



A Carbon-Balance Model of Stand Growth: A Derivation Employing the Pipe-Model Theory and the Self Thinning Rule

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WORKING PAPER

A CARBON-BALANCE MODEL OF STAND GROWTH: A DERIVATION EMPLOYING THE PIPE-MODEL THEORY AND THE SELF-THINNING RULE

Harry T. Valentine

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Preface

This paper represents an advance in the effort of IIASA's Acid Rain Project to develop a model of the possible damage caused by acid rain to forests. The paper reports a derivation of a stand-level model that describes how changes in the rate of carbon fixation and pattern of allocation, as affected by pollutants, may affect the growth and yield of a forest stand and its susceptibility to decline syndrome. The paper also represents a contribution to the field of forest ecology. In the course of the derivation, connections among different theories and observations of stand structure, self-thinning, and metabolism are demonstrated which previously had gone unnoticed.

Leen Hordijk
Leader
Acid Rain Project

Abstract

The pipe-model theory is used as a framework for the derivation of models describing the growth of average stem length, total basal area, and total volume of an even-aged, self-thinning, mono-species stand. Variations of the models are derived for two situations: (1) where the annual rates of substrate production and feeder-root turnover can be assumed constant over time, and (2) where these rates are expected to change over time, such as in polluted environments. The model describing the growth of stand volume for the first situation has been studied previously and shows good agreement with yield tables. Growth rate models applicable to individual trees are described and preferred over similar models derived previously by the author.

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**A Carbon-Balance Model of Stand Growth:
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1. INTRODUCTION

Carbon-balance modeling (e.g., McMurtrie and Wolf, 1983; Mäkelä and Hari, 1986), the pipe-model theory (Shinozaki *et al.*, 1964 a,b ; Oohata and Shinozaki, 1979; Waring *et al.*, 1982), and the self-thinning of even-aged stands (e.g., Yoda *et al.*, 1963; White, 1981; Westoby, 1984) have been three important, though rather distinct, topics of research in forest ecology. Recently, however, the pipe-model theory was used in connection with derivations of carbon-balance models of the growth of individual trees (Valentine, 1985; Mäkelä, 1986). In the present article, I use the pipe-model theory as a framework for the derivation of a model of the growth of an even-aged, self-thinning, mono-species stand. Two variations of the model are described: 1) for stands where the annual rates of substrate production and feeder-root turnover can be considered constant over time, and 2) for stands where these rates are expected to change over time due to changing environments caused by air pollution/acid rain or other factors.

The pipe-model theory of Shinozaki *et al.* (1964 a,b) provides a simple interpretation of the structures of plants and stands. In the present model, a stand of trees is assumed to be comprised of leaves, feeder roots, active pipes, and disused pipes (Fig. 1). The woody components of the stand – branches, stems, and transport roots – are modeled in aggregate as an assemblage of active and disused pipes. Active pipes extend from leaves to feeder roots, and have both supporting and vascular functions. In accordance with the pipe-model theory, a constant ratio is maintained between total

foliar dry matter and the total cross-sectional area of the active pipes in the stand. In addition, I assume that feeder-root dry matter is proportional to foliar dry matter. Disused pipes have a supporting function but do not serve as vascular connections between leaves and feeder roots. An active pipe becomes disused when the foliage and feeder roots attached to it die (or are not renewed). The distal portion of a disused pipe is lost from the stand when the branch of which it is a part, is shed or pruned off. However, the basal portion of a disused pipe remains a part of a specific tree and a part of the stand until that tree dies. Consequently, the basal area of a stand equals the aggregate basal area of its active pipes (active-pipe area) plus the aggregate basal area of its disused pipes (disused-pipe area) at 1.37 m.

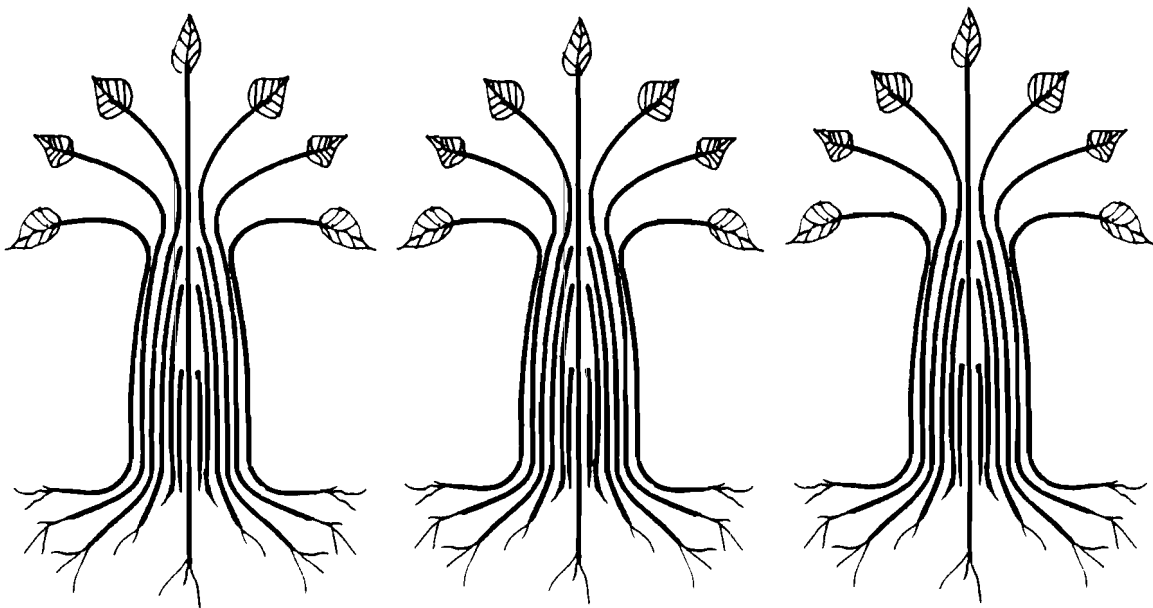


Figure 1. In this pipe model, active pipes connect leaves to feeder roots and have both vascular and supporting functions. Disused pipes – vestiges of old active pipes – no longer connect leaves to feeder roots and have only a supporting function. The active and disused pipes, in aggregate, represent all of the woody components of the stand: branches, boles, transport roots.

The development of an even-aged stand can be divided into two stages according to foliar dynamics. In the first stage, the total foliar dry matter of the stand increases over time. The growth of the basal area of the stand in this stage is due, in large part, to the growth of active-pipe area which is proportional to the growth of foliar dry

matter. The second stage of a stand's development begins when foliar dry matter reaches its maximum. In some stands the maximum may be reached within four years after establishment (Mohler *et al.*, 1978). Cross-sectional samples of stands have furnished evidence that once the maximum of foliar dry matter is reached, it tends to be sustained until senescence (Marks, 1974; Sprugel, 1974; Mohler *et al.*, 1978). Other cross-sectional data have been interpreted as indicating that foliar dry matter peaks and then declines slightly, but rapidly, to a constant level that is sustained until senescence (Forrest and Ovington, 1970; Kira and Shidei, 1967). Regardless of whether the maximum of foliar dry matter is a peak or a plateau, the growth of the basal area of a stand in the second stage of development is due to the growth of the aggregate basal area of disused pipes. Increases in the active-pipe areas of some trees are compensated by reductions in the active-pipe areas of other trees. A tree dies when its active-pipe area decreases to zero.

2. MODEL FRAMEWORK

The present model applies to stands in the second stage of development, where foliar dry matter and active-pipe area are maximal (or nearly so) and more or less constant. In deriving the model, I assume that ingrowth into an even-aged stand is nil; all changes in the tree count are negative and due to tree death.

Variables

N = the number of trees in the stand.

A = the total active-pipe area of the stand (m^2).

\bar{B} = the average basal area per tree (m^2).

B = the total basal area of the stand (m^2).

L = the average length of an active pipe (m).

V = the total volume of the stand (m^3).

V' = the total aboveground volume of the stand (m^3).

X = the total disused-pipe area of the stand (m^2).

Growth rate of basal area

The growth rate of the basal area of a stand equals the sum of the net growth rates of active-pipe and disused-pipe areas:

$$dB/dt = dA/dt + dX/dt \quad (1)$$

The net growth rate of active-pipe area, dA/dt , can be split into a positive fraction (dA^+/dt) and a negative fraction ($-dA^-/dt$), i.e., $dA/dt = dA^+/dt - dA^-/dt$. The positive fraction is the rate of production of new active-pipe area by the living trees in the stand, and in the absence of tree mortality, this rate equals the growth rate of the total basal area of the stand. The negative fraction, $-dA^-/dt$, is the rate of conversion of active-pipe area to disused-pipe area. This conversion neither adds nor subtracts from the basal area of the stand. Similarly, the net growth rate of disused-pipe area, dX/dt , can be split into a positive fraction (dX^+/dt) and a negative fraction ($-dX^-/dt$), i.e., $dX/dt = dX^+/dt - dX^-/dt$. The positive fraction equals dA^-/dt . The negative fraction is the rate at which disused-pipe area is lost from the stand to mortality. Because $-dA^-/dt + dX^+/dt = 0$, the growth rate of stand basal area can be rewritten as:

$$dB/dt = dA^+/dt - dX^-/dt \quad (2)$$

Growth rate of active-pipe length

The growth rate of average, active-pipe length, dL/dt , also can be split into two fractions: a metabolic fraction (dL_M/dt) and a numerical or non-metabolic fraction (dL_N/dt), i.e.,

$$dL/dt = dL_M/dt + dL_N/dt \quad (3)$$

The metabolic fraction, dL_M/dt , is the rate at which average, active-pipe length increases due to the apical growth of shoots and roots. The non-metabolic fraction, dL_N/dt , is the rate at which average, active-pipe length increases due to the suppression and disuse of pipes that are, on average, shorter than L .

A model of the metabolic rate, dL_M/dt , is derived below, along with a model of dA^+/dt , with a carbon-balance approach. First, however, I show that both the non-metabolic rate, dL_N/dt , and the rate of loss of disused-pipe area to mortality, dX^-/dt , can be expressed as functions of dA^+/dt .

Disuse of short pipes

By definition, the growth rate of the active-pipe volume of a stand is

$$d(AL)/dt = A(dL_M/dt + dL_N/dt) + L(dA^+/dt - dA^-/dt) \quad (4)$$

and the rate of production of new active-pipe volume, through metabolic processes, is $LdA^+/dt + AdL_M/dt$. Disused pipes do not increase in length, so if the average length of a deactivating pipe is ϑL ($0 < \vartheta < 1$), then the rate of production of new disused-pipe volume is $-\vartheta L dA^-/dt$ and conservation of active-pipe volume requires that:

$$-(1-\vartheta)L dA^-/dt + AdL_N/dt = 0 \quad (5)$$

Substituting $dA^+/dt - dA^-/dt$ for dA^-/dt and solving for the non-metabolic fraction of the growth rate of average, active-pipe length, therefore

$$dL_N/dt = [(1-\vartheta)L/A](dA^+/dt - dA/dt) \quad (6)$$

Restricting consideration to stands for which $dA/dt = 0$ and $A \approx A_{\max}$, eqn (6) reduces to

$$dL_N/dt = [(1-\vartheta)L/A_{\max}]dA^+/dt \quad (7)$$

Self-thinning

To derive a model for dX^-/dt , I use Reineke's (1933) precursor of the self-thinning rule. The self-thinning of even-aged stands has been an active topic of ecological research for the last two decades (e.g., Yoda *et al.*, 1963; White, 1981; Westoby, 1984) and a topic of forestry research for considerably longer. Numerous reports in the forestry literature since the seminal paper by Reineke (1933) indicate that the number of trees comprising an even-aged, mono-species stand, given an average basal area per tree, \bar{B} , is $N \leq N_R$, where

$$N_R = k\bar{B}^{-c} \quad (8)$$

$$(dN_R/dt)/N_R = -c(d\bar{B}/dt)/\bar{B} \quad (9)$$

and c (≈ 0.8 for most species) and k are constants. Multiplying eqn (9), the time derivative of eqn (8), by an arbitrary scalar, $-\psi$, and rearranging gives:

$$-\psi\bar{B}dN_R/dt - \psi cN_Rd\bar{B}/dt = 0 \quad (10)$$

By definition, $B = \bar{B}N$ and therefore

$$dB/dt = \bar{B}dN/dt + Nd\bar{B}/dt \quad (11)$$

Adding zero in the form of the left-hand side of eqn (10) to the right-hand side of eqn (11) gives the dynamics of B , \bar{B} , and N_R of a stand growing according to eqns (8) and (9) (i.e., a stand for which $N = N_R$):

$$dB/dt = (1-\psi c)N_Rd\bar{B}/dt + (1-\psi)\bar{B}dN_R/dt \quad (12)$$

If ψ is scaled such that the average basal area of a dying tree is $(1-\psi)\bar{B}$, then $(1-\psi)\bar{B}dN_R/dt$ is the rate that basal area is lost from the stand to mortality which equals $-dX^-/dt$ of eqn (2). Setting the positive and negative fractions of eqn (2) equal to those of eqn (12), therefore:

$$dA^+/dt = (1-\psi c)N_Rd\bar{B}/dt \quad (13)$$

$$-dX^-/dt = (1-\psi)\bar{B}dN_R/dt \quad (14)$$

Solving eqns (13) and (14), respectively, for $d\bar{B}/dt$ and dN_R/dt , and inserting the resultant expressions into (9), yields

$$dX^-/dt = \varphi dA^+/dt \quad (15)$$

where $\varphi = c(1-\psi)/(1-c\psi)$ is assumed constant. Substituting eqn (15) into (2), therefore

$$dB/dt = (1-\varphi)dA^+/dt \quad (16)$$

3. CARBON BALANCE

I use a carbon-balance approach (Thornley, 1976; Chapt. 6) to derive models of dA^+/dt and dL_M/dt . Dry matter of foliage, feeder roots, and pipes is measured in kg of equivalent CO_2 as is dry-matter substrate produced by the foliage and consumed in respiration for construction or maintenance of foliage, feeder roots, and active pipes.

Foliar dry matter

The following quantities pertain to the growth, maintenance, and renewal of foliar dry matter:

z = units of foliar dry matter in mid-summer per unit active-pipe area (kg $[\text{CO}_2]/\text{m}^2$).

r_z = units of dry matter substrate consumed in the construction of a new unit of foliar dry matter.

b_z = units of dry-matter substrate consumed per year for maintenance of a unit of foliar dry matter. In addition, $(r_z + 1)/T_z$ units of dry-matter substrate are consumed per unit of foliar dry matter per year for renewal, where

T_z = the average ultimate leaf age (growing seasons) for the species.

It follows from these definitions that the total foliar dry matter in the stand is zA . The rate of production of new foliar dry matter is $z dA^+ / dt$ and the rate of constructive respiration for new foliar dry matter is $z r_z dA^+ / dt$. The rates of production and constructive respiration are defined with dA^+ / dt because it is the positive fraction of dA / dt . The negative fraction of dA / dt is the rate of production of new disused-pipe area, for which there is no corresponding consumption of dry-matter substrate. The rate of respiration for maintenance and renewal of extant foliar dry matter on an annual basis is $z [b_z + (r_z + 1) / T_z] A$.

Feeder-root dry matter

Constants analogous to z , r_z , b_z , and T_z are assumed to apply to feeder-root dry matter and are denoted, respectively, by f , r_f , b_f , and T_f . Feeder-root dry matter in the stand is fA , the rate of production of new feeder-root dry matter is $f dA^+ / dt$, the rate of constructive respiration is $f r_f dA^+ / dt$, and the rate of respiration for maintenance and renewal is $f [b_f + (r_f + 1) / T_f] A$. Combined terms for foliar and feeder-root dry matter are defined as follows

$$z' = z + f$$

$$r' = zr_z + fr_f$$

$$b' = z[b_z + (\tau_z + 1)/T_z] + f[b_f + (\tau_f + 1)/T_f]$$

Thus, the rates of production and constructive respiration of new foliar plus feeder-root dry matter are denoted, respectively, by $z'dA^+/dt$ and $r'dA^+/dt$. The rate of respiration for maintenance plus renewal of existing foliar plus feeder-root dry matter is $b'A$.

Woody dry matter

Quantities pertaining to the growth and maintenance of active-pipe (woody) dry matter are defined as follows:

u = units of woody dry matter per unit woody volume ($\text{kg } [\text{CO}_2]/\text{m}^3$).

r_p = units of substrate consumed in the construction of a new unit of woody dry matter.

b_p = units of dry-matter substrate consumed per year for maintenance of a unit of active-pipe dry matter. Disused-pipe dry matter is assumed to be devoid of respiring cells.

The total active-pipe dry matter in the stand is uAL and the rate of respiration for maintenance of the living woody dry matter is ub_pAL . The rate of production of new active-pipe dry matter is $u(LdA^+/dt + AdL_M/dt)$ and, the rate of constructive respiration for new active-pipe dry matter is $ur_p(LdA^+/dt + AdL_M/dt)$.

Dry-matter substrate

Production of dry-matter substrate by a stand is a function of the foliar dry matter. For the present model:

α = the maximum units of dry-matter substrate produced per year per unit foliar dry matter.

To account for a suboptimal environment for substrate production, the actual rate of substrate production is defined in terms of a scaling variable (I) so that

αI = the actual units of dry-matter substrate produced per year per unit foliar dry matter.

Thus, I varies between 0 and 1, and $\alpha z AI$ is the rate of dry-matter substrate production by a stand.

Production rates

The sum of the rates of production and constructive respiration of new foliar, feeder-root, and active-pipe dry matter in the stand equals the rate of substrate production minus the sum of the rates of maintenance respiration for existing foliar, feeder-root, and active-pipe dry matter

$$u(1+r_p)AdL_M/dt + [z'+r'+u(1+r_p)L]dA^+/dt = A[\alpha zI - b' - ub_pL] \quad (17)$$

As was noted, branches, stem, and transport roots are modeled in aggregate as an assemblage of active and disused pipes. The lengthening of existing active pipes corresponds roughly to apical growth, and the production of new active pipes corresponds roughly to cambial growth. Because apical growth tends to occur over a more or less fixed portion of each growing season for many species, it seems natural to assume that a constant proportion of the available dry-matter substrate is used for this growth and associated constructive respiration. Thus, eqn (17) is split into 2 parts according to the type of growth with constant partitioning coefficients, (λ) and $(1-\lambda)$, ($0 < \lambda < 1$):

$$u(1+r_p)AdL_M/dt = (1-\lambda)A[\alpha zI - b' - ub_pL] \quad (18)$$

$$[z'+r'+u(1+r_p)L]dA^+/dt = \lambda A[\alpha zI - b' - ub_pL] \quad (19)$$

Solving eqns (18) and (19), respectively, for dL_M/dt and dA^+/dt , therefore

$$dL_M/dt = (1-\lambda)[aI - b^* - bL] \quad (20)$$

$$dA^+/dt = \lambda A[aI - b^* - bL] / [z^* + L] \quad (21)$$

where

$$a = \alpha z / (u + ur_p)$$

$$b^* = b' / (u + ur_p)$$

$$b = ub_p / (u + ur_p)$$

$$z^* = (z' + r') / (u + ur_p)$$

4. STAND-LEVEL MODEL

Active-pipe length

The growth rate of average, active-pipe length is obtained by substituting eqn (21) into (6) and adding the result to eqn (20), i.e.,

$$dL/dt = [aI - b^* - bL] [(1-\lambda) + \lambda(1-\vartheta)L / (z^* + L)] - [(1-\vartheta)L / A] dA/dt \quad (22)$$

When dA/dt equals 0, eqn (22) is integrable from t to $t + \Delta t$ if I is assumed constant over that span. However, the value of $L / (z^* + L)$ should be fairly constant and close to 1 for large L , so eqn (22) reduces to

$$dL/dt = \kappa_0 [aI - b^* - bL] \quad (23)$$

Integration of this simpler function yields

$$L(t + \Delta t) = \kappa_1 + \kappa_2 I(t) + \kappa_3 L(t) \quad (24)$$

where

$$\begin{aligned} \kappa_0 &\approx 1 - \vartheta\lambda \\ \kappa_1 &= -b^* (1 - \kappa_3) / b \\ \kappa_2 &= a (1 - \kappa_3) / b \\ \kappa_3 &= \exp(-\kappa_0 b \Delta t) \end{aligned}$$

It is noted, on the one hand, that if I were constant for all t , then eqn (24) would reduce to a Mitscherlich growth function in L . On the other hand, if the specific rate of feeder-root turnover (T_f^{-1}) is variable, but can be assumed constant over the span from t to $t + \Delta t$, then the constant κ_1 in eqn (24) should be replaced by

$$\kappa_1(t) = \kappa_4 + \kappa_5 / T_f(t)$$

to give

$$L(t + \Delta t) = \kappa_4 + \kappa_5 / T_f(t) + \kappa_2 I(t) + \kappa_3 L(t) \quad (25)$$

where

$$\begin{aligned} \kappa_4 &= -\{z [b_z + (r_z + 1) / T_z] + f b_f\} (1 - \kappa_3) / u b_p \\ \kappa_5 &= -f (r_f + 1) (1 - \kappa_3) / u b_p \end{aligned}$$

Basal area

The growth rate of basal area of an actively self-thinning stand is obtained by substituting eqn (21) into (16), i.e.,

$$dB/dt = (1-\varphi)\lambda A_{\max}[\alpha I - b^* - bL]/(z^* + L) \quad (26)$$

Substituting eqn (23) into (26) furnishes the rate of change of B with respect to L

$$dB/dL = (1-\varphi)\lambda A_{\max}/[\kappa_0(z^* + L)] \quad (27)$$

Integration of eqn (27) from t to $t + \Delta t$ gives a function describing the annual growth of the basal area of the stand

$$B(t + \Delta t) = B(t) + \kappa_6 \{ \ln[L(t + \Delta t) + z^*] - \ln[L(t) + z^*] \} \quad (28)$$

where $\kappa_6 = (1-\varphi)\lambda A_{\max}/\kappa_0$. Substitution of $\exp\{[B(t) - c_1]/\kappa_6\} - z^*$, where c_1 is a constant, for $L(t)$ into eqn (25) furnishes a model of the growth of stand basal area as a function of the rates of feeder-root turnover and substrate production, i.e.,

$$B(t + \Delta t) = \kappa_6 \ln \{ \kappa_7 + \kappa_8 / T_f(t) + \kappa_9 I(t) + \kappa_3 \exp[B(t)/\kappa_6] \} \quad (29)$$

where

$$\kappa_7 = [\kappa_4 + z^* (1 - \kappa_3)] \exp(c_1 / \kappa_6)$$

$$\kappa_8 = \kappa_5 \exp(c_1 / \kappa_6)$$

$$\kappa_9 = \kappa_2 \exp(c_1 / \kappa_6)$$

Total volume

The growth rate of the woody volume of a stand (dV/dt) equals the rate of production of new active-pipe volume minus the rate that disused-pipe volume is lost to mortality and the shedding of branches. Let $v_1 L (dA^+ / dt - dA / dt)$ denote the rate that volume is lost to shedding of branches in connection with the disuse of pipes and let $v_2 L (dX^- / dt)$ denote the rate that disused-pipe volume is lost to mortality so that

$$dV/dt = L dA^+ / dt + A dL_M / dt - L [v_1 (dA^+ / dt - dA / dt) + v_2 dX^- / dt] \quad (30)$$

where v_1 and v_2 are assumed constant. Eqn (15) applies to a self-thinning stand where $dA / dt = 0$, in which case eqn (30) reduces to

$$dV/dt = (1 - v_1 - \varphi v_2) L dA^+ / dt + A dL_M / dt \quad (31)$$

The rate of change of V with respect to L is obtained by substituting eqns (20), (21), and (23) into (31), i.e.,

$$dV/dL = (A/\kappa_0)[(1-\lambda)+(1-\nu_1-\varphi\nu_2)\lambda L/(z^*+L)] \quad (32)$$

Because $A \approx A_{\max}$ when $dA/dt = 0$, and $L/(z^*+L) \approx 1$ for large L , eqn (31) can be integrated to yield

$$V(t+\Delta t) = V(t) + \kappa_{10}[L(t+\Delta t) - L(t)] \quad (33)$$

where $\kappa_{10} = A_{\max}[1-(\nu_1+\varphi\nu_2)\lambda]/\kappa_0$. Substitution of $[V(t)-c_2]/\kappa_{10}$, where c_2 is a constant, for $L(t)$ into eqn (25) furnishes a model of growth of woody volume as a function of the rates of feeder-root turnover and substrate production, i.e.,

$$V(t+\Delta t) = \kappa_{11} + \kappa_{12}/T_f(t) + \kappa_{13}I(t) + \kappa_3V(t) \quad (34)$$

where $\kappa_{11} = \kappa_4\kappa_{10} + c_2(1-\kappa_3)$, $\kappa_{12} = \kappa_5\kappa_{10}$, and $\kappa_{13} = \kappa_2\kappa_{10}$.

The growth of volume, like the growth of L , is described by a Mitscherlich function if $I(t)$ and $T_f(t)$ are constant for all t , and if the assumptions leading to eqn (34) are not overly Procrustean.

Aboveground volume

Eqn (34) applies to aboveground plus belowground woody volume, but if aboveground woody volume, V' , is assumed to be a constant fraction (ν) of total woody volume, then the growth fraction of V' is

$$V'(t+\Delta t) = \kappa_{14} + \kappa_{15}/T_f(t) + \kappa_{16}I(t) + \kappa_{17}V'(t) \quad (35)$$

where $\kappa_{14} = \nu\kappa_{11}$, $\kappa_{15} = \nu\kappa_{12}$, and $\kappa_{16} = \nu\kappa_{13}$. In an invariant environment, where I and T_f are constant, the growth function of V' is

$$V'(t+\Delta t) = \kappa_{18} + \kappa_{17}V'(t) \quad (36)$$

where $\kappa_{18} = \kappa_{14} + \kappa_{15}/T_f + \kappa_{16}I$.

5. DISCUSSION

Previously, Khil'mi (1957) used a model analogous to eqn (36) to describe the aboveground growth of closed, self-thinning stands and obtained good agreement

between the model and yield tables. The parameter κ_{17} was shown to be more or less constant among stands of a given species in the same geographical region, regardless of site quality, whereas the value of κ_{18} increased from poor to good sites. The assumptions of the present model are in accordance with the findings of Khil'mi inasmuch as κ_{17} is a constant, i.e.,

$$\kappa_{17} = \nu \cdot \exp[(1 - \theta\lambda)b_p \Delta t / (1 + r_p)]$$

and κ_{18} is a function of the rate of feeder-root turnover and the rate of substrate production which is known to vary among stands, depending on site quality. These properties also may hold for some even-aged, mixed-species stands (Fig. 2).

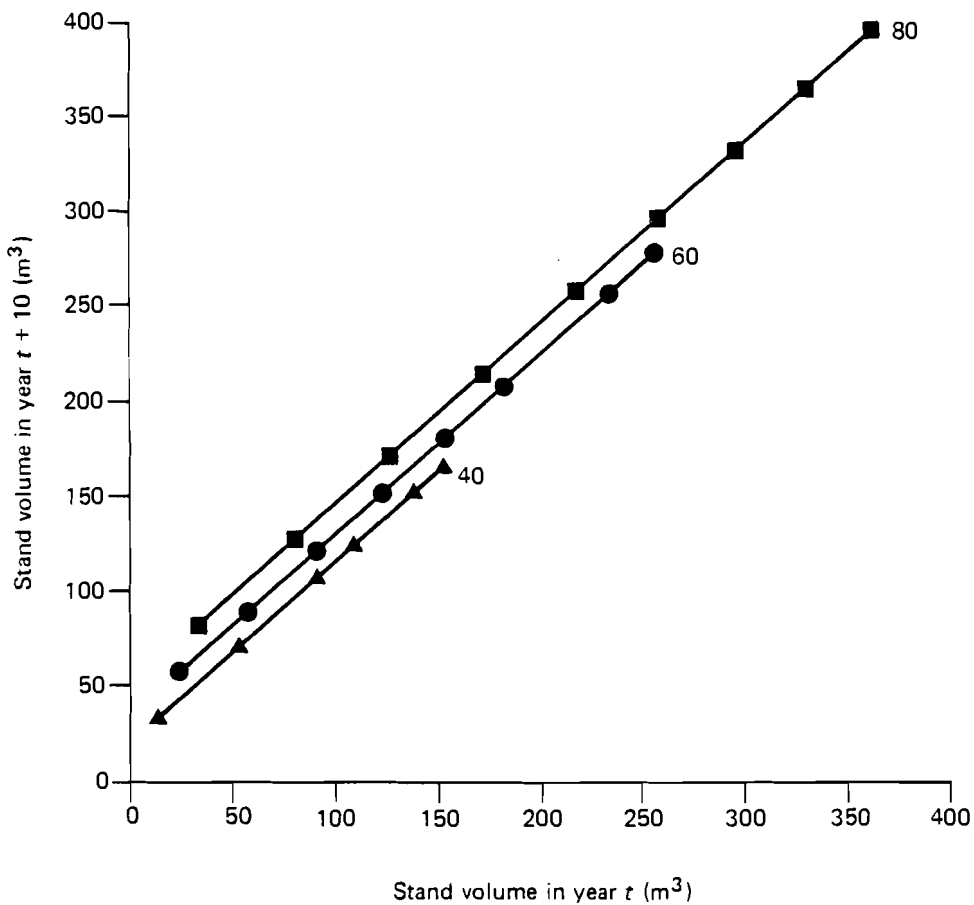


Figure 2. Total predicted aboveground volume in year $t + 10$ vs. volume in year t ($t = 10, 20, \dots, 90$) for mixed oak (*Quercus* spp.) stands of site index 40, 60, or 80 in the northeastern United States. Data are from Schnur (1937: Table 12). The common slope of the three regression lines is 0.951. Intercepts for site indices 40, 60, and 80, respectively are 21.1, 35.4, and 50.4 ($r^2 = 0.99$; $se = 1.35$).

Periodic increment ($\Delta V'$) from t to $t+\Delta t$ in a single self-thinning stand with constant T_f and I is obtained by subtracting $V'(t)$ from eqn (36), i.e.,

$$\Delta V' = \kappa_{18} + (\kappa_{17} - 1)V'(t) = \kappa_{14} + \kappa_{15}/T_f + \kappa_{16}I + (\kappa_{17} - 1)V'(t) \quad (37)$$

The asymptotic yield (V'_{\max}) of the stand equals $V'(t)$ when $\Delta V'$ equals zero

$$V'_{\max} = \kappa_{18} / (1 - \kappa_{17}) = (\kappa_{14} + \kappa_{15}/T_f + \kappa_{16}I) / (1 - \kappa_{17}) \quad (38)$$

Corresponding to V'_{\max} is the asymptotic, average, active-pipe length (L_{\max}) which is obtained from eqn (25)

$$L_{\max} = (\kappa_4 + \kappa_5/T_f + \kappa_2I) / (1 - \kappa_3) \quad (39)$$

Unlike V'_{\max} , which depends on the values of the self-thinning and pruning parameters ($\varphi, \vartheta, v_1, v_2$), L_{\max} depends only on the fundamental carbon-balance parameters, i.e.,

$$L_{\max} = \{ \alpha z I - z [b_z + (r_z + 1)/T_z] - f [b_f + (r_f + 1)/T_f] \} / u b_p \quad (40)$$

By the present theory, L_{\max} is the active-pipe length (i.e., average stem length from z units of foliar dry matter to f units of feeder-root dry matter) at which the rate of substrate production balances the rate of maintenance respiration so that there is no further growth by the stand. With constant T_f and I , L_{\max} is truly an asymptote, a value that is approached, but never reached. However, in a changing environment, where T_f and I or both can be expected to vary in closed, self-thinning stands, a better definition for L_{\max} is potential active-pipe length.

It has been hypothesized that air pollution/acid rain is causing or contributing to certain forest declines in Europe, Japan, and parts of North and South America, and Southeast Asia. Bossel (1986) noted that such hypotheses fit into two categories: 1) those concerning direct damage to foliage by pollutants with consequent deceleration of the rate of substrate production, and 2) those concerning damage to feeder roots or mycorrhizae in acidifying soils with consequent acceleration of the rate of feeder-root turnover. The present model suggests that either kind of damage should cause decreases in stand growth rate, potential active-pipe length and, correspondingly, potential yield, V'_{\max} . If changes in T_f^{-1} or I were of such magnitude that

$$[\kappa_4 + \kappa_5 / T_f(t) + \kappa_2 I(t)] / (1 - \kappa_3) < L(t)$$

then actual active-pipe length would exceed the potential and widespread dieback or tree death should occur within the stand because the demand for substrate for the maintenance of existing living tissue would not be met. This situation should be more likely where $L(t)$ is large, which is consistent with observations that dieback is more severe in older than in younger stands.

The onset of dieback creates a situation for which the present model does not apply. Self-thinning and the constancy of foliar dry matter are disrupted by the death or dieback of suppressors, in addition to suppressed individuals, and the resultant creation of gaps in the canopy of the stand. Moreover, the metabolic aspects of stand growth for instances where the rate of respiration exceeds the rate of substrate production is not formulated in the present carbon-balance model.

A situation for which the application of the present model could be extended is the period before the canopy closes following the establishment of a stand (or following a silvicultural thinning) where foliar dry matter is increasing and self-thinning is nil or just beginning (or resuming). Such an extension should require functions describing $I(t)$, dA/dt , and dX^-/dt where $A < A_{\max}$. Regarding the latter two rates, it is expected that in general

$$0 \leq dA/dt \leq dA^+/dt$$
$$0 \leq dX^-/dt \leq \varphi(dA^+/dt - dA/dt)$$

where φ is the constant of eqn (15) and $(dA^+/dt - dA/dt)$ equals the rate of production of new disused-pipe area, dX^+/dt . The degree of closure achieved by a stand before the onset of the production of disused-pipe area ($dA^+/dt > dA/dt$) or the onset of self-thinning ($dX^-/dt > 0$) depends largely on the variation in the sizes of the trees and their spacial arrangement. In natural stands of irregularly spaced trees, the onset of self-thinning may occur nearly coincident with the onset of production of disused-pipe area, but in plantations of regularly spaced trees, self-thinning may not occur until after disused-pipe area comprises a sizable fraction of the stand's basal area.

Individual trees

Previously, I used a pipe-model framework to derive a model of the growth rate of an individual tree (Valentine, 1985). Eqns (1), (3) through (6), and (17) through (23) of the present article also apply at the tree level, and are preferred over the earlier model. Because an individual tree retains the basal portions of all of its disused pipes within its bole, the rate of production of new active-pipe area, dA^+/dt , equals the growth rate of the basal area of the tree, dB/dt . Therefore, at the tree level, eqn (21) gives the basal area growth rate, viz.

$$dB/dt = \lambda A [aI - b^* - bL] / [z^* + L] \quad (41)$$

The growth rate of total volume at the tree level is obtained by dropping the term involving dX^-/dt from eqn (30) and substituting dB/dt for dA^+/dt , whence

$$dV/dt = L [v_1 dA/dt + (1 - v_1) dB/dt] - A dL_M/dt \quad (42)$$

The growth rate of the fraction, ν , of the total volume that is aboveground is simply

$$dV'/dt = \nu dV/dt \quad (43)$$

The rates dL_M/dt and dL/dt , respectively, are described at the tree level by eqns (21) and (23) without change. The foliar dry matter of an individual tree and its rate of substrate production per unit of foliar dry matter are unlikely to remain constant over time. Consequently, functions describing dA/dt and $I(t)$ are needed to complete the individual tree model and remain to be formulated.

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