

A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning

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Abstract

This paper describes a stand growth model, based on physiological processes, which incorporates a number of steps and procedures that have allowed considerable simplification relative to extant process-based models. The model, called 3-PG (use of Physiological Principles in Predicting Growth), calculates total carbon fixed (gross primary production; P_G) from utilizable, absorbed photosynthetically active radiation ($\phi_{p.a.u.}$), obtained by correcting the photosynthetically active radiation absorbed by the forest canopy ($\phi_{p.a.}$) for the effects of soil drought, atmospheric vapour pressure deficits and stand age. P_G is obtained from $\phi_{p.a.u.}$ and the canopy quantum efficiency, values of which are becoming available. The ratio of net (P_N) to gross primary production is emerging as relatively constant for trees. This eliminates the need to calculate respiration and is used to estimate P_N —the net amount of carbon converted to biomass. 3-PG uses a simple relationship to estimate the amount of carbon allocated below ground and a procedure based on allometric ratios—widely available for many species and situations—to determine the allocation of carbon to foliage and stems and constrain tree growth patterns. The effects of nutrition are incorporated through the carbon allocation procedure; the amount of carbon allocated below ground will increase with decreasing soil fertility. Recently acquired knowledge about the physiological factors causing decline in forest growth rates with age is used to model that decline. Changes in stem populations (self-thinning) are derived from a procedure based on the $-3/2$ power law, combined with stem growth rates.

The model requires weather data as input, works on monthly time steps and has been run for periods up to 120 years, producing realistic patterns of stem growth and stem diameter increments. The time course of leaf area index is realistic for a range of soil conditions and atmospheric constraints. 3-PG can be run from remotely-sensed estimates of leaf area index coupled to weather data and basic, readily available information about soils and stand characteristics. It is being tested as a practical tool against forestry data from New South Wales, Tasmania, Victoria and New Zealand. Test results show excellent correspondence between stand growth measurements and simulated stem growth over 30 years. © 1997 Elsevier Science B.V.

Keywords: Forest model; Carbon balance; Partitioning; Physiological processes; Weather

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1. Introduction

A number of process-based models aimed at calculating forest productivity have been developed within the last 10–15 years. Among these, FOREST-BGC (Running and Coughlan, 1988; Running and Gower, 1991) is one of the best known and most widely used, while others such as BIOMASS (McMurtrie et al., 1992), PnET (Aber and Federer, 1992) and TREGROW (Weinstein et al., 1991) are also well established. FOREST-BGC has been generalised to BIOME-BGC (Running and Hunt, 1993) and BIOMASS provided the basis for the G'DAY model (Comins and McMurtrie, 1993), which incorporates nitrogen uptake and movement within trees and allows evaluation of the long-term consequences of changes in atmospheric CO₂ and the effects of the soil nitrogen balance on carbon accumulation by trees. All these models, however, are essentially research tools and have yet to be simplified to the point where they are of value—or indeed of interest—to practical forest managers. There is good reason for this: the calculation of forest growth from physiological processes is complicated and has necessarily involved the use of detailed, multi-variable models that generally require a great deal of information and careful parameterisation before they can be run. There is progress in simplification—FOREST-BGC has been streamlined to the point where it requires only an estimate of projected leaf area index (L^*), and appropriate weather data, making it suitable for use with satellite measurements (White and Running, 1994), but the result remains an estimate of carbon fixed and biomass produced, which is of limited value to those concerned with forest growth in the conventional sense of changes in tree mass and the distribution of that mass to trees and their component parts.

We believe that the detailed models have now developed to the point where they can be used to generate simplified relationships, soundly based in biophysical processes yet accessible to practitioners as well as to scientists. To generate practical tools these process-based calculations must be combined with empirical relationships derived from experiments and measurements made over long periods in forests and plantations. This paper describes a model

called 3-PG (the acronym is derived from the use of Physiological Principles in Predicting Growth) developed using this approach. The model is based on a number of well-established principles and some recently confirmed constants that greatly simplify calculations. It required little adjustment to obtain realistic forest growth estimates from a simple (spreadsheet) program, and can easily be parameterised for particular forest types. The constraints that lead to the actual amounts of intercepted photosynthetically-active radiation (light) that is utilised by forests are soundly-based in physiology and consistent with much more detailed models. This model, moreover, can be applied to ground-based forest inventory maps incorporated into a Geographical Information System (GIS), or to maps derived from an analysis of satellite images, to extend estimates of forest growth over large, heterogenous areas.

The 3-PG model (see Table 1 for summary of abbreviations and symbols):

- calculates gross primary production (P_G) from utilisable absorbed photosynthetically active radiation ($\phi_{p.a.u.}$) and a canopy quantum efficiency coefficient (α_c). $\phi_{p.a.u.}$ is obtained by reducing the values of absorbed photosynthetically active radiation ($\phi_{p.a.}$) by amounts determined by modifiers—dimensionless factors (f_i) with values varying between zero and unity. The modifiers reflect the constraints imposed on the utilisation of absorbed radiation by leaves because of stomatal closure, caused by high atmospheric vapour pressure deficits (D), soil drought, defined by the ratio of the amount of water in the root zone to the maximum possible amount (θ), or the effects of sub-freezing temperatures (T) (see Landsberg, 1986; McMurtrie et al., 1994; Runyon et al., 1994).
- uses the ratio of net (P_N) to gross primary production ($P_N/P_G = c_{pp}$), which is emerging as relatively constant for trees (Schulze et al., 1977; Benecke and Evans, 1987; Ryan, 1991; Ryan et al., 1996a; Williams et al., 1997; Heather Keith, personal communication, 1996) to estimate P_N from P_G .
- uses a simple relationship, derived from information in the literature about root growth and turnover (Santantonio, 1989; Beets and White-

head, 1996) and the effects of growing conditions on them (Runyon et al., 1994), to estimate the amount of carbon allocated below-ground.

- uses a sub-model derived from the $-3/2$ power law (see Drew and Flewelling, 1977; Landsberg, 1986) and stem growth rates to calculate changes in stem numbers per unit area with time (self-thinning).
- uses an equation based on allometric ratios—widely available for many species and situations—to determine the allocation of carbon to foliage and stems and constrain tree growth patterns.
- uses recently acquired knowledge about the physiological factors causing decline in forest

growth rates (Yoder et al., 1994; Mencuccini and Grace, 1996; Ryan et al., 1996b) with age to model that decline.

Section 2 presents an outline of the 3-PG model, which provides a framework for the description of the simplifying concepts used in it. The ideas that we believe have allowed us to make significant progress in calculating the carbon balance of, and carbon partitioning in forests, are dealt with in some detail in separate sections. Some results of sensitivity analyses to illustrate the performance and potential of 3-PG are presented, as well as the results of comparisons between simulated and measured stem growth rates.

Table 1
Abbreviations and symbols used in the text and in equations

| | |
|----------------------|---|
| ϵ | Radiation utilisation efficiency (g MJ^{-1}) based on above-ground standing biomass |
| α_c | Canopy quantum efficiency coefficient ($\text{mol C (mol photon)}^{-1}$) |
| η_i | Carbon allocation coefficients for foliage (η_f), stems (η_s) and roots (η_r) |
| ϕ_s | Short-wave incoming radiation (MJ m^{-2}) |
| ϕ_p | Photosynthetically active radiation (mol m^{-2}) ($\approx 0.5 \phi_s$) |
| $\phi_{p.a.}$ | Absorbed photosynthetically active radiation (MJ m^{-2} or mol m^{-2}) |
| $\phi_{p.a.u.}$ | Utilisable $\phi_{p.a.}$ (MJ m^{-2} or mol m^{-2}), determined by environmental constraints |
| θ | Available water in the root zone (mm, depth equivalent) |
| c_{pp} | Ratio P_N/P_G (0.45 ± 0.05) |
| c_γ, k_γ | Empirical constant and coefficient in Eq. (4) describing litterfall during early growth |
| D | Average monthly vapour pressure deficit (kPa) |
| f_θ | Dimensionless modifier derived from average monthly soil moisture ratio |
| F_a | Relative stand age (actual age/estimated maximum age) |
| f_{age} | Dimensionless modifier based on stand age and associated decrease in stem hydraulic conductivity |
| f_D | Dimensionless modifier derived from average monthly vapour pressure deficit |
| f_T | Dimensionless temperature modifier based on number of frost days |
| g_c | Canopy conductance (m s^{-1}) |
| g_{cmax} | Maximum canopy conductance (m s^{-1}) |
| P_G | Gross primary production (carbon fixed per unit time; mol m^{-2} or Mg ha^{-1}) |
| k_g | Empirical coefficient in Eq. (1), describing the relationship between stomatal and canopy conductance and D |
| k_s | Coefficient in the power-law equation describing change in maximum stem mass with stem population |
| L^* | Leaf area index |
| m | Variable in Eq. (15), reflecting the effect of fertility on carbon allocation to roots |
| n_θ, c_θ | Power and coefficient in Eq. (2), describing f_θ in terms of r_θ |
| n_{age} | Empirical power term in Eq. (3), for calculating the age modifier (f_{age}) |
| P_N | Net primary production (Mg ha^{-1}) = (P_G - autotrophic respiration). In 3-PG, P_N is assumed to be a constant fraction ($c_{pp} = 0.45$) of P_G |
| $P_{f,s}$ | Ratio of the growth rates of foliage and stem mass |
| r_θ | Moisture ratio (current soil moisture content/ θ) |
| σ_f | Specific leaf area ($\text{m}^2 \text{kg}^{-1}$), based on projected leaf areas |
| W | Total tree mass (kg) at any time |
| w_i | Mass of component parts of trees: w_f , foliage mass; w_s , stem mass; w_r , root mass |
| $w_{s,max}$ | Maximum stem mass at a given stem population |

2. Model structure

A flow diagram outlining the calculations that comprise the model is presented in Fig. 1. The model uses a monthly time step and requires as input data

- values of total short-wave (375–2500 nm) incoming radiation (ϕ_s);
- monthly mean day-time vapour pressure deficit (D);
- total monthly precipitation;
- number of days per month with frost.

Starting values of foliage, stem and root mass are also required, appropriate to the age of the stand at the start of a run, together with appropriate allometric equations and some soil water parameters. Start-

ing values can be obtained from the literature, or reasonable guessed values will suffice. L^* is determined from foliage mass and input values of specific leaf area (σ_f , $\text{m}^2 \text{kg}^{-1}$), which are widely available. ϕ_p is assumed to be $0.5 \phi_s$ and the model calculates $\phi_{p,a}$ using Beer's law. This assumes that foliage is uniformly distributed across the stand, which is not an unreasonable assumption from the time stands are approaching canopy closure (for comparisons between the performance of detailed and simple radiation interception models, integrated over time see Wang et al., 1992). It is a poor assumption for widely-spaced young trees, so radiation interception, and hence rates of dry mass production, calculated by 3-PG for young forests, may be significantly in error. Whether this is important over the life of a stand requires investigation; the matter can be relatively easily rectified by using a more complex radiation interception model, at least for early stage growth (see, for example the procedure used by Kuuluvainen, 1991).

2.1. Vapour pressure deficit modifier (f_D)

If $L^* < 3$, canopy conductance (g_c) is calculated as maximum stomatal conductance ($g_{c,max}$) (for values see Körner, 1993) corrected for the effects of D (specified by f_D) multiplied by L^* . If $L^* > 3$, canopy conductance is derived from maximum conductance values (Kelliher et al., 1993, 1995) corrected for the effects of D . The correction applied to g_c is given by

$$g_c = g_{c,max} \exp(-k_g D) \quad (1)$$

where the coefficient k_g is based on well-established relationships between stomatal conductance and vapour pressure deficit (see, e.g. Dye and Olbrich, 1993; Leuning, 1995; Granier et al., 1996). We used a value of $k_g = 2.5$ (with D in kPa). The model is sensitive to this relationship. Eq. (1) is also used to calculate the D modifier applied to $\phi_{p,a}$, i.e. $f_D = \exp(-k_g D)$, so that $f_D \rightarrow 1$ as $D \rightarrow 0$. Support for the applicability of this relationship directly to $\phi_{p,a}$ has been provided by Landsberg and Hingston (1996), who showed that monthly growth increments of plantation eucalypts were negatively correlated with monthly average D , and that the relationship between growth and $\phi_{p,a}$ was improved by correct-

Flow diagram: 3-PG

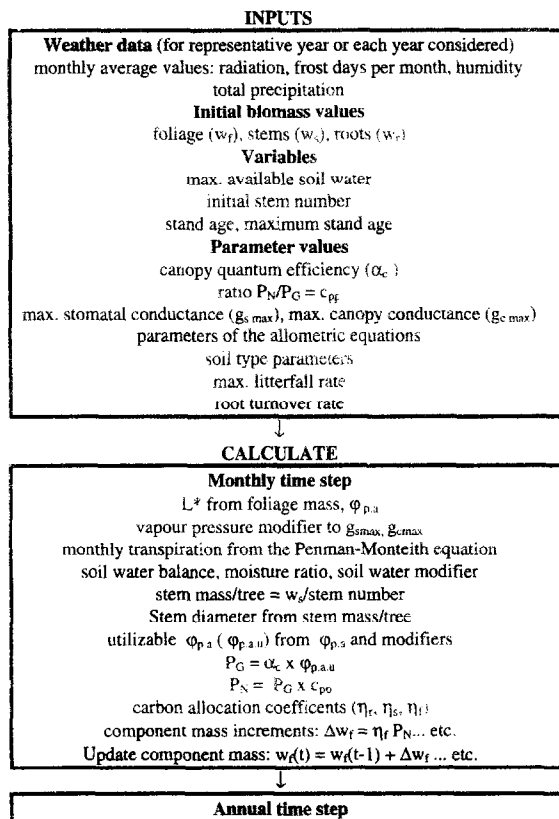


Fig. 1. Flow diagram showing the sequence of calculations in 3-PG. The model was developed using a spreadsheet and 'Visual Basic' and exists in this form. It has also been programmed using a powerful modelling package, which runs much faster and can be used in association with satellite data and GIS.

ing for the effects of D . They obtained a value of $k_g = 1.9$.

2.2. Soil water modifier (f_θ)

The soil water balance is obtained as the difference between total monthly transpiration (mm), calculated using the Penman–Monteith equation with the appropriate g_c value, and monthly precipitation. The model is initialised with soil water content = maximum available waters (θ mm) in the rooting zone. This is dependent on the water holding characteristics of the soil and the rooting depth of the trees (see Landsberg and Gower, 1997). The moisture ratio (r_θ) for the stand is calculated as

$$r_\theta = \frac{\text{Current soil water content} + \text{water balance}}{\text{Available water}}$$

The water balance in any month will be negative if transpiration exceeds precipitation, and vice versa. If the numerator of the expression for r_θ exceeds θ , it is set to θ , i.e. the excess water is assumed to have run off or drained out of the system. If it is negative, $r_\theta = 0$. Available water can be set to any value considered appropriate to the forest under consideration. Values in the range 25–250 mm occur in the literature (Waring and Major, 1964).

The soil water modifier, f_θ , is calculated from

$$f_\theta = \frac{1}{1 + \left[\frac{(1 - r_\theta)}{c_\theta} \right]^{n_\theta}} \quad (2)$$

where c_θ and the power n_θ take different values for different soil types. We suggest $c_\theta = 0.7, 0.6, 0.5$ and 0.4 for sand, sandy-loam, clay-loam and clay, respectively, and $n_\theta = 9, 7, 5$ and 3 for the same soil types. These values produce the curves shown in Fig. 2, which are essentially the same as those for relative transpiration rate vs. volumetric water content published by Denmead and Shaw (1961) and, much later, by Dunin et al. (1985) for *Eucalyptus maculata*. The curve shift from sand to clay, causing f_θ to fall earlier in clay, but not as rapidly as in the sand, reflects the differences in the hydraulic characteristics of soils with different proportions of clay. At a given soil water content the water potential of clay soils is significantly lower than in sandier soils (see Williams et al. (1983) for data illustrating this, and

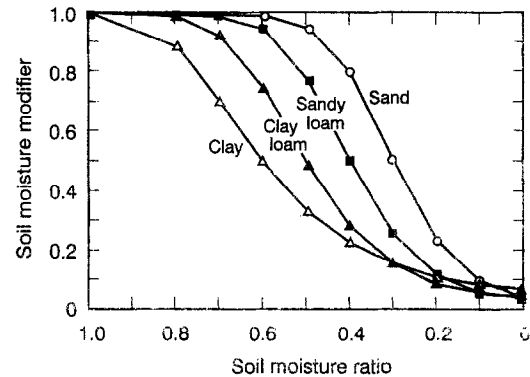


Fig. 2. Relationship between the soil water modifier (f_θ) and the moisture ratio (r_θ) for four soil types.

Landsberg and Gower (1997) for a detailed discussion). The values of c_θ and n_θ are, nevertheless, chosen without specific empirical justification. If appropriate experimental results become available these values may need to be altered.

2.3. Temperature (frost) modifier (f_T)

The present version of the model accounts for temperature only in terms of the occurrence of frost. We assume that there is no photosynthesis on any day that temperatures fall below zero (this could easily be altered, on the basis of appropriate empirical evidence, to more than 1 day). The frost modifier is, therefore

$$f_T = 1 - \left(\frac{\text{frost days per month}}{\text{number of days per month}} \right)$$

2.4. Nutrition

A number of models have used the relationship between leaf photosynthesis and nitrogen concentration to scale carbon assimilation at stand levels. However, this relationship is not well-founded for conifers (see Landsberg and Gower, 1997) and we have chosen to deal with nutrition through the mechanism of carbon allocation rather than attempt to calculate a nutritional modifier that would require information on nutrient availability, and uptake by trees, which would be extremely difficult to simulate. Detailed discussion of this is deferred until after the section on carbon allocation.

2.5. The age effect (f_{age})

As a forest ages, its above-ground net primary production decreases, a fact well documented in all forestry yield tables. Until recently, the observed decrease in P_N with age was thought to be related to an increase in maintenance respiration of woody biomass, but direct measurements of stem respiration at times when growth is not occurring suggest that less than 12% of annual P_G is required for maintenance of the small number of living cells present in woody tissue, even in subtropical climates (Ryan et al., 1995). Some have speculated that above-ground production decreases because soil nutrient supply declines as more woody material is incorporated into litter and soil organic matter and nutrients are increasingly immobilised (Gower et al., 1996; Murty et al., 1996). However, nutrient availability in old stands can be similar to or greater than in younger stands (Ryan et al., 1996b). Paired young and old-tree comparisons made on the same site (with, presumably, similar nutrient availability) showed that older trees had similar maximum rates of photosynthesis in the early morning but during the day these rates fell 25–30% more than those observed on the foliage of younger trees. The differences were attributed to differences in the relative sensitivity of stomata to atmospheric vapour pressure deficits (Yoder et al., 1994), and appear to be associated with hydraulic limitations to the flow of water through an increasingly long and torturous path as trees age (Tyree and Sperry, 1988; Ryan and Yoder, 1997). This interpretation is supported by data presented by Mencuccini and Grace (1996) who showed that, in Scots pine stands differing more than a half-century in age, changes in the total hydraulic conductance in stems and branches closely paralleled annual variation in above-ground net primary productivity as the forest aged (Fig. 3). Hydraulic conductance, calculated on a unit leaf area basis, was lower by a factor of more than four in mature trees compared to the values in stands at maximum productivity. Because of the reduction in stomatal conductance associated with reductions in hydraulic conductivity as trees age, photosynthesis is reduced, and less carbon is available to maintain the previously acquired leaf area. The canopy, as a result, must open as a forest ages.

In the 3-PG model we use an empirical expres-

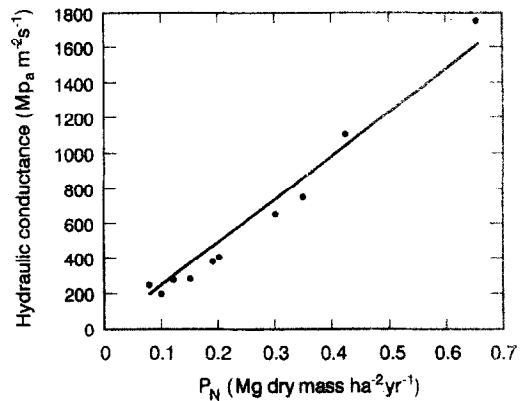


Fig. 3. The linear relationship between hydraulic conductance and P_N obtainable from the data published by Mencuccini and Grace (1996). The low values of P_N and conductance were measured in old stands and the highest values in young stands. The relationship supports the assumption that stem conductance declines with age, inducing lower stomatal conductance and hence lower photosynthesis and stand productivity.

sion, in terms of relative stand age, to account explicitly for the reduction in maximum stomatal conductance as stands age. The age modifier (f_{age}), is given by an equation that mimics the changes in (normalised) above-ground wood production shown by data collated by Ryan et al. (1996b). Relative age (denoted F_a) is the ratio of actual age (in years) to the maximum age likely to be attained by a forest or plantation

$$f_{age} = \frac{1}{1 + (F_a/0.95)^{n_{age}}} \quad (3)$$

The constant (0.95) causes $f_{age} = 0.5$ when $F_a = 0.95$; the power in the denominator controls the rate of change of the function. We have used $n_{age} = 4$. Either of these parameter values can be varied as deemed appropriate by users. The expression is not sensitive to the maximum age specified for a forest, although it will clearly cause large differences in growth rates of stands that are, say, 20 years old, if the maximum age is specified as 80 years—as may be the case for some plantations in sub-tropical areas—or 300 years, which would be a normal age for a mature forest in many parts of the world.

Regardless of growing conditions, Eq. (3) results in patterns of biomass production that decrease at rates comparable to the reported decrease in above-

ground production published in forestry yield tables appropriate for a given region.

2.6. Calculation of $\phi_{p.a.u.}$

Utilizable, absorbed photosynthetically active radiation is calculated by applying the modifiers for D (f_D), soil water (f_θ), temperature (f_T) and age (f_{age}) to $\phi_{p.a.}$. The soil water and vapour pressure deficit modifiers are not multiplicative relative to each other. 3-PG uses the lower value of f_D and f_θ , on the assumption that if stomata are closed by D , limiting transpiration rate (and CO_2 uptake) so that the rate of water movement to the roots is fast enough to maintain the transpiration rate even in relatively dry soil, then soil water content is not a limiting factor. The reverse holds: if water cannot move to roots fast enough to meet transpiration demand then g_c must be reduced to a value appropriate to the supply rate, even if that is below that determined by D , otherwise the trees would become desiccated. In this case soil water is the limiting factor, not canopy conductance.

2.7. Dry mass production (radiation conversion efficiency)

P_G is calculated by multiplying $\phi_{p.a.u.}$ by the canopy quantum efficiency coefficient α_c (see below), and P_N follows. Carbon allocation is calculated monthly (see Section 2.11) and L^* for 1 month is derived from the leaf mass at the end of the previous month.

3-PG uses a 'universal' canopy quantum efficiency coefficient α_c , with a value of $0.03 \text{ mol C (mol photon)}^{-1}$, equivalent to 1.8 g C MJ^{-1} . This is based on three studies. McMurtrie et al. (1994) analysed pine productivity at five sites ranging from Sweden through the USA to Australia and New Zealand, and found simulations of P_G at those sites produced values which fell on a straight line with a slope of 1.77 g C MJ^{-1} when plotted against $\phi_{p.a.u.}$. Waring et al. (1995), in conjunction with an independent estimate of gross primary production derived from eddy correlation data collected over the Harvard Forest, a mixed deciduous forest in north-east USA, showed the average value of maximum canopy quantum efficiency to be $0.03 \text{ mol C (mol photon)}^{-1}$. Reductions in α_c occurred seasonally in direct pro-

portion to the break-down in chlorophyll pigmentation, a change easily assessed visually from the ground or from satellites (Yoder and Waring, 1994; Prince and Goward, 1995). In another study, Williams et al. (1997) computed P_G for predominantly evergreen forests distributed across western Oregon by adding estimates of foliage, stem, and root respiration to previously published estimates of P_N and $\phi_{p.a.}$ (Runyon et al., 1994). They confirmed that the maximum canopy quantum efficiency has a value for forests near $0.03 \text{ mol C (mol photon)}^{-1}$ and does not vary widely about that value. On severely nutrient deficient soils, or where atmospheric pollutants cause chlorosis of foliage, α_c will decrease below the maximum (Johnson and Linberg, 1992). Tests of the constancy of α_c can be expected from any forest experiment involving long-term CO_2 flux measurements, or from experiments where most of the terms in the dry mass balance are accounted for and a reliable process-based model is used to calculate P_G .

The use of a linear relationship between $\phi_{p.a.}$ and dry mass production by plant canopies, stemming largely from Monteith (1977), is now widespread and there are many values of the dry mass conversion factor (ϵ , g MJ^{-1} or $\text{mol C (mol photon)}^{-1}$) in the literature (see review by Landsberg et al., 1996). It is often not entirely clear, however, whether the analyses refer to above-ground or total biomass production in relation to $\phi_{p.a.}$. When above-ground biomass is referenced there is always uncertainty about the below-ground component. Large variations in ϵ can be explained on this basis alone. Furthermore, many analyses leading to values of ϵ have not taken account of constraints on radiation utilisation by plant canopies. 3-PG allows analysis of the above and below-ground biomass fractions, so that ϵ values can be examined. We propose that the symbol ϵ be used only for above-ground P_N per unit utilisable $\phi_{p.a.}$ and the symbol α_c be used for P_G .

The relationships are conceptually simple. Standing biomass at any time is $W(t)$ —the integral of the processes of dry mass production (P_G) and respiration (R) up to that time, i.e.

$$W(t) = P_G - R \quad (4)$$

so that

$$\alpha_c = P_G / \phi_{p.a.u.} \quad (5)$$

and

$$\epsilon = (1 - p_a) P_G / \phi_{p.a.u.} \quad (6)$$

where p_a is the mass fraction (integrated over time) allocated to root growth and turnover.

2.8. Litterfall

It is important to include litterfall in the model. Any value considered appropriate can be used; we find that a constant monthly litterfall rate ($\gamma_{f,max}$) of about 0.02 (i.e. about 25% per year) gives good results. It would be simple to make litterfall a variable function of some cumulative drought index (see, e.g. experimental results of Pook, 1986; Linder et al., 1987). We have not done this but we have made litterfall a function of age for young stands—increasing asymptotically to the maximum ('standard') litterfall rate from near zero at 1 year to the maximum at 5 years (Eq. (7))

$$\gamma_f = \frac{\gamma_{f,max}}{1 + c_\gamma \exp(-k_\gamma t)} \quad (7)$$

where γ_f is the foliage (and small branch) litterfall rate (year^{-1}), c_γ is an empirical constant, k_γ is an empirical coefficient and t is time, in months. We set $c_\gamma = 15$ and $k_\gamma = 0.12$.

3-PG includes root turnover rates, although these have no effect on its general performance because we do not use root mass to modify estimates of rooting depth. It would be a simple procedure to do this if it were considered justified by the knowledge available about a particular system.

2.9. Stem populations

The model requires stem numbers because the allometric ratios used to partition carbon are invariably determined for single trees (see Section 2.11); also, forest managers are not interested in the total biomass produced by a forest—they want to know stem growth rates and final stem volumes. 3-PG exploits the (virtually universal) relationship between stem populations and maximum achievable individual stem mass ($w_{s,max}$ (Eq. (8)); see Drew and Flewelling, 1977; White, 1981; Landsberg, 1986) to calculate changes in stem populations (p)

$$w_{s,max} k_s p^{-3/2} \quad (8)$$

k_s is a coefficient for which a value is required. This can be obtained either from empirical data—the average mass of individual stems in stands near the end of their life cycle—or a value can be obtained from 3-PG by running the model through an appropriate rotation length with low stocking (100–150 trees ha^{-1}) with the mortality function 'switched off', to estimate maximum achievable stem mass for the environmental conditions and allometric ratios used in the simulation.

To run the population sub-model, initial stem mass is provided as an input, and from the end of Year 1 mean stem mass (w_s) generated by stem growth in the model is tested against $w_{s,max}$ for the current population ($p(w_{s,max})$). If $w_s > w_{s,max}$ we solve Eq. (8) for $p(w_s)$ and reduce stem numbers by $\Delta p = [p(w_s) - p(w_{s,max})]$, i.e. Δp is stem mortality. The procedure is illustrated diagrammatically in Fig. 4. By the end of the following year, mean stem mass will have increased and the procedure is repeated. It has the disadvantage that stem numbers fluctuate above the $w_{s,max}/p$ line, instead of below it (see Drew and Flewelling, 1977; Landsberg, 1986), but in view of the approximations involved in the solution for k_s , this is not important.

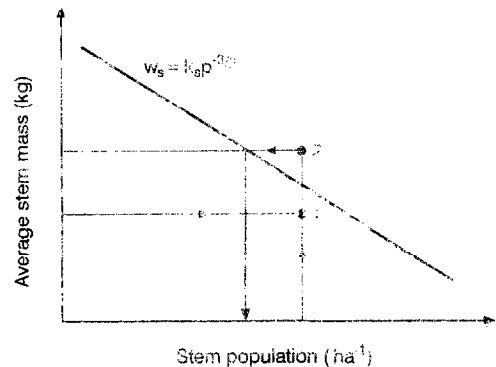


Fig. 4. Diagrammatic representation of the stem population sub-model. The line describes the relationship between average maximum individual stem mass ($w_{s,max}$) and population. If mean stem mass (w_s) is less than $w_{s,max}$ (point 1) the population remains unchanged. If $w_s > w_{s,max}$ (point 2), p is reduced by the number necessary to conform to the relationship. Values of k_s have to be provided. They can be obtained from empirical data or calculated using the model. We calculated k_s from stem mass values obtained by running the model for 120 years using initial stem populations of 150 ha^{-1} , with the normal environmental constraints.

The mass of the stems that die must be discarded from standing biomass. Stem mortality largely occurs among the smaller stems in a population so in this version of the model we divide Δp by 3 and calculate stem mass loss as $(\Delta p/3)w_s(1/3 + 1/6 + 1/9)$. We do not reduce leaf mass, on the assumption that dying stems would have few leaves, and that the stand foliage mass is distributed among the living stems.

2.10. Respiration, P_N and root turnover

Ryan's work, in recent years (Ryan, 1991; Ryan et al., 1995, 1996a), has contributed greatly to our knowledge of the respiration rates of trees and their various component parts. It has resulted in useful relationships between respiration rates and variables such as temperature and leaf nitrogen content but, because they require information such as sapwood volume, fine root mass, tissue temperatures and nitrogen content, these are of limited value in stand-level models. However, by combining these studies with increasingly reliable estimates of P_G , derived from measurements (Schulze et al., 1977; Benecke and Evans, 1987; Waring et al., 1995; Williams et al., 1997) and models such as BIOMASS (Ryan et al., 1996a) new information about the relationship between P_G and P_N is emerging, from which it appears that the ratio $P_N/P_G (= c_{pp})$ is remarkably constant, averaging about 0.45 ± 0.05 for a wide variety of forests, including deciduous hardwoods and evergreen conifers, both young and old. (This value was derived from data in the papers cited above, and from data made available to us by Michael Ryan, personal communication, and—relating to eucalypts—by Heather Keith, personal communication.)

Two important generalisations have emerged from recent analyses of carbon allocation in trees: (1) there is a strong inverse relationship between stem growth and the fraction of P_N allocated below ground (Beets and Whitehead, 1996); (2) as environmental conditions become harsher, the fraction of P_N allocated annually to fine root growth increases from about 25% to nearly 60% (Santantonio, 1989; Runyon et al., 1994; Beets and Whitehead, 1996; Heather Keith, personal communication). In 3-PG the environmental modifiers provide a measure of the

'harshness' of the environment: under zero-stress conditions f_D , f_θ and the temperature modifier (f_T) are unity, and $\phi_{p.a.u.} = \phi_{p.a.}$, so operationally we define the harshness of the environment in terms of the ratio of $\phi_{p.a.u.}$ to $\phi_{p.a.}$ —i.e. the smaller the proportion of radiation absorbed by foliage that could be utilised, the more harsh the environment (Eq. (11); Section 2.11).

2.11. Carbon allocation

Carbon products derived from photosynthesis in leaves are transported to the various parts of trees, where they are used for respiration and as structural material. The mechanisms determining the amount of carbon allocated to any part of a tree are not well understood; study of these processes remains one of the major challenges facing physiological ecologists and various models have been developed to describe them (see Ågren, 1983; Ågren and Ingestad, 1987; Thornley, 1972a,b and the review by Cannell and Dewar, 1994).

In models aimed at simulating the growth of real forests, as opposed to exploring the mechanisms that influence growth patterns, carbon allocation is sometimes estimated using allocation coefficients (η_i) derived from the (allometric) equations that describe the observed relationships between the mass or size of different parts of plants (see, e.g. McMurtrie and Landsberg, 1992). These allocation coefficients are dimensionless, but the problem of their dynamics has not, up to now, been solved.

Allometric relationships for single trees can, almost invariably, be described by equations of the form

$$W_i = a_i W^{n_i} \quad (9)$$

where W is the total mass of the plant and i denotes any component part. It is reasonable to assume that the parameter values—particularly n_i —reflect the genetic characteristics of species. There are many examples in the literature where experimentalists have obtained improved descriptions of data by fitting equations of other forms, usually with more parameters, but the fact remains that almost all data sets can be described, with high statistical r^2 values, by Eq. (9), which is a very tractable and useful form (see Pearson et al., 1984; where a summary of data

for *Pinus contorta* indicates remarkable stability across stands with different stem populations). More complex statistical descriptions seldom contribute much additional useful information. Foresters normally use stem diameter at 'breast height' (B , formally $B \approx 1.4$ m) as a measure of stem size; this can be used as a surrogate for W . The values of the parameters of Eq. (9) may be expected to vary with age (see Table 2) and site water and fertility conditions, although there are few studies available where these factors have been examined. However, the empirical values available for the power (n_i) are remarkably similar (for a summary of experimental data from many sources see Gholz et al., 1979; Pastor et al., 1984 and Landsberg, 1986 for discussion).

If the net rate of dry mass production of a tree is dW/dt , then the rates of growth in leaf (w_f), root (w_r) and stem (w_s) mass are

$$\frac{dw_f}{dt} = \frac{dW}{dt} \eta_f - \gamma_f w_f \quad (10)$$

$$\frac{dw_r}{dt} = \frac{dW}{dt} \eta_r - \gamma_r w_r \quad (11)$$

$$\frac{dw_s}{dt} = \frac{dW}{dt} \eta_s - \gamma_s w_s \quad (12)$$

where γ_f , γ_r and γ_s represent litterfall, root turnover and stem mortality rates (cf. Eq. (7) and the outline of the procedure for calculating stem mortality, following Eq. (8)).

Eqs. (10)–(12) were originally written in that form by McMurtrie and Wolf (1983). They have since been used in numerous models; see, e.g. McMurtrie (1985) and McMurtrie and Landsberg (1992) for an application to analysis of experimental data.

To obtain the allocation coefficients for 3-PG we specified the way η_r is expected to vary with growing conditions (see Section 2.10). The equation used is a simple hyperbola

$$\eta_r = \frac{0.8}{1 + 2.5(\phi_{p.a.u.}/\phi_{p.a.})} \quad (13)$$

making η_r dependent on the relative harshness of the growing conditions, defined by the ratio $\phi_{p.a.u.}/\phi_{p.a.}$. Eq. (13) reflects the accumulating evidence that trees allocate increased amounts of carbon to their roots when growing conditions deteriorate—a strategy that seems intuitively 'sensible' in terms of the need to survive adverse conditions—and imposes limits to the proportion of carbon allocated to root growth, maintenance and turnover that are consistent with many studies and observations and physiologically plausible.

It is clear from Eqs. (10)–(12) that the allocation coefficients are, essentially, given by the ratio(s) $(dw_i/dt)/(dW/dt) = dw_i/dW$ so, accepting B as a good surrogate for W , we can assume that the allocation coefficients for foliage and stems are proportional to dw_f/dB and dw_s/dB . The ratio of the stem and leaf allocation coefficients (applicable to P_N)

Table 2

The parameters of Eq. (9) ($w_i = a_i B^{n_i}$) describing the relationships between the mass of foliage (w_f , kg) and stems (w_s , kg; this includes branches and bark) and diameter at breast height (B , cm) for a number of species and—in the case of eucalypts—different age classes. The data are intended to be illustrative, not comprehensive

| Species | | a_f | n_f | a_s | n_s | Data source |
|----------------------------|----------------|-------|-------|-------|-------|----------------------------------|
| <i>E. globulus</i> | 2 years | 0.252 | 1.11 | 0.257 | 1.66 | Robin Cromer, CSIRO |
| <i>E. globulus</i> | 4 years | 0.036 | 1.98 | 0.173 | 2.02 | Robin Cromer, CSIRO |
| <i>E. globulus</i> | 6 years | 0.013 | 2.45 | 0.126 | 2.23 | Robin Cromer, CSIRO |
| <i>E. globulus</i> | 9 years | 0.010 | 2.42 | 0.091 | 2.48 | Robin Cromer, CSIRO |
| <i>E. pauciflora</i> | 55 years | 0.050 | 1.61 | 0.031 | 2.61 | Dr Heather Keith, CSIRO |
| <i>Pinus</i> spp. | Various ages | 0.009 | 2.32 | 0.040 | 2.65 | Gower et al. (1994) ^a |
| <i>Pinus contorta</i> | Various popns. | 0.018 | 2.06 | 0.153 | 2.27 | Pearson et al. (1984) |
| <i>Pinus contorta</i> | ? | 0.027 | 1.84 | 0.050 | 2.43 | Gholz et al. (1979) |
| <i>Acer saccharum</i> | About 60 years | 0.006 | 2.22 | 0.073 | 2.56 | Pastor and Bockheim (1981) |
| <i>Populus tremuloides</i> | About 60 years | 0.024 | 1.50 | 0.171 | 2.20 | Pastor and Bockheim (1981) |

^a Calculated from data presented by Gower et al., including various pine species of different ages grown in various locations

can, therefore, be obtained from Eq. (9) with numerical values of a_i and n_i appropriate to each component of the tree(s) and the species under consideration. This gives us

$$p_{f,s} = \frac{(dw_f/dB)}{(dw_s/dB)} \quad (14)$$

where $p_{f,s}$ is the ratio of the growth rates of foliage and stems, in terms of their changes in relation to B . Now, given that $\eta_f + \eta_r + \eta_s = 1$ and that we have η_r from Eq. (13), then

$$\eta_s = (1 - \eta_r) / (p_{f,s} + 1) \text{ and } \eta_f = 1 - \eta_r - \eta_s$$

Operationally, in 3-PG, average stem mass is calculated from total (stand) stem mass and stem number. Eq. (9) is inverted and solved for B to provide the value for use in Eq. (14). Foliage and stem mass are never calculated directly from Eq. (9).

This procedure has proved remarkably stable and well-behaved. If P_N is reduced by poor growing conditions, η_r is increased (Eq. (13)) and stem and foliage growth are reduced in a way that conserves the allometric balance of the trees.

2.12. Effects of nutrition

There is evidence that nutrition affects the amount of carbon allocated to roots (see review by Santantonio, 1989; Fig. 5), with a greater proportion going to the roots of trees on infertile sites than those on fertile sites. Of the carbon going to roots, most goes

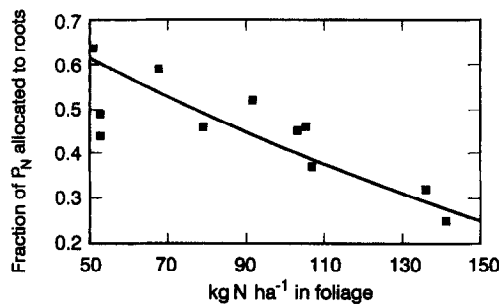


Fig. 5. Relation between total nitrogen content of *Pinus radiata* canopies and the fraction of P_N allocated to roots. The data were obtained from experiments on 7–11 year old trees reported by Beets and Madgwick (1988) and Beets and Whitehead (1996). The line was drawn by eye to indicate that these data are consistent with the relationships described by Eqs. (13) and (14).

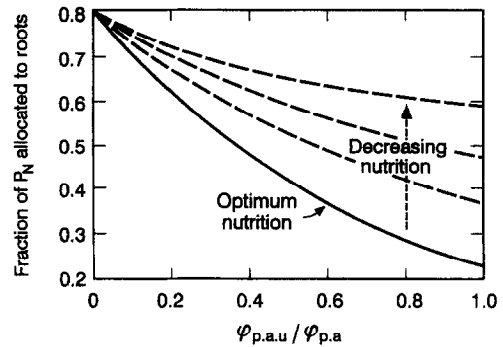


Fig. 6. Variation of the carbon allocation coefficient (see Eq. (13)) with site nutritional status, or nutrient availability, introduced as a modifying variable. The curves are described by Eq. (15).

to the fine roots, but a minimum of about 20% goes to coarse roots (Beets and Whitehead, 1996). In general, climatic constraints over-ride nutritional limitations—trees in the most fertile soil will not grow without adequate water, or in very cold conditions (see Linder et al., 1987; Specht and Specht, 1989; Snowdon and Benson, 1992) for examples of data illustrating the way water relations can over-ride nutrition—but, when water is adequate, improved nutrition usually results in increasing the proportion of P_N allocated above ground.

Quantifying the relationship is difficult—our understanding of nutrient dynamics and uptake processes is not yet good enough, at the tree/stand level, to allow formulation of definitive, deterministic relationships so we have used a simple scaling procedure, whereby the allocation of carbon below ground is minimised on fertile sites and increases as fertility decreases. The proposed relationships are presented in Fig. 6, which presents a set of curves derived from Eq. (13) with a new variable (m) introduced:

$$\eta_r = \frac{0.8}{1 + 2.5m(\phi_{p.a.u.}/\phi_{p.a.})} \quad (15)$$

m has a maximum value of 1, on a highly fertile site, reducing towards zero as site fertility decreases. The curves in Fig. 6 indicate that differences in carbon allocation caused by soil fertility are greatest under good growing conditions ($\phi_{p.a.u.}/\phi_{p.a.} \rightarrow 1$) and least when growth is restricted by vapour pressure deficits, soil water or temperature. We can only suggest, at

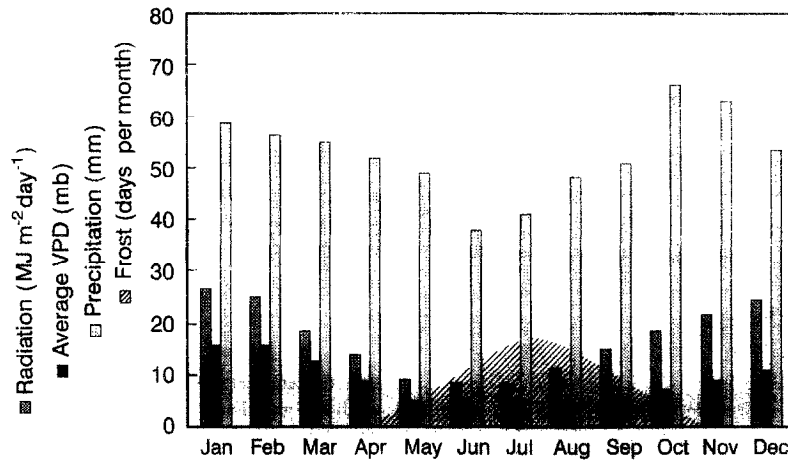


Fig. 7. Climatic data from Canberra, Australia, used in all the simulations reported in this paper. The lightly shaded columns are monthly rainfall (mm), the more intensely shaded columns are monthly incoming radiation ($\text{MJ m}^{-2} \text{day}^{-1}$) and the solid columns are average vapour pressure deficit (D), here given in millibars for presentational reasons ($10 \text{ mbar} = 1 \text{ kPa}$). The hatched area indicates frost days per month.

this stage, that values of m be allocated on the basis of measures of fertility such as litterfall nitrogen or nitrogen mineralisation rates, as well as conventional analyses of soil phosphorus content (see Landsberg and Hingston, 1996).

3. Results

We present, in this section, results of sensitivity analyses with 3-PG and some results from tests of model output against measured stand growth.

The model may be run with observed climatic data (monthly values for a number of years) or run for as many years as required using the same set of data. For illustrative purposes in the sensitivity analysis we have chosen the latter option, using climatic data from Canberra, in the Australian Capital Territory, shown in Fig. 7. This allows us to explore the behaviour of the model without confounding the comparisons by using different weather data for each year. We have not varied nutrition; the stands are assumed to be in fertile soils (i.e. $m = 1$ in Eq. (14)), but m was varied to account for soil fertility to give the results of the model tests presented in Fig. 11.

In all the simulations shown here the allometric ratios used were for generic pine (see Table 2), but with $n_f = 2.42$, unless otherwise stated. Starting

biomass values were $1, 3$ and 6 t ha^{-1} dry mass for foliage, roots and stems, respectively. The soil was a sandy-loam (see Eq. (2) and Fig. 2). All runs were carried through to 100 years.

Fig. 8 shows the leaf area index changes (L^*

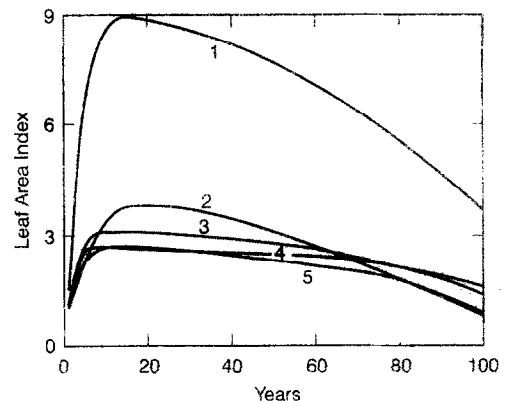


Fig. 8. Trends in leaf area index (L^*) under different environmental constraints. All simulations were performed using the Canberra climatic data, with initial stem populations (stocking density) of 1000 ha^{-1} . The environmental conditions relating to each curve are given in Table 3. Note that frost has relatively little effect because radiation during winter months is low. Increasing soil water storage has some effect, but limitations imposed by vapour pressure deficits still dominate during months with high radiation. Removing the vapour pressure deficit limitation results in more rapid exhaustion of the soil water supply.

Table 3

Stem growth data relating to Fig. 8, where trends in L^* under different environmental conditions are shown. The numbers in the left-hand column correspond to the numbers on the curves in the figure

| Run | Constraints | Max. growth rate (Mg ha ⁻¹ year ⁻¹) | Max. L^* | Final stem biomass (Mg ha ⁻¹) | Final stem number (no. ha ⁻¹) |
|-----|---------------------------------------|---|------------|--|--|
| 1 | None | 31.2 | 9 | 2217 | 226 |
| 2 | D ; θ non-limiting, frost | 10.8 | 3.8 | 773 | 199 |
| 3 | D ; θ non-limiting, no frost | 9.7 | 3.1 | 728 | 239 |
| 4 | No D ; $\theta = 150$ mm, frost | 8.1 | 2.7 | 680 | 345 |
| 5 | D , $\theta = 150$ mm, frost | 8.2 | 2.7 | 601 | 229 |

values at the end of the last month of each year) with time. The top line (Curve 1) shows the time course of L^* when growth was not constrained either by soil water or D ; the environmental conditions relating to the other curves are given in Table 3. The main point that emerges from Fig. 8 is the very strong constraint imposed on the development of leaf area by water limitations, whether caused by shortage of soil water or by high atmospheric vapour pressure deficits. The stem growth data from these runs are given in Table 3, where we see that maximum growth rates, which occur early, reflect θ values before stored soil water (set to θ at the start) is exhausted and the water balance is dominated by rainfall. However, high growth rates in the first 10–15 years do not necessarily result in high final yields. These were very high where growth was

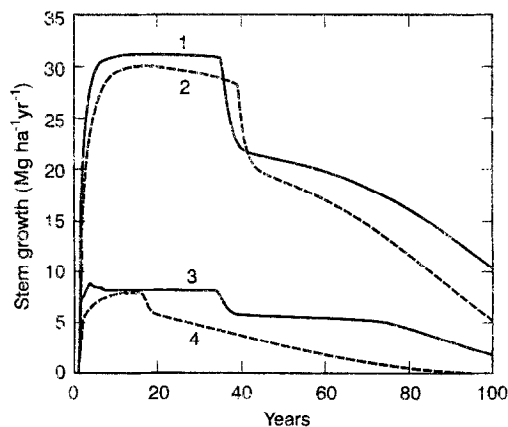


Fig. 9. Stem growth rates calculated with different values of n_f (Eq. (9)), which determines allocation of carbon to foliage growth. The values used and environmental conditions relating to each curve are given in Table 4.

always unconstrained, but not very different in the other cases.

In Fig. 9 we explore the consequences of changing the allocation of dry mass to leaves by changing the exponent for foliage (n_f in Eq. (9)) from 2.42,

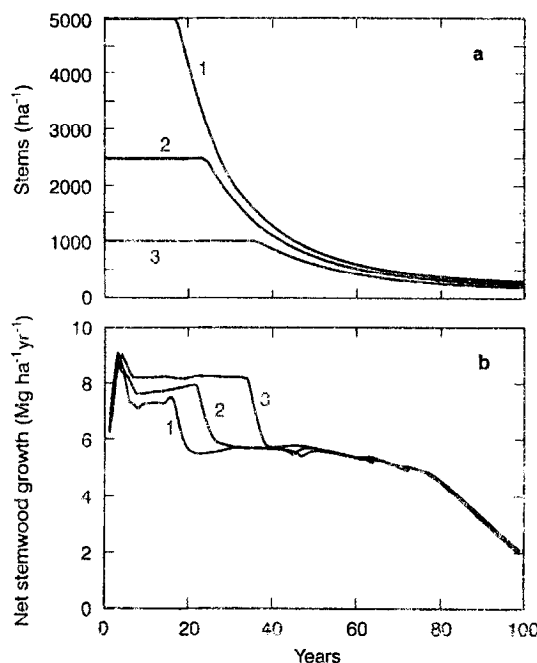


Fig. 10. (a) Changes in stem population with different initial stem numbers: 1, 5000 stems ha⁻¹; 2, 2500 stems ha⁻¹; 3, 1000 stems ha⁻¹. Note that stem populations begin to fall at different times. (b) Net stemwood growth rates at the three populations used in (a). Note that, at the two high populations (curves 1 and 2, starting values 5000 and 2500 stems ha⁻¹, respectively), stemwood growth rate begins to fall after about 5 years, falling faster in 1. The low population stand (starting value 1000 stems ha⁻¹) sustained high growth rates for much longer, and ended with higher yields.

Table 4

Stem growth data relating to Fig. 9, where the stem growth patterns resulting from the use of different allometric ratios, determined by n_f (Eq. (8)), with and without environmental constraints, are illustrated. The numbers in the left-hand column correspond to the numbers on the curves in the figure

| Run | Constraints | n_f | Max. growth rate (Mg ha ⁻¹ year ⁻¹) | Max L^* | Final stem biomass (Mg ha ⁻¹) | Final stem number (no. ha ⁻¹) |
|-----|--------------------------------|-------|---|-----------|--|--|
| 1 | None | 2.42 | 32.8 | 9 | 2217 | 226 |
| 2 | None | 2.32 | 30.0 | 4.7 | 1960 | 308 |
| 3 | D , $\theta = 150$ mm, frost | 2.42 | 8.2 | 2.7 | 601 | 229 |
| 4 | D , $\theta = 150$ mm, frost | 2.32 | 8.0 | 1.5 | 320 | 127 |

used in all other runs, to 2.32. The exponent for stems (n_s) remained at 2.65 (see Section 2.11). The upper lines show that, in the absence of environmental constraints, allocating a larger proportion of available carbon to leaves ($n_f = 2.42$) results in slightly higher growth rates and final yield (Table 4) than the lower allocation rate ($n_f = 2.32$). Stem mortality, which starts when average stem weights reach $w_{s,max}$, begins about the same time. The lower lines (3 and 4) were calculated with $\theta = 150$ mm and normal vapour pressure deficit constraints. Here we find that the greater allocation of carbon to leaves is an advantage. Maximum growth rates are similar but higher growth rates are sustained for longer by the canopy with the greater leaf area and the final yield is almost double that achieved with $n_f = 2.32$. The biomass data for these curves are given in Table 4.

Fig. 10(a) shows the reduction in stem popula-

tions over 100 years with $\theta = 150$ mm and vapour pressure deficit constraints. Fig. 10(b) presents the respective stem growth rates (net of stem losses) over 100 years with different initial stocking levels (1000, 2500 and 5000 stems ha⁻¹). The population curves follow the course determined by Eq. (8), from the time $w_s = w_{s,max}$. Stemwood growth rates were sustained at relatively high levels for about 35 years at the lowest population (1000 ha⁻¹), but fell quite early at the higher populations.

Fig. 11 shows comparisons between 3-PG output and the growth of *P. radiata* at Tumut, in New South Wales, and Haupapa, in North Island, New Zealand over 30 years. Tumut (35.25°S, 148.5°E) is at an elevation of 1100 m, with average precipitation of 1360 mm year⁻¹ and incoming solar radiation (ϕ_s) of 7540 MJ m⁻². Frost occurs on about 120 days year⁻¹. The soils at Tumut are poor and were rated 0.3 on a scale of 0–1 (i.e. in Eq. (15), $m = 0.3$), with an average (estimated) 150 mm of water available in the root zone. Haupapa (38.5°S, 176.4°E) is at an elevation of 580 m, with average precipitation of 1150 mm year⁻¹ and $\phi_s = 7615$ MJ m⁻² year⁻¹. There are less than 10 frost days per year. The soils are excellent, rated $m = 1$, with 400 mm water available in the root zone. For the simulations initial stocking was set to 1500 ha⁻¹ for both sites—the normal commercial planting density. The k_s value (Eq. (8)) which determined natural mortality, was set to 6×10^6 at both sites, although it should perhaps have been higher for Haupapa. The data with which simulated values are compared are measured growth rates in plantations at the two sites, provided by forestry officers there.

The correspondence between measured and simulated stem growth is clearly excellent, for both sites.

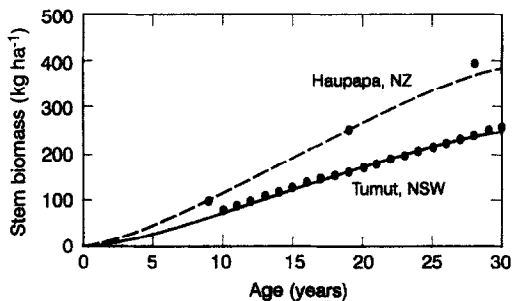


Fig. 11. Simulated (lines) vs. measured values (points) of cumulative stem biomass at Haupapa, New Zealand, and Tumut, New South Wales, over 30 years. The simulated values were calculated with 3-PG, using appropriate weather data and values for available water in the root zone and fertility modifiers in Eq. (15). Initial stem populations were taken as 1500 ha⁻¹. No fitting procedures or adjustments were used.

4. Discussion

4.1. Utilisable radiation

One of the major simplifications in 3-PG, which make it possible to keep the model relatively simple, is the use of modifiers to calculate utilisable radiation, applied to monthly averages. There may be some semantic objections to the term ‘utilisable’ radiation, applied to the fraction of $\phi_{p.a.}$ that is finally converted into dry mass by the canopy, on the grounds that there are constraints other than those we have allowed for—such as high light intensities in the top layers of canopies on bright days. However, we regard the term as a useful and legitimate description at the level of complexity with which we are concerned. The procedure is well founded in physiological research and modelling using time steps of days (see Runyon et al., 1994; Waring et al., 1995), but will need to be tested against long-term, detailed flux measurements, such as those now being gathered at a number of sites (Wofsy et al., 1993; Goulden et al., 1996; Grace et al., 1996). It can also be evaluated in relation to models that use more detailed light interception routines and physiological response algorithms. Such experimental measurements and models will provide data that allow the range of variation in α_c to be examined.

4.2. Soil water modifier

The hydrology in this version of 3-PG is extremely simple and may need to be reconsidered. The problem lies in the use of monthly water balances, which are inherently unsatisfactory. They assume (implicitly) that rainfall is evenly distributed over the month, which is obviously not the case, so that soil recharge and depletion patterns are distorted. The problem could be solved by using daily precipitation data and water balances, but this would be a move back to high data demands and increased complexity—including the need to introduce interception as a function of foliage mass, evaporation from the canopy, etc. We do not currently consider this justified, and simply accept that the soil water modifier is rather crude. The fact that the soil water modifier affects the transpiration rates—reducing them, for example, in months when the moisture

ratio is low, so that relatively small amounts of precipitation improve the water balance—provides feedback that ensures that the system generally behaves realistically.

4.3. Constant P_N/P_G

The use of a constant ratio (c_{pp}) between P_N and P_G eliminates the need for detailed calculations of respiration for the various tissues and components of trees, a procedure which, despite recent progress, would lead to large errors. The c_{pp} values available to us range from 0.37 to 0.5, but cluster round 0.45, suggesting that we can be relatively confident that the value 0.45 ± 0.05 that we have accepted can be used with confidence. The errors in doing so are almost certainly smaller than those that would result from calculating respiration. Much more work is needed in this area, but we consider that this simplification, which allows a major step forward in forest modelling, is justifiable.

4.4. Carbon allocation

In later and more complex versions of this model it may prove worthwhile (given a sound basis for doing so) to introduce accelerated leaf fall as a consequence of long periods of drought, but we have not done this.

Given that we can calculate realistic values of P_N , the carbon allocation problem is one of the major obstacles to the simulation of tree growth patterns. We have solved it by assuming that the allometric ratios obtained from measurements or destructive harvesting of trees are genetically determined and that the trees tend to conserve these ratios by conserving the ratios of the rates of change of foliage and stem mass (Eq. (14)); i.e. allometric ratios are the end result of carbon allocation up to the time they are measured. This is a robust assumption; examination of the behaviour of Eq. (14) indicates that it leads to variation with B of the type that would be expected as trees age and stem diameters increase. For any set of allometric equations where $n_f < n_s$ (Eq. (9))—which is the usual situation (see Table 2)— $p_{f.s}$ declines with B , so we do not end up with enormous foliage mass, as would be the case if partitioning was determined by the allometric equa-

tions used independently in their integral form. We note that if

$$w_f = a_f W^{n_f}$$

then

$$\frac{dw_f}{dt} = \eta_f \frac{w_f}{W} \frac{dW}{dt}$$

Similarly

$$\frac{dw_s}{dt} = \eta_s \frac{w_s}{W} \frac{dW}{dt}$$

hence

$$P_{f,s} = \frac{\eta_f w_f}{\eta_s w_s}$$

showing explicitly that $P_{f,s}$ depends on η_f/η_s and declines as w_s increases.

Although we assume that allometric ratios are genetically determined and therefore reflect species differences (see Table 2 and Fig. 4), they are undoubtedly modified by environmental conditions. We know that the rate of foliage production—and hence η_f in Eq. (9)—is lower for a given species in a harsh, as opposed to a mild environment. Similarly, stem biomass increases less with diameter in harsher environments as a result of less height growth and more taper in stems (Waring, 1983; Waring and Schlesinger, 1985). There is also evidence in both angiosperms and gymnosperms that increases in aridity are associated with a reduction in specific leaf area (Specht and Specht, 1989; Pierce et al., 1994). As the environment becomes more arid, the leaf area is reduced but the carbon required to produce a unit of leaf area more than doubles, affecting the growth rate and final tree size in predictable ways.

The procedure we have presented here is sensitive to differences in the parameters of Eq. (9), particularly because the key equation (Eq. (14)) is a ratio of derivatives. This may impose stringent requirements on experimental technique and field measurements, but it does result in clear and testable hypotheses.

4.5. The age effect

Allowing for the reduction in P_N with stand age is essential for any carbon balance model that is intended to be run over periods approaching the

maximum age of forest stands. Eq. (3) which serves this purpose in 3-PG, is entirely empirical and does not invoke any particular mechanism, but it would be an advantage, in relation to testing the equation, if the underlying mechanism(s) could be unambiguously identified. We have indicated that, in our view, one of the most important of the various factors that may be involved in the reduction in F_N as stands age is hydraulic conductivity, which feeds back to stomata and hence photosynthesis (see Yoder et al., 1994). The results of Mencuccini and Grace (1996) are consistent with this idea (see Fig. 3). The matter is currently receiving considerable attention and clarification will, no doubt, emerge in due course.

4.6. 3-PG as a practical forestry tool

The excellent correspondence between simulated and measured cumulative stem biomass at Tatum and Haupapa (Fig. 1), achieved simply by using the appropriate weather, soil moisture and fertility values in 3-PG, gives confidence that the model is ready to be used as a practical tool. We tested it against *L. radiata*, which is, we acknowledge, a simple system, because good growth measurements were available from these plantations, which is seldom the case with native forests. However, we can, equally successfully, simulate the biomass accumulation curves that give the time course of current annual increment (CAI), developed by West and Mattay (1993). In the case of eucalypts the decrease in P_N is much more rapid than in pines, and there has to be some element of fitting by adjusting the constant in Eq. (3) that controls the point at which F_N begins to fall. It will be important, if 3-PG is to be established as a practical tool, that many tests against measured stem growth rates be carried out; the problem, in most cases, will be obtaining growth measurements good enough to do this. Observations of L' would also be of great value. Model outputs can be provided in terms of changes in average B and it will be possible to apply to these data standard distributions, such as the Weibull distribution, to indicate the stem size distribution that can be expected. Thinning procedures have been written for the model, but these will be described elsewhere.

A matter of great interest, from the practical forestry point of view, is the variation in wood

density. Physiological models of necessity work in terms of mass of carbon, and a value for wood density of 500 kg m^{-3} is generally accepted as 'reasonable'. However, wood density may in fact vary by a factor of more than two between species: Kingston and Risdon (1961) provide comprehensive data for Australian trees, which show the density of *P. radiata* to be about 400 kg m^{-3} and that of some of the 'Ironbark' eucalyptus species as more than 900 kg m^{-3} . Such differences must reflect directly the volume growth that can be achieved by different species.

4.7. The use of remote sensing to parameterise the model

One of the primary aims in developing the 3-PG model was to scale up predictions of stand growth to region-wide estimates of P_N so they could be compared with independent estimates derived from satellites, which monitor seasonal and yearly variation in L^* based on the ratio of the reflectances in the infra-red and near infra-red wavebands. One of the most commonly used indices, in this respect, is the normalised difference vegetation index (NDVI; Running et al., 1989). It is also possible to estimate $\phi_{p.a.}$ directly from satellites and to derive estimates of the environmental constraints (Goward et al., 1994; Prince and Goward, 1995). Remote sensing offers the only opportunity to observe changes in phenology over large areas, and of indirectly obtaining an estimate of soil water storage capacity in those areas where water balance calculations have been made and correlated with seasonal reductions in L^* . Coops et al. (1997) have used a modified version of 3-PG with remotely sensed measurements and have obtained good correspondence between growth rates derived from the average of forest plot measurements over large areas ($8 \text{ km} \times 8 \text{ km}$) and estimates of mean annual growth made with this model.

5. Conclusions

To conclude, we consider that our knowledge of the physiological processes underlying forest growth has reached the point where we can, with reasonable confidence, make simplifications that have allowed

us to develop a model which should be of value as a research tool and has considerable potential value as a practical means of analysing forest growth and the reasons for its variations from place to place, and in time. The model also has potential as a tool for ecological analysis. The carbon partitioning procedure, based on allometric ratios, provides interesting insights into tree growth patterns and may be a useful tool in genetic studies. The stem population sub-model, based on the $-3/2$ power law, may also warrant further study in its own right.

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