Equations 11 and 13; Hypothesis 3), we have modified G'DAY to incorporate these aging mechanisms.

The C sinks associated with maintenance and construction respiration were incorporated in Equation 1:

$$NPP = GPP - (R_c + R_m) \quad (14a)$$

where GPP is gross primary production, and R_c and R_m are construction and maintenance respiration rates, respectively. Gross primary production is defined here as net daytime carbon gain and is proportional to APAR:

$$GPP = \epsilon_o E(n_f) APAR, \quad (14b)$$

where ϵ_o is maximum gross PAR utilization efficiency.

We assumed that total construction respiration represents 25% of NPP (Ryan 1991):

$$R_c = 0.25 NPP. \quad (15a)$$

Following Ryan (1991) and Ryan and Waring (1992), we model maintenance respiration as the sum of:

$$R_m = R_{mf} + R_{mr} + R_{msw}, \quad (15b)$$

where R_m is total annual maintenance respiration, and R_{mf} , R_{mr} and R_{msw} are annual maintenance respiration rates of foliage (dark period only), fine roots and sapwood, respectively. Both foliage and fine root respiration rates are functions of mean annual air temperature (T_a) and their nitrogen contents (N_f and N_r , respectively):

$$R_{mf} = 0.5 R_0 N_f Q_{10}^{T_a/10} \quad (15c)$$

$$R_{mr} = R_0 N_r Q_{10}^{T_a/10}, \quad (15d)$$

where the value of R_0 , the respiration rate per unit nitrogen content corresponding to a temperature of 0 °C, is derived from Ryan (1991) and Q_{10} is 2.0. The factor of 0.5 is included because GPP, given by Equation 14b, is net of daytime foliar respiration, so that R_{mf} represents night respiration only.

Sapwood respiration is assumed to depend on mean air temperature and sapwood volume. Assuming constant mean sapwood density (Ryan 1991), we convert Ryan and Waring's (1992) equation for sapwood respiration to a function of temperature and sapwood C content (C_{sw}):

$$R_{msw} = 0.00876 C_{sw} Q_{10}'^{T_a/10}, \quad (15e)$$

where $Q_{10}' = 1.94$. An empirical equation for sapwood C is derived from measurements of woody biomass for three lodgepole pine stands aged 40, 65 and 245 years and assuming that branches and coarse roots are composed entirely of sapwood (Ryan 1991):

$$C_{sw} = 1.11 C_w^{0.77}. \quad (16)$$

Thus, given values of N_f , N_r and C_w , maintenance respiration can be calculated from Equations 15 and 16.

Substituting Equations 3, 14b and 15a into Equation 14a, we obtain a modified photosynthetic constraint:

$$1.25 NPP = \epsilon_o E(n_f) I_0 \left(1 - \exp \left(- \frac{k \sigma a_f NPP}{s_f} \right) \right) - R_m \quad (17)$$

R_m is given by Equations 15b to 16 evaluated at the fast-variable equilibrium where

$$N_f = \frac{n_f a_f NPP}{s_f}$$

and

$$N_r = \frac{n_r a_r NPP}{s_r},$$

with sapwood maintenance respiration calculated using observed values of C_w in the young and old stands.

Equation 17 can be solved to express NPP as a function of n_f . This relationship replaces Equation 5 as the photosynthetic constraint to production. It is illustrated in Figure 3a for parameter values given in Appendix 1.

Age-dependent stomatal conductance and photosynthetic efficiency

Stomatal conductance, hydraulic conductance and canopy architecture are not explicitly represented in CM's model. We assume that gross PAR utilization efficiency (ϵ_o) declines with age; the implicit assumption here is that photosynthesis correlates with stomatal conductance.

Woody litter decay

The net rate of N release through woody litter decay is:

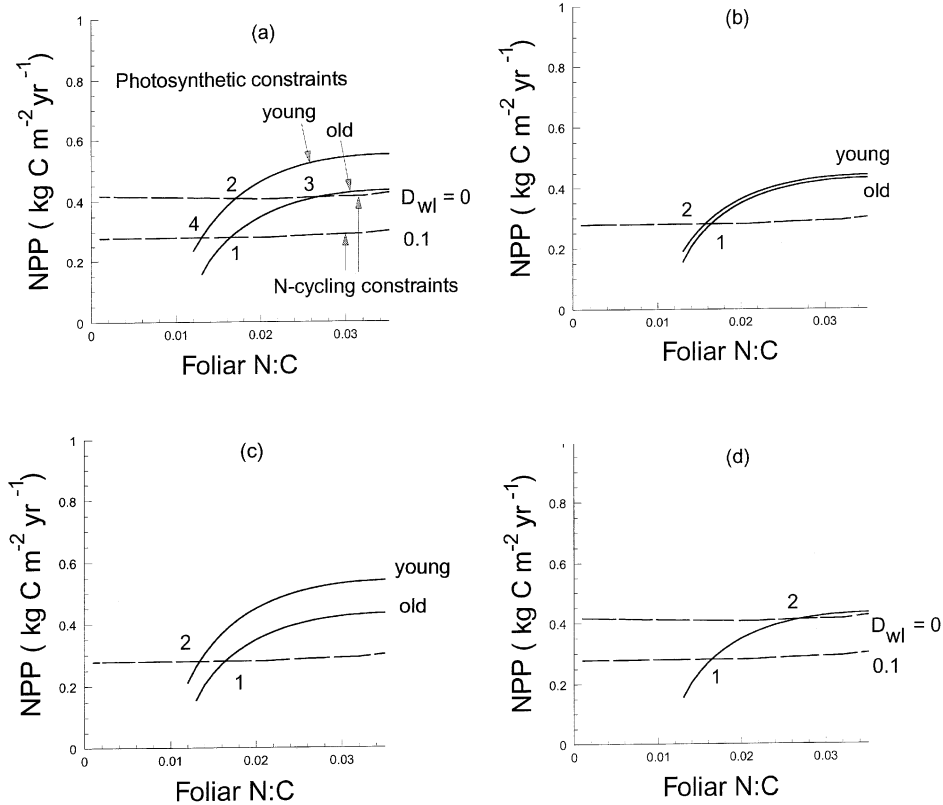


Figure 3. Photosynthetic constraints for the young and old stand and medium-term N-cycling constraints obtained with woody litter decay rates (D_{wl}) of 0.0 and 0.1 kg C m⁻² year⁻¹. We assume fixed soil N/C ratios. The long-term equilibrium NPP of the old stand corresponds to Point 1 at the intersection of the old photosynthetic constraint and the lower N-cycling constraint. Curves are shown for four cases: (a) assuming the young stand has lower maintenance respiration (Hypothesis 1), higher ϵ_o (Hypothesis 2) and zero woody litter (Hypothesis 3) (The young stand equilibrium corresponds to Intersection 2 between the young stand photosynthetic constraint and the upper N-cycling constraint.); (b) incorporating Hypothesis 1 only; (c) incorporating Hypothesis 2 only; and, (d) incorporating Hypothesis 3 only. In (b) and (c) the two medium-term N-cycling constraint curves coincide. In (d) the two photosynthetic constraint curves coincide.

$$N_{Rwl} = d_{wl}C_{wl}(n_{wl} - b_{sw}n_{so} - b_{pw}n_{po}), \quad (18a)$$

where C_{wl} is woody litter carbon, n_{wl} is N/C ratio of woody litter, d_{wl} is its specific decay rate, and b_{sw} and b_{pw} are fractions of decomposing woody litter carbon which subsequently enter the slow and passive soil pools. Equation 18a applies at the medium-term equilibrium. In the long-term, once the slow soil pool is equilibrated, the net rate of N release in woody litter decay is

$$N_{Rwl}' = d_{wl}C_{wl}(n_{wl} - b_{pw}'n_{po}) \quad (18b)$$

where b_{pw}' is the fraction of woody litter decay entering passive SOM in the long-term:

$$b_{pw}' = b_{pw} + \frac{b_{sw}b_{ps}}{1-b_{ss}}. \quad (18c)$$

Because n_{wl} is much less than that of SOM, woody litter decay usually leads to immobilization of N from soil reserves (i.e., $N_{Rwl} < 0$); in that case, inclusion of the woody litter decay term (N_{Rwl}) in Equation 11 will lower the N-cycling constraint curve. However, N immobilization in decomposing woody litter does not continue indefinitely. In the long term, woody litter decay can become an N source (i.e., N_{Rwl}' , given by Equation 18b, can be positive even though N_{Rwl} given by Equation 18a is negative); this sign difference between N_{Rwl}

and N_{Rwl}' is possible because the value of $b_{ps}/(1 - b_{ss})$ is considerably less than one.

Parameterization of the model for stands of lodgepole pine

To test the hypotheses put forward to explain the decline in productivity during stand development, we parameterized the model for two adjacent even-aged stands of lodgepole pine (*P. contorta*) growing in Frazer Experimental Forest near Winter Park, Colorado, USA. The forest lies in the subalpine region (39°54' N, 105°52' W, 2800 m asl) with a 3-month growing season, mean annual air temperature of 3.8 °C, mean growing season temperature of 14.5 °C, and mean growing season incident PAR of 1.164 GJ m⁻² (averaged over 10 years). Stands were aged 40 and 245 years at the time of measurement. Methods used to estimate tree biomass components, above-ground NPP, belowground C allocation and respiration rates are described by Ryan (1991) and Ryan and Waring (1992).

Estimated stand properties and parameter values for the older stand are listed in Table 1 and Appendix 1, respectively. Woody biomass (C_w) of the younger stand was 35% less than that of the older stand (5.47 versus 8.5 kg C m⁻², Ryan and Waring 1992) and gross PAR utilization efficiency (ϵ_o) was assumed to be 16% lower for the older stand (Yoder et al. 1994).

Our objective in parameterizing the model was to derive the photosynthetic and N-cycling constraint curves for the two

Table 1. Values of some variables estimated from field data for the 40- and 245-year-old stands of *P. contorta*.

Variable	40-Year-old stand	245-Year-old stand
NPP (kg C m ⁻² year ⁻¹)	0.47	0.25
C _f (kg C m ⁻²)	0.65	0.41
n _f	0.0175	0.017
C _w (kg C m ⁻²)	5.47	8.5
R _{msw} (kg C m ⁻² year ⁻¹)	0.051	0.065

lodgepole pine stands. Values of several parameters listed in Appendix 1 were estimated indirectly, as enumerated below.

1. Potential gross PAR utilization efficiency (ϵ_o), defined in Equation 14b, was inferred from estimated GPP and APAR, and n_f .

2. Foliar senescence rate (s_f) was estimated from the fraction of the total foliar C present in 1-year-old foliage (Schoettle 1989).

3. Fahey (1983) obtained a specific woody litter decay rate (d_{wl}) for lodgepole pine of 0.016 year⁻¹, which is comparable to the rates found in other cold temperate forests (Harmon et al. 1986). However, because d_{wl} was not measured in either lodgepole pine stand under study, and there is evidence that total woody litter (C_{wl}) was lower in the young stand than in the old stand, we used four different values of D_{wl} , represented by the product of $d_{wl}C_{wl}$ (Equations 18a and 18b); namely, 0.0 in the young stand and 0.05, 0.1 and 0.07 kg C m⁻² year⁻¹ in the old stand. The value 0.07 kg C m⁻² year⁻¹ represents the value of D_{wl} for the long-term equilibrium of woody litter biomass (when $D_{wl} = d_{wl}C_{wl} = s_wC_w = a_wNPP$).

4. The N/C ratio of new wood (n_w) was derived based on relative values of sapwood and heartwood N/C given by Pearson et al. (1987).

5. Fractions of leaf and root litter entering slow and passive SOM (b_{if} and b_{ir} , where $i = s$ or p) and other soil C partition coefficients were derived from an analysis of the CENTURY model of Parton et al. (1987).

6. The gaseous N emission fraction ($x = 0.01$) was taken from Kirschbaum et al. (1994).

7. Estimates of slow and passive SOM are required to evaluate net release of N from the slow and passive pools (N_{Rs} and N_{Rp} , respectively). Measurements of total SOM are available (10.6 kg C m⁻²), but not of its breakdown into active, slow and passive components. We assumed constant passive SOM for both stands ($C_p = 4$ kg C m⁻², N. Scott, personal communication). For the old stand, we estimated slow SOM by assuming that its soil C and N contents are in equilibrium.

8. For the young stand, there is considerable uncertainty about slow SOM and woody litter decay rate. We made two assumptions: (1) the young stand has the same amount of slow SOM as the old stand; and (2) all woody litter has been removed from the young stand ($C_{wl} = 0$ and consequently $D_{wl} = 0$ and $N_{Rwl} = 0$). We thus assume that soil C and N reserves of the younger stand are identical to the older stand (the young stand had been reestablished on an old forest site which had equilibrated soil pools); this assumption is reasonable because

the two stands had similar histories and there were no large losses of slow SOM during reestablishment of the young stand.

Results

We used the equilibrium-based analysis of G'DAY to make predictions under a variety of assumptions about how the two stands differ in amount of respiring sapwood (Hypothesis 1), gross PAR utilization efficiency (ϵ_o) (Hypothesis 2), and rates of N immobilization in decaying woody litter (Hypothesis 3).

Hypotheses 1, 2 and 3 combined

Figure 3a illustrates the photosynthetic and N-cycling constraints derived for the stands assuming that, compared with the old stand, the young stand has lower maintenance respiration (Hypothesis 1), higher gross PAR utilization efficiency (Hypothesis 2), and lower woody litter decay rate ($D_{wl} = 0.1$ and 0 kg C m⁻² year⁻¹ in the old and young stands, respectively; Hypothesis 3). The photosynthetic constraint curve (Equation 17) was higher for the young stand than the old stand because of its greater photosynthetic efficiency and reduced respiratory costs. For the old stand, the appropriate medium-term N-cycling constraint curve was given by Equation 11 with equilibrated slow soil pool (Point 7 above), whereas the medium-term N-cycling constraint for the young stand was given by Equation 11 with $N_{Rwl} = 0$ and C_s and N_s equal to their values for the old stand (Point 8 above).

The N-cycling constraint of the young stand was higher than that of the older stand because the young stand had less woody litter, and hence reduced N immobilization. Woody tissue has a low N/C ratio and decaying woody litter immobilizes large amounts of N (Equation 18a), which reduces soil N availability to support tree growth. Predicted NPPs of the old and young stands, which are given by Intersections 1 and 2, respectively, in Figure 3a, were 0.28 and 0.41 kg C m⁻² year⁻¹; i.e., modeled NPP was 45% higher for the young stand. The model predicts n_f ratios of 0.0164 and 0.017 for the old and young stands, respectively. The comparable measured NPPs were 0.25 and 0.47 kg C m⁻² year⁻¹ and the measured n_f ratios were 0.017 and 0.0175 for the old and young stands, respectively.

Hypotheses 1, 2 and 3 considered separately

Figure 3a incorporates all three hypotheses for the decline of NPP as stands age. Figures 3b–d consider three other cases, each incorporating only one of the hypotheses. For Case 1, which incorporates Hypothesis 1 only (Figure 3b), we assume that sapwood maintenance respiration rate is lower in the younger stand but assume no change in photosynthetic efficiency (ϵ_o) and no reduction of woody litter with stand age (i.e., $D_{wl} = 0.1$ kg C m⁻² year⁻¹ in both stands). Modeled NPPs of the old and young stands, which are given by Intersections 1 and 2, respectively, were not significantly different (see Table 2) because reduced maintenance respiration had little impact on the photosynthetic constraint curve and no effect on the N-cycling constraint (Figure 3b).

For Case 2, we assume that the younger stand has higher gross PAR utilization efficiency (ϵ_o) but that the stands have

equal amounts of sapwood C and the same woody litter C (Hypothesis 2 only, Figure 3c). Under these assumptions, there was a negligible difference in modeled NPPs of the young and old stands (cf. Intersections 1 and 2, Table 2) because, even though the photosynthetic constraint curves differed considerably, the N-cycling constraints were almost horizontal.

For Case 3, we assume that the only difference between the stands is that the young stand has no woody litter (Hypothesis 3 only, Figure 3d). This assumption affects the N-cycling constraint curve, but not the photosynthetic constraint. Modeled NPP of the younger stand was $0.41 \text{ kg C m}^{-2} \text{ year}^{-1}$ (Intersection 2). Thus Case 3 accounts for the entire NPP difference seen in Figure 3a. However, Case 3 was unable to reproduce the n_f ratios. Figure 3d gave $n_f = 0.0164$ and 0.0269 for the old and young stands, respectively, whereas the measured values were 0.017 and 0.0175 (Table 1).

Hypotheses 1 and 2 considered jointly

Hypotheses 1 and 2 affect the photosynthetic constraint only, whereas Hypothesis 3 affects the N-cycling constraint only. Thus, the photosynthetic constraints for the old and young stands in Figure 3a differed because the younger stand had higher photosynthetic efficiency and reduced respiration. Similarly, the N-cycling constraints differed because of reduced woody litter decay rate (D_{wl}) in the young stand. In Figure 3, Intersection 3 between the old stand photosynthetic constraint and the upper N-cycling constraint therefore repre-

sents the equilibrium obtained for Case 3 (Hypothesis 3 only). Similarly, Intersection 4 in Figure 3a represents the equilibrium obtained when Hypotheses 1 and 2 are combined. Thus the four intersections in Figure 3a can be used to determine whether the reduced growth of the young stand was due to changes in C substrate availability (Hypotheses 1 and 2) or N availability (Hypothesis 3).

Variable soil N/C ratio

For Figure 3a, we assume that slow soil N/C is a fixed constant throughout stand development. However, there is evidence that soil N/C may vary depending on the quality of litter substrate (Aber et al. 1990, Baldock et al. 1992, Escudero et al. 1992). Figure 4 illustrates the consequences of assuming that the N/C ratio of newly formed slow SOM is proportional to n_{fl} . (We use the relationship $n_{so} = 4.0n_{fl}$.) The shape of the medium-term N-cycling constraint is highly sensitive to assumptions about variability of soil N/C (McMurtrie and Comins 1995). Under the assumption of fixed soil N/C, the medium-term N-cycling constraint was almost horizontal (Figure 3). However, for variable soil N/C ratio, the N-cycling constraint declined steeply with increasing n_f (Figure 4) because, if the N/C ratio of newly formed SOM increases, N_{ss} increases relative to N_{Rs} thereby reducing availability of soil N to support plant growth. When all three aging hypotheses are included (Figure 4), modeled NPPs of the old and young stands were 0.28 and $0.40 \text{ kg C m}^{-2} \text{ year}^{-1}$ (Intersections 1 and 2, respectively), repre-

Table 2. G'DAY parameter values and predicted NPP and n_f for young and old stands for each figure. (Predictions for the old stand for Figures 3a–d are identical.) Symbols: R_{msw} = sapwood maintenance respiration ($\text{kg C m}^{-2} \text{ year}^{-1}$), derived from Equations 15e and 16, ϵ_o = maximum gross PAR utilization efficiency (kg C GJ^{-1}), ϵ = maximum net PAR utilization efficiency (kg C GJ^{-1} , value given for Figure 2 only), D_{wl} = woody litter decay rate ($\text{kg C m}^{-2} \text{ year}^{-1}$), soil N/C = fixed (F; $n_{so} = 0.035$) or variable (V; $n_{so} = 4.0n_{fl}$), NPP = predicted net primary production ($\text{kg C m}^{-2} \text{ year}^{-1}$), and n_f = predicted foliar N/C ratio.

Figure	Stand (Intersection)	R_{msw}	ϵ_o	D_{wl}	Soil N/C	a_r	NPP	n_f
2	-	0	($\epsilon = 0.46$)	0	F	0.58	0.327	0.0206
3a	Old (1)	0.065	1.05	0.1	F	0.58	0.280	0.0164
	Young (2)	0.046	1.25	0	F	0.58	0.407	0.0170
	(3)	0.065	1.05	0	F	0.58	0.411	0.0269
	(4)	0.046	1.25	0.1	F	0.58	0.280	0.0129
	Young (Case 1)	0.046	1.05	0.1	F	0.58	0.280	0.0157
3b	Young (Case 2)	0.065	1.25	0.1	F	0.58	0.280	0.0134
3c	Young (Case 3)	0.065	1.05	0	F	0.58	0.411	0.0269
4	Old (1)	0.065	1.05	0.1	V	0.58	0.280	0.0164
	Young (2)	0.046	1.25	0	V	0.58	0.400	0.0167
	(3)	0.065	1.05	0	V	0.58	0.342	0.0196
	(4)	0.046	1.25	0.1	V	0.58	0.335	0.0144
	Old	0.065	1.05	0.1	V	0.58	0.280	0.0164
5	Young	0.046	1.25	0	V	0.41	0.458	0.0188
	Old	0.065	1.05	0.05	V	0.58	0.309	0.0177
6a	Young	0.046	1.25	0	V	0.58	0.397	0.0166
	Old	0.065	1.05	0.05	V	0.58	0.309	0.0177
6b	Young	0.046	1.25	0	V	0.41	0.455	0.0187
	Old	0.065	1.05	0.07	V	0.58	0.303	0.0164
-	Young	0.046	1.25	0	V	0.58	0.405	0.0159
	Old	0.065	1.05	0.07	V	0.58	0.303	0.0164
-	Young	0.045	1.25	0	V	0.41	0.465	0.0178
	Old	0.065	1.05	0.07	V	0.58	0.303	0.0164

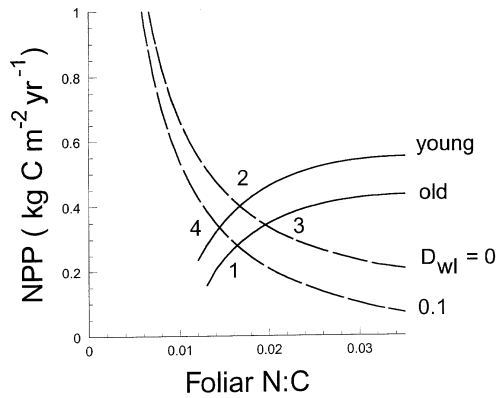


Figure 4. Photosynthetic and N-cycling constraint curves analogous to Figure 3a, but assuming that soil N/C ratios vary with n_f . We assume the relationship $n_{so} = 4.0n_f$, where n_{so} and n_f are N/C ratios of newly formed SOM and senescent foliage, respectively.

sending 43% higher productivity in the young stand than in the old stand. Simulated n_f ratios were 0.0164 and 0.0167 in the old and young stands, respectively; these values were slightly lower than the measured values of 0.017 and 0.0175. If we assume that ϵ_o and respiratory load are identical in the two stands, but that woody litter decay (D_{wl}) is zero in the young stand (Intersection 3, Figure 4), then modeled NPP of the young stand was $0.34 \text{ kg C m}^{-2} \text{ year}^{-1}$ (i.e., 22% higher than that of the old stand); this represents the response to Hypothesis 3 alone. Alternatively, if we assume that woody litter decay is unaltered in the young stand, but that both sapwood respiration and photosynthetic efficiency differ (Intersection 4, Figure 4), then the model predicts an NPP of $0.335 \text{ kg C m}^{-2} \text{ year}^{-1}$ (i.e., 20% higher than in the old stand); this represents the combined response to Hypotheses 1 and 2. (If we consider responses to the two hypotheses influencing the photosynthetic constraint separately, we find that the increased productivity was predominantly due to higher ϵ_o , cf. Figures 3b and 3c.)

Sensitivity to allocation of NPP below ground

Figures 3 and 4 consider the consequences of declining N availability under the assumption that carbon allocation is unaltered as stands age. There is evidence, however, that reduced N availability leads to increased belowground allocation (Keyes and Grier 1981, Cannell 1985, Santantonio 1989, Lambers and Poorter 1992, Ågren and Wikström 1993, Kirschbaum et al. 1994). Biomass studies indicate that root allocation is higher and wood allocation is lower in the old stand than in the young stand ($a_f/a_r/a_w = 0.17/0.41/0.42$ in the young stand compared with $0.19/0.58/0.23$ in the old stand). The effect of altered allocation on the constraint curves is shown in Figure 5 where N-cycling constraints are shown for the young and old stands with litter decay rates, $D_{wl} = 0$ and $0.1 \text{ kg C m}^{-2} \text{ year}^{-1}$, respectively. The N-cycling constraint of the young stand was considerably higher than the corresponding curve in Figure 4, where we assumed $a_f/a_r/a_w =$

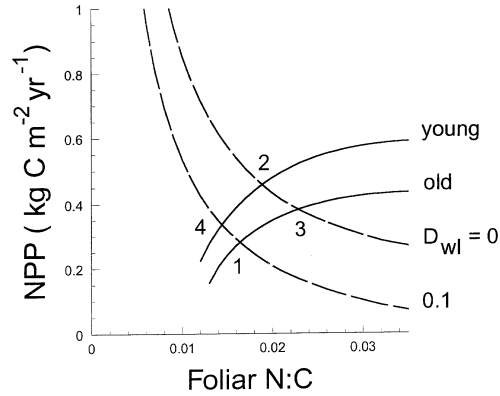


Figure 5. Photosynthetic and N-cycling constraint curves analogous to Figure 4, but assuming that belowground allocation is lower in the young stand ($a_f/a_r/a_w = 0.19/0.58/0.23$ for the old stand and $0.17/0.41/0.42$ for the young stand).

$0.19/0.58/0.23$. Hence, simulated NPP of the young stand ($0.46 \text{ kg C m}^{-2} \text{ year}^{-1}$) was higher than that obtained assuming that allocation changes with age ($0.40 \text{ kg C m}^{-2} \text{ year}^{-1}$, Figure 4). The simulated n_f of the young stand (0.0188) was also higher than in Figure 4. Of the simulations discussed, the results shown in Figure 5 are most consistent with field data (cf. Tables 1 and 2).

Sensitivity to woody litter decay rate

For both stands, there is uncertainty about the assumed rate of woody litter decay (D_{wl}). For Figures 3–5, we assumed $D_{wl} = 0$ and $0.1 \text{ kg C m}^{-2} \text{ year}^{-1}$ for the young and old stands, respectively. Figure 6 illustrates the consequences of assuming $D_{wl} = 0.05 \text{ kg C m}^{-2} \text{ year}^{-1}$. In this case, predicted NPPs of the old and young stands were 0.31 and $0.40 \text{ kg C m}^{-2} \text{ year}^{-1}$, respectively (assuming fixed allocation, Figure 6a) and 0.31 and $0.46 \text{ kg C m}^{-2} \text{ year}^{-1}$, respectively (assuming lower belowground allocation in the young stand, Figure 6b). The constraint curves shown in Figures 6a and 6b were similar in shape to those of Figures 4 and 5, respectively; the main difference was that, with lower D_{wl} , the N-cycling constraints were closer together. Consequently, the difference between modeled NPPs of the young and old stands was less than predicted with $D_{wl} = 0.1 \text{ kg C m}^{-2} \text{ year}^{-1}$ (Table 2).

As an alternative to the above values of D_{wl} , we considered the consequences if woody biomass and woody litter are equilibrated in the old stand. At this old-growth equilibrium, D_{wl} can be derived by equating wood production, woody litter production and woody litter decay:

$$a_w \text{NPP} = s_w C_w = d_{wl} C_{wl} = D_{wl}. \quad (19)$$

For the parameter values listed in Appendix 1, Equation 19 gave $D_{wl} = 0.07 \text{ kg C m}^{-2} \text{ year}^{-1}$ for the old stand. Predicted values of NPP for the young and old stands were 0.40 and $0.30 \text{ kg C m}^{-2} \text{ year}^{-1}$, respectively, assuming fixed allocation coefficients but variable soil N/C ratios, and 0.46 and 0.30 kg C m^{-2}

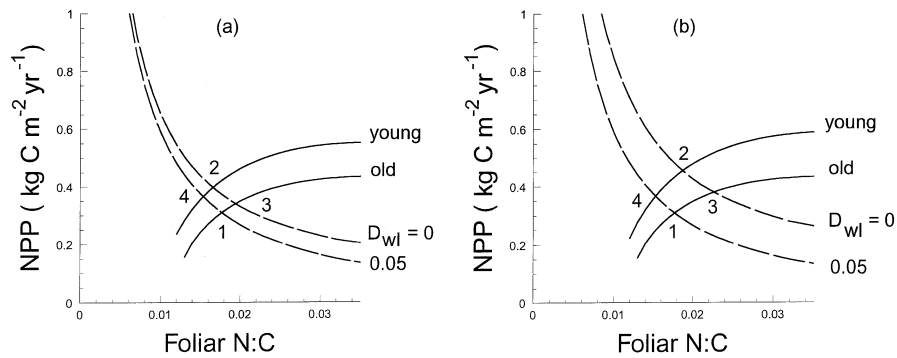


Figure 6. Photosynthetic and N-cycling constraint curves analogous to Figures 4 and 5, but assuming that forest floor woody litter decay rate of the old stand is $0.05 \text{ kg C m}^{-2} \text{ yr}^{-1}$ and (a) with constant allocation fractions, as assumed in Figure 4, and (b) with variable allocation fractions, as assumed in Figure 5.

year^{-1} , respectively, assuming variable allocation coefficients and variable soil N/C ratios.

Discussion

The simulations indicate that, for N-limited stands, changes in NPP with age can be explained in terms of two interacting processes: declining gross canopy photosynthetic efficiency and declining N availability as a result of increasing N immobilization in woody litter. The effect of declining N availability is even more important than the decline in gross canopy photosynthetic efficiency if it leads to increased allocation below-ground (Figure 5). The decline in NPP was only weakly associated with increasing sapwood respiration. However, our conclusions about the relative importance of the three competing hypotheses are sensitive to assumptions about the flexibility of soil N/C ratios. Thus, if we assume that the soil N/C ratio varies significantly with stand age, then both N availability and gross photosynthetic efficiency are important, whereas if soil N/C ratios are constant, declining N availability is primarily responsible for the modeled decline in NPP.

For a given n_f , the photosynthetic constraint of the young lodgepole pine stand can be 25% or more higher than that of the older stand (Figure 3a). This difference arises because the young stand has higher PAR utilization efficiency (ϵ_o) than the old stand; changes in sapwood respiratory load contributed little to the difference (Figure 3b versus Figure 3c). Such a large percentage change in modeled photosynthetic productivity might suggest that high ϵ_o can explain the higher productivity of young stands. However, scrutiny of both constraint curves reveals that nutrient cycling processes play a more important role than either ϵ_o or respiratory costs.

The main features of the analysis are summarized below.

1. Our explanation of aging process is strongly dependent on several assumptions, particularly woody litter decay rates and soil N/C ratios; hence to obtain reliable estimates of forest NPP it is important to model both woody litter accumulation and cycling of soil N and C correctly.

2. Declining soil N availability significantly reduced simulated NPP for the older lodgepole pine stand. The decline in NPP was related to woody litter accumulation on the ground and to a lesser extent increasing belowground allocation.

3. The age-related decline in NPP cannot be attributed solely to the young stand's lower stemwood respiratory load and higher PAR utilization efficiency.

We assumed that both young and old stands can be regarded as effective equilibrium systems. However, several studies suggest that woody biomass and woody litter pools are rarely in equilibrium because of frequent disturbance and species succession (Cottam 1980, Franklin and Hemstrom 1980, Harmon and Hua 1991). Often the whole or a part of the forest is destroyed by fire or wind before equilibrium is established (Heinselman 1980, Harmon et al. 1991). Therefore, the validity of our equilibrium-based approach depends on the frequency of major disturbances and the time required to achieve effective equilibrium after a disturbance. McMurtrie and Comins (1995) provide evidence that the effective equilibrium is achieved within two decades of disturbance.

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Appendix 1

Model variables and parameters, including parameterization for the old stand for Figure 3. Abbreviations: APAR = absorbed photosynthetically active radiation, C = carbon, GPP = gross primary production, N = nitrogen, NPP = net primary production, PAR = photosynthetically active radiation, SOM = soil organic matter. Subscripts: f = foliage, p = passive, r = fine roots, s = slow, w = wood, wl = woody litter.

Symbol	Definition	Value	Units
Variables			
b_{ij} ($i = p, s; j = f, r$)	Fractions of leaf and root litterfall C which are sequestered in passive and slow SOM	-	-
$C_f, C_w, C_{wl}, C_s, C_{sw}$	C Content of foliage, wood, and woody litter slow SOM and sapwood	-	kg C m ⁻²
$C_{sf}, C_{sr}, C_{swf}, C_{swr}$	C Fluxes into slow SOM from decomposing foliage, fine root and woody litter, and passive SOM	-	kg C m ⁻² year ⁻¹
C_{Rs}	Net C release from slow SOM decay	-	kg C m ⁻² year ⁻¹
d_{we}	Specific decomposition rate of woody litter	-	year ⁻¹
E	Function for N dependence of ϵ	-	-
GPP, NPP	Gross and net primary production	-	kg C m ⁻² year ⁻¹
N_{Rp}, N_{Rs}, N_{Rwl}	Net rates of N release from passive and slow soil and woody litter pools	-	kg N m ⁻² year ⁻¹
N_{Sp}, N_{Ss}, N_{Sw}	Rates of N sequestration in passive and slow SOM and wood	-	kg N m ⁻² year ⁻¹
N_f, N_r	N Contents of foliage and fine roots	-	kg N m ⁻²
N_{min}	Rate of N mineralization	-	kg N m ⁻² year ⁻¹
n_f, n_r, n_{fl}, n_{rl}	N/C Ratio of foliage, fine roots, foliage litter and fine root litter	-	-
R_c, R_m	Rates of construction and maintenance respiration	-	kg C m ⁻² year ⁻¹
R_{mf}, R_{mr}, R_{msw}	Rates of foliage, fine root and sapwood maintenance respiration	-	kg C m ⁻² year ⁻¹
U	Rate of N uptake	-	kg N m ⁻² year ⁻¹
Parameters			
a_f, a_r, a_w	Fraction of NPP allocated to foliage, fine roots and wood in the old stand	0.19, 0.58, 0.23	-
b_{ps}	Fraction of C release from slow SOM entering passive SOM	0.032	-
b_{sp}	Fraction of C release from passive SOM entering slow SOM	0.16	-
b_{ss}	Fraction of C release from slow SOM which re-enters slow SOM	0.15	-
b_{sw}, b_{pw}	Fraction of C release from woody litter pool entering slow and passive SOM	0.32, 0.0017	-
C_p	Carbon content of passive SOM	4.0	kg C m ⁻²
D_{wl}	Woody litter decay rate: first value for the young stand and the following three values for the old stand	0, 0.05, 0.1, 0.06	kg C m ⁻² year ⁻¹
d_p, d_s	Specific decomposition rates of passive and slow SOM	0.00046, 0.013	year ⁻¹
I_o	Incident PAR over active growing season	1.164	GJ m ⁻²
k	PAR extinction coefficient	0.5	-
N_A	Rate of atmospheric N deposition	0.00021	kg N m ⁻² year ⁻¹
N_F	Rate of N fixation	0	kg N m ⁻² year ⁻¹
n_w, n_{wl}	N/C Ratios of passive SOM, new wood and senescing woody litter	0.1, 0.00139, 0.0007	-
n_{po}, n_{so}	N/C Ratios of newly formed passive and slow SOM	0.1, 0.035	-
n_{crit}	Foliar N/C ratio below which photosynthesis is N limited	0.035	-
Q_{10}, Q_{10}'	Temperature dependence of maintenance respiration	2.0, 1.94	-
r_w	Fraction of N in new wood obtained by retranslocation from existing wood	0.6	-
R_0	Respiration rate corresponding to 0 °C	27	kg C kg ⁻¹ N year ⁻¹
s_f, s_r	Rate of foliage and fine roots senescence	0.12, 1	year ⁻¹
T_a	Mean annual air temperature	3.8	°C
x	Gaseous N emission fraction	0.01	-
ϵ	Maximum net PAR utilization efficiency	0.46	kg C GJ ⁻¹
ϵ_o	Maximum gross PAR utilization efficiency	1.05	kg C GJ ⁻¹
σ	Leaf area per unit of carbon	7.6	m ² kg ⁻¹ C
λ_f, λ_r	Ratio of leaf and root litter N/C relative to live tissue N/C	0.5, 1	-

Appendix 2

Equilibrium C content of the slow pool

Estimates of slow soil pool C and N are required to evaluate net release of N from slow SOM (N_{Rs}). We estimate slow SOM of the old stand under the assumption that slow pool C and N are equilibrated, i.e., that C flux into the slow pool matches efflux:

$$C_{sf} + C_{sr} + C_{sp} + C_{swl} = C_{Rs}, \quad (A1)$$

where C_{sf} , C_{sr} , C_{swl} and C_{sp} are influxes to the slow pool arising from decomposition of leaf, fine root, woody litter and passive SOM, respectively, and C_{Rs} is net release of C through decomposition of slow SOM:

$$C_{Rs} = d_s C_s (1 - b_{ss}), \quad (A2)$$

where b_{ss} represents the fraction of decomposing slow pool C which reenters the slow pool. Analysis of the CENTURY model gives $b_{ss} = 0.15$.

We let b_{sf} and b_{sr} represent the proportions of leaf and fine root litter C subsequently entering slow SOM, to obtain:

$$C_{sf} + C_{sr} = (a_l b_{sf} + a_r b_{sr}) NPP. \quad (A3)$$

When passive SOM decomposes, a proportion (b_{sp}) of its carbon loss enters slow SOM, giving:

$$C_{sp} = d_p C_p b_{sp}, \quad (A4)$$

where d_p is the decay rate of passive SOM and b_{sp} , representing the fraction of C released through decomposition of passive SOM, which subsequently enters slow SOM, is evaluated from the CENTURY model of Parton et al. (1987).

The C flux from decaying woody litter into slow SOM is

$$C_{swl} = d_{wl} C_{wl} b_{sw}, \quad (A5)$$

where d_{wl} is the woody litter decay rate, C_{wl} represents forest floor woody litter C and b_{sw} is the fraction of woody litter C subsequently entering slow SOM.

There are no measurements of forest floor woody litter for either of the *P. contorta* stands considered here; in this paper we ran the model for four constant values of the product $d_{wl} C_{wl} = D_{wl}$ (0 for the young stand and 0.05, 0.1 and 0.07 kg C m⁻² year⁻¹ for the old stand). Equilibrium slow pool C is obtained by substituting Equations A2–A5 into Equation A1:

$$C_s = \frac{(a_l b_{sf} + a_r b_{sr}) NPP + d_p C_p b_{sp} + D_{wl} b_{sw}}{d_s (1 - b_{ss})}, \quad (A6)$$

where C_p and D_{wl} are given and NPP is evaluated for the older stand by solving Equations 5 and 13.