Performance of the forest productivity model 3-PG applied to a wide range of forest types

J.J. Landsberg[a,*,1], R.H. Waring[b], N.C. Coops[c]

[a]Landsberg Consulting, 22 Mirning Crescent, Aranda, Canberra ACT 2614, Australia
[b]College of Forestry, Oregon State University, Corvallis, OR 97331-5752, USA
[c]CSIRO Forestry and Forest Products, Private Bag 10, Clayton, Vic. 3169, Australia

Abstract

The structure of the 3-PG model is outlined indicating the input data and parameter values required to run it and the changes introduced since the model description was originally published. Calibration procedures are described and the capacity of 3-PG to fit a wide range of forest growth data sets, from experimental and commercial plantings, is evaluated. The data came from the environmental range from sub-tropical Africa and Australia (Kwa-Zulu Natal 28°S and Queensland) to northern Europe (Flakaliden, 64°N, in Sweden). In all cases it was possible to simulate the observed data with useful accuracy. Values of the key parameters, and the way they vary are provided. To test whether the model can predict stand growth when it has not been fitted to the data we used independent sets of measurements, providing tests of model performance at three levels of severity: a test against data from the same site, where different treatments were applied; a test on data from a different location, where a similar experiment had been carried out; and a test against data from a spacing and thinning experiment. The results of the tests are assessed in terms of simple statistics (r^2 and bias). In the first and second tests, the r^2 values were all >0.9 (with one exception, where $r^2 = 0.85$), although the bias in some of the results for the first test was relatively high (>20% in above-ground and >50% in below-ground variables). The second test produced unbiased results; r^2 values in the third test were lower, but the results were also essentially unbiased. The results presented show that the 3-PG model is robust and reliable and can be used with confidence to predict growth in areas where trees have not been grown, i.e. the model can be used to estimate site productivity. The model can also be used to explore the effects of environmental conditions on tree growth and productivity. Parameters in 3-PG that allow the model to account for species differences, and the problem of determining the appropriate values for the fertility rating used in the model are discussed.
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1. Introduction

The model called 3-PG (Physiological Principles Predicting Growth), developed by Landsberg and Waring (1997),[2] is a simple process-based model requiring few parameter values and only readily available data as inputs. It is a generalised stand model (i.e.

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* Corresponding author.
E-mail addresses: joe.landsberg@landsberg.com.au
(J.J. Landsberg), richard.waring@orst.edu (R.H. Waring),
nicholas.coops@ffp.csiro.au (N.C. Coops).
[1] Visiting fellow, Department of Forestry, Australian National University.

[2] Subsequently denoted as L&W.

it is not site-specific, but needs to be parameterised for individual species) applicable to plantations or even-aged, relatively homogeneous forests. 3-PG was developed in a deliberate attempt to bridge the gap between conventional, mensuration-based growth and yield, and process-based carbon balance models. The output variables produced are of direct interest and applicability to forest managers. Software, with operating instructions and a technical description of the model is available on the internet (see Acknowledgements).

In this paper, we describe the procedures for calibrating 3-PG and present results obtained by fitting the model to a number of forest growth data sets obtained from experiments and commercially managed plantations. We also test the performance of the model by simulating the growth of plantations for which it had not been calibrated. These analyses, as well as our increasing experience with this model in a range of applications (Coops et al., 1998a,b; Landsberg et al., 2000; Coops and Waring, 2001; Waring, 2000; Tickle et al., 2001a; Sands and Landsberg, 2001; White et al., 2001) have allowed us to establish that the principles underlying 3-PG are sound and hold for a wide range of (evergreen) forest types. The model is robust and although it is desirable, wherever possible, to have accurate data against which to calibrate it, parameter values that provide reasonable predictions of the growth of particular forest types can be estimated from relatively limited data. The analyses have also allowed us to evaluate which of the parameter values are most critical, as well as the variation in parameter values derived from fitting 3-PG to different sets of measurements made on the same species subjected to different treatments.

One of the strengths of this model is that it must produce values of a number of output variables that correspond to those observed, these include the time course of stand biomass, average stem diameter (and hence stand basal area) and leaf area index (L^*), as well as reasonable values of monthly transpiration rates. (There are many measurements and estimates of water use by closed canopy forests, which provide a sound basis for determining what values are 'reasonable'.) Growth, in terms of carbon fixed by the stand, and water use, are linked through the stomata, which are explicitly dealt with in the model. The analyses presented also indicate the measurements that are most important for calibrating and testing the model.

2. Model structure and outputs

2.1. Structure

Details of the structure of 3-PG are given in L&W (see also Sands and Landsberg, 2001); here we provide a general outline indicating changes introduced since the model description was originally published. The structure of the model is simple: 3-PG consists, essentially of two sets of calculations—those that lead to biomass values, and those that allocate biomass between various components of the trees, and hence determine the growth pattern of the stand. 3-PG is a conservation of mass model. The state of the stand is updated at each monthly time step. Output is monthly or annual values of L^*, stem mass and volume, stem growth rate, mean annual (volume) increment (MAI) and stem number. Given the appropriate geometrical relationships, 3-PG can also provide estimates of stand height. The model can be run for any number of years, using actual weather data for each month or monthly averages for many years. Using averages is the normal procedure unless there is particular interest in specific events such as droughts.

3-PG uses the principles that underlie earlier models such as FOREST-BGC (Running and Coughlan, 1988) and BIOMASS (McMurtrie et al., 1990). Like these, it is based on the calculation of radiation interception, canopy photosynthesis or gross primary production (GPP[3], P_G), estimation of net primary production (NPP, P_N) and the allocation of the resultant carbohydrates to component parts of the trees. GPP is obtained by applying a canopy quantum efficiency (QE, α_c) value to the photosynthetically active radiation (PAR, ϕ_p) absorbed by a stand (APAR, $\phi_{p.a.}$). The effective value of QE (α_c) is obtained by constraining a maximum value (α_o) by atmospheric vapour pressure deficit (VPD) through its effects on stomatal conductance (g_s) and hence canopy conductance (g_c), and by

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[3] Commonly used variable names are frequently abbreviated, and these abbreviations are used in the text. They are also allocated symbols for use in any mathematical expression. Thus, PAR and ϕ_p both denote photosynthetically active radiation. In some cases (e.g. L^*) the same symbol is used in text and equations.

air temperature, frost, water balance and nutrition. Soil nutritional status is represented by an index—the fertility rating (FR)—which takes values between 0 and 1. NPP is calculated from a simple ratio of NPP to GPP (see Waring et al., 1998; Malhi et al., 1999; Law et al., 2002); the assumption of constancy in the ratio of NPP to GPP eliminates the need to calculate respiration.

The allocation equations are fully developed by L&W, but the central result is reproduced here because it is essential to some of the analyses presented in this paper. Carbohydrate allocation is on a single-tree basis. The coefficient that determines allocation to roots (η_r) is calculated first, with the proportion of NPP going to roots being influenced by moisture relations and soil nutrition. Allocation to stems and foliage relies on the ratio of the derivatives ($p_{f,s}$) of the allometric equations ($w_i = a_i B_i^n$) describing leaf (w_f) and stem (w_s) mass in terms of stem (bole) diameter at 'breast' height (B)

$$p_{f,s} = \frac{\eta_f}{\eta_s} = \left(\frac{dw_f/dB}{dw_s/dB}\right) = \frac{a_f n_f B_f^{(n-1)}}{a_s n_s B_s^{(n-1)}} \equiv a_p B_p^{\,n} \qquad (1)$$

When calibrating 3-PG it is convenient to parameterise $p_{f,s}$ in terms of its values at two stem diameters, say $B = 2$ and 20 cm, i.e. $p_{f,s}2$ and $p_{f,s}20$, the ratio of carbohydrate allocation to foliage and stems at these values of B (see Sands, 2001). The model calculates monthly values of the average mass of individual stems; the stem allometric equation is then inverted (solved for average B), so the relationship between B and w_s determines stand basal area and volume at any time. The carbon allocation procedure allows L^* to vary with growing conditions, but forces the allocation of carbon to follow patterns that lead to realistic structures; use of the $p_{f,s}$ ratios provides a convenient way to estimate the rate of change of foliage mass with stem diameter. The effects of varying $p_{f,s}$ on carbohydrate allocation are illustrated in Fig. 1, which shows relationships with B, and the time course of L^* generated by varying values of $p_{f,s}2$ and $p_{f,s}20$. Note that, since $n_p = \ln(p_{f,s}20/p_{f,s}2)/\ln(10)$ and $a_p = p_{f,s}2/2_p^{\,n} = p_{f,s}20/20_p^{\,n}$, the value of $p_{f,s}$ at any value of B (Eq. (1)) can be determined from the values of $p_{f,s}2$ and $p_{f,s}20$. Furthermore, given the coefficients (a_s and n_s) of the stem/B allometric equation, the corresponding coefficients for the foliage/B equation can be determined, since $n_p = n_f - n_s$ and $a_p = a_f n_f/a_s n_s$.

Initial tree populations are specified and changes in stem populations caused by natural mortality are calculated using the well-established $-3/2$ power law. Stem populations may also be changed by thinning.

Soil water balance is calculated monthly, using the well-established and widely used Penman-Monteith equation to calculate transpiration. Canopy conductance is estimated from g_s and L^* (see L&W). The effects of soil water balance and atmospheric VPD are not additive or multiplicative—the most limiting factor in any interval is the one that applies, i.e. if soil water is more limiting than VPD, growth is assumed to be constrained by soil water during that period.

2.2. Inputs

3-PG runs can be started at any stand age, although normal procedure is to simulate stand growth from year 2. The input data required by the model are weather data, soil water holding capacity in the root zone (θ, mm depth equivalent), initial stem number (n_{st}), initial total stem, foliage and root mass (w_s, w_f and w_r, t ha^{-1}), appropriate to the stand at the starting age, and a value for the FR (see below). Parameter values needed are the constants (a_s) and coefficients (n_s) of the allometric equations for stem mass (including bark) in terms of diameter. Values for the foliage allometric equation are useful as guides but values obtained from destructive measurements are seldom useful in fitting 3-PG to evergreen species that hold more than one year's foliage because estimates of leaf mass on stems of a given size at any time do not include foliage previously produced and subsequently lost, whereas the model calculates the total leaf mass that would be produced at a given stem size. To get appropriate parameter values for the foliage/B equation from measurements, cumulative litterfall/stem has to be included in the foliage mass. Values are also needed for specific leaf area (SLA, σ_f), for the cardinal temperatures (see below), litterfall rate, maximum stomatal conductance and, the most important, for canopy quantum efficiency. The model allows for changes in the time course of SLA and (branches + bark) as the proportion of above-ground biomass (see Sands and Landsberg, 2001).

The weather data required by 3-PG are monthly average values of solar radiation, atmospheric VPD,
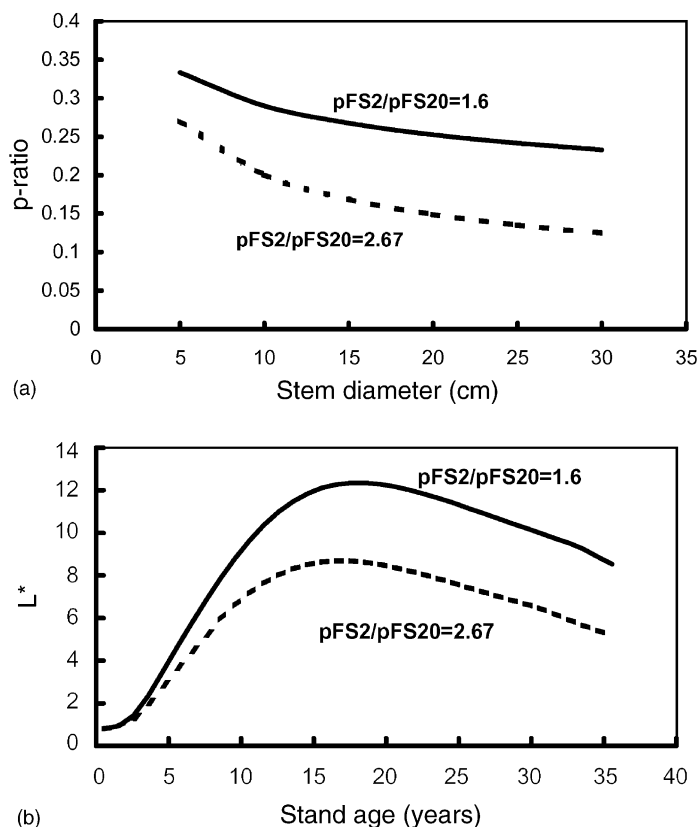
Fig. 1. (a) Variation with stem diameter of the parameter $p_{f,s}$ (Eq. (1)) which directly affects carbon allocation. The values are those used to generate the time course of leaf area index (L^*) in (b). (b) Time course of L^* for Sitka spruce (*Picea sitchensis*) using input data from Perthshire, Scotland and the parameter values obtained by analysis of this species across 12 sites in England (see Tables 2 and 3).

rainfall, frost days per month and average temperature. All these are routinely available, except—in some cases—solar radiation, which can be calculated from temperature data (Bristow and Campbell, 1984; Thornton et al., 1997; Coops et al., 1998a, 2000).

Nutrition is obviously an important variable but unfortunately, despite many years of research effort all over the world, our ability to describe soil nutrient status in terms usable in quantitative models of plant growth is extremely limited. The question of the appropriate FR is difficult for several reasons: first, because there are few plantation and forested areas for which good quality information about soil physical and chemical properties is available, and second, because there is unlikely to be a simple relationship between some 'state' measure of soil fertility and tree growth. Nutrient availability depends on biogeochemical cycling (see Waring and Schlesinger, 1985;

Landsberg and Gower, 1997; Waring and Running, 1998), particularly in relation to nitrogen, so although chemical analyses may provide a guide to FR, a degree of expert knowledge will often be useful. The use of FR therefore remains a somewhat problematical and unsatisfactory—albeit pragmatic—approach. It can also be used as a tunable parameter in the model.

2.3. Canopy quantum efficiency and fertility

The range of values allowed for α_o is constrained by experimental measurements and observations. L&W originally used a default value of 0.03 mol C (mol quanta)$^{-1}$ (equivalent to 1.65 g C MJ^{-1} (APAR), assuming 0.5 g C (g dry biomass)$^{-1}$). Law et al. (1999) used 0.04 for *Pinus ponderosa* and Bond et al. (1999) reported values of 0.05 for *Pseudotsuga menziesii* and other highly productive conifers native

to the Pacific northwest region of the USA. An analysis by Landsberg and Hingston (1996) indicated that eucalyptus plantations in Western Australia were producing above-ground biomass at rates that indicated radiation conversion efficiency of up to 0.05 mol C (mol quanta)$^{-1}$ or 2.73 g C MJ^{-1} (APAR)—approaching the value that seems to be about the norm for intensively managed field crops (see Landsberg et al., 1997). Correcting for (estimated) below-ground production, converting the biomass to carbon and allowing for litterfall indicated that values of α_c up to 0.07 mol C (mol quanta)$^{-1}$ would be realistic. This is consistent with the highest values given by Leverenz and Öquist (1987) for a number of C_3 plants and is taken as the upper allowable limit for calibrating 3-PG.

Based on published information, reviewed by Landsberg and Gower (1997, p. 137), Linder and Murray (1998) and Ågren and Ingestad (1987), we have made QE a linear function of FR (but see Bauer et al. (2001, 2002), who indicated that the relationships maybe non-linear). This is a change from the original L&W formulation of the model. The equation used (Sands and Landsberg, 2001) is

$$\alpha_c = \alpha_0(f_{N_0} + (1 - f_{N_0})FR) \qquad (2)$$

where α_0 is the maximum value of QE, at FR = 1 and $\alpha_0 f_{N_0}$ gives the minimum value of QE, at very low fertility. Based on the values given above and extensive experience with the model, we assume $\alpha_0 = 0.05$ mol C (mol quanta)$^{-1}$ for conifers and 0.07 mol C (mol quanta)$^{-1}$ for eucalyptus species. A default value of 0.5 for f_{N_0} has proved suitable when calibrating the model against growth data from a range of soil types (range of FR values).

A temperature response function has proved to be an essential part of the model. It is described in detail by Sands and Landsberg (2001). Here, we illustrate the need for it, and the results it gives, by a seasonal comparison of modelled and measured GPP for *P. ponderosa* growing in its home range. During the first 6 months of the year, when water is not limiting, growth is limited by suboptimal temperatures. When fT was not included in the model, modelled GPP values were generally more than twice those measured. Applying the temperature correction, with $T_{min} = -2$ °C, $T_{opt} = 20$ °C and $T_{max} = 40$ °C, resulted in reasonable correspondence between measured
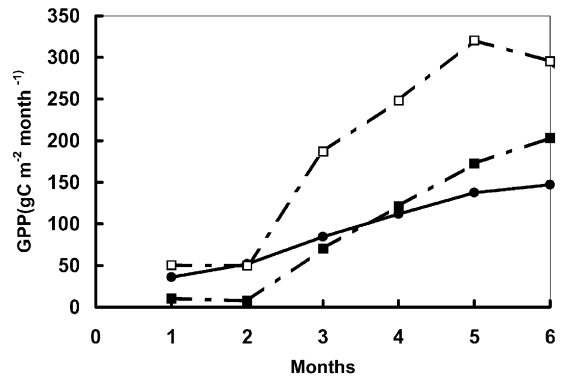

Fig. 2. GPP by ponderosa pine forests in Oregon (Latitude 44°N) during the first 6 months of the year when water is not limiting. The upper dot-dash line (open squares) shows simulated growth when no temperature correction was applied. The lower dot-dash line (solid squares) is simulated growth with temperature correction applied (see text). The solid line is measured GPP (Law et al., 1999).

and modelled values of GPP (Fig. 2). Suboptimal temperatures reduce the quantum efficiency of boreal species such as *Pinus sylvestris* to near zero in some months (Overdieck et al., 1998). As a result, all growth ceases during such months, a point well made by considering the simulations of *Picea abies* in northern Sweden and *P. sylvestris* in Finland, where temperatures completely determine the growing season. This
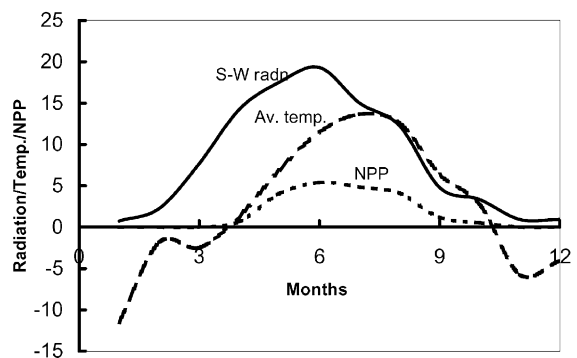

Fig. 3. Time course of short-wave radiation (MJ month^{-1}), average monthly temperature (°C) and above-ground growth rate (Mg ha^{-1} month^{-1}) of Norway spruce (*P. abies*) at Flakaliden in northern Sweden. The growth curve was calculated using 3-PG with FR = 1 and temperature limits of −2, 15 and 22 °C (weather data provided by Professor Sune Linder simulated growth rates correspond well to those observed at Flakaliden, see also Fig. 5).

is illustrated by Fig. 2, which shows short-wave radiation, average monthly temperature and the simulated time course of NPP for a fertilised stand of *P. abies*. Simulated NPP data for *P. abies* in Sweden are presented in Fig. 3 (see also Figs. 5 and 6).

3. Calibration procedures and results

3-PG is calibrated by fitting to individual sets of observational data: in general biomass production is determined by QE, the FR, weather conditions and soil moisture holding capacity at the site. With SLA and litterfall as inputs, average monthly weather data relevant to the site and the best available estimates of soil water holding capacity and fertility, an iterative procedure is used to optimise parameter values and match model output to field observations. Time series observations are preferable for calibration, but the model can be calibrated to reproduce a single set of measurements made at some specified age.

The calibration procedure involves running the model and comparing output with observed values. Parameter values are then adjusted to improve the fit and the model re-run. Successive adjustments lead, in most cases, to good fits between observed and simulated variable values. The more observed/measured data available, the more precise will be the calibration. For example, if the time course of L^* is available or, failing that, a reliable estimate of the maximum L^* and the age at which it was produced, then clearly the maximum value of L^* produced by 3-PG must correspond closely to this value. Similarly, the values of B, stem mass and stand volume produced by the model, and the time course of change in the values of these variables, must correspond to observation. In the rare cases that root mass values are also available these provide an additional constraint (see Table 4). Calibration of the soil water balance against measurements of soil water content provides the opportunity to adjust the parameter controlling the rate of change of stomatal conductance with VPD (see Ewers et al., 2000).

A number of parameter values can be varied to alter the output of the model, e.g. litterfall rates and the relationship between carbohydrate allocation to roots and growing conditions, but normal procedure is to use standard default or the best available empirical values for as many parameters as possible; if too much flexibility is allowed it becomes very difficult to identify the factors that are determining growth and yield differences, little is learned and we have little guidance about parameter values to use in the model when predictive calculations are to be made. Since the values of the constant (a_s) and power (n_s) of the stem allometric equation provide the estimates of stem diameter when the equation is solved for B from mean stem mass they should, if possible, be based on experimental data. Because of the non-linearity of the equations small variations in the parameter values can cause significant differences in the values of B, basal area and stand volume. Having established the values of a_s and n_s they are not altered; the usual procedure is to adjust the values of $p_{f,s}2$ and $p_{f,s}20$ until the time course of L^* corresponds to that observed (or expected) in the field. Because of the uncertainty in estimates of FR based on information about soils it may be treated as an adjustable parameter within limits of, say ± 0.1 or 0.2 units to match observed and simulated biomass production. (Adjustments to FR alter above-ground biomass production by altering α_c (see Eq. (2) and carbohydrate allocation to roots.)

Examples of calibration curves for 3-PG, in the form of observed and simulated variable values after adjustment of parameter values are shown in Fig. 4 (see also Figs. 5 and 6). The data in Fig. 4a are from one of the spacing treatments in an experiment with *E. grandis* in Kwambonambi (Kwa-Zulu Natal, South Africa; see Tables 1 and 2); those in Fig. 4b from the fertilised treatment in the fertiliser × irrigation experiment at Gympie (southern Queensland, Australia; see Tables 1 and 2). We note that the fit to L^* for the Kwambonambi data is not good after about 6–7 years. It seems likely that, in this case, the modelled results are more accurate than the experimental data: the 'observed' L^* values were calculated from an empirical relationship between stem size and leaf mass, established from a few harvested trees. This was scaled up by stem number and size to give leaf mass, and hence L^* (assuming SLA was 3.5 m^2 kg^{-1}), leading to the high L^* values after about 7 years of age. Separate studies by Dye et al. (1997a,b) using a LICOR[4] leaf area meter showed maximum L^* in an

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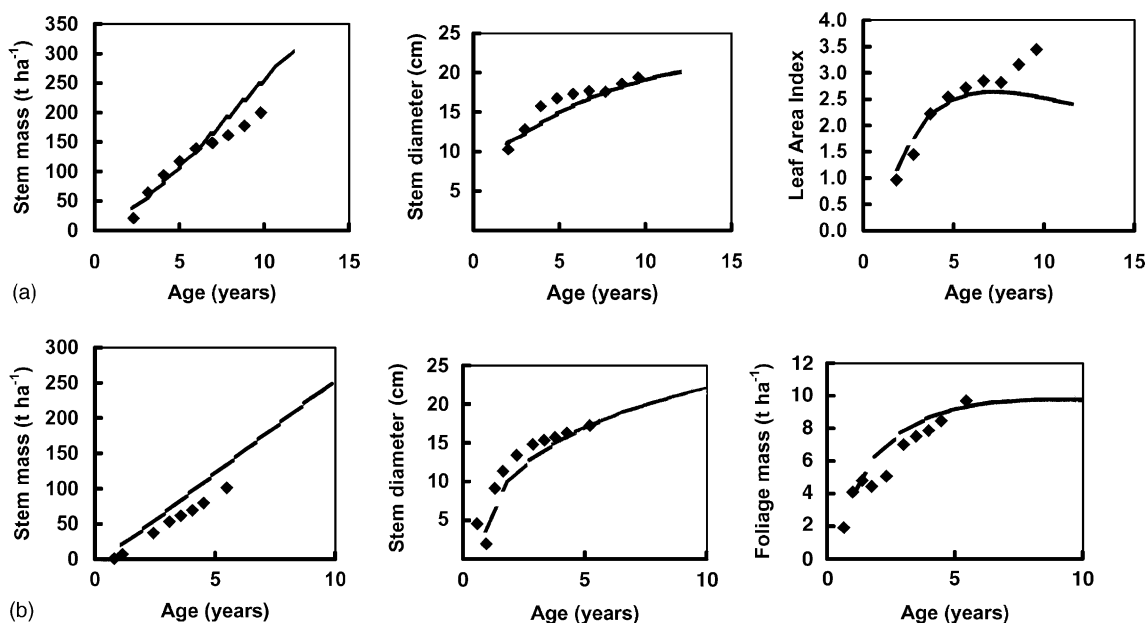[4] The product name is provided for information; mention of it does not imply endorsement.

Fig. 4. Calibration of 3-PG against data from *E. grandis* experiments in Kwa-Zulu Natal, South Africa (a, data set 8) and an intensive fertiliser + irrigation experiment in Gympie, Queensland (b, data set 13). The points are measured values and the lines are the best-fit obtained (simultaneously for all variables) by adjusting parameter values in the model (evaluation of best-fit did not involve statistical analysis).

unthinned stand of *E. grandis* in an optimal growing area, with rainfall of >1400 mm, did not exceed 3, while in another clonal experiment at Kwambonambi (concerned with water use efficiency) L^* did not exceed 1.5 (Dye et al., 1997b). The asymptotic foliage mass values in Fig. 4b about 9 t ha^{-1} are equivalent to $L^* \approx 3$.

3.1. Results for a range of species

To evaluate the generality of the 3-PG model, and the way parameter values vary, we analysed data from sites across the environmental range from sub-tropical Africa and Australia (Kwa-Zulu Natal 28°S and Queensland) to northern Europe (Flakaliden, 64°N, in Sweden) see Tables 1 and 2. They could be divided into two sets: data from experiments and data derived from measurements made in commercial plantations. The experiments included spacing experiments in South Africa and experiments designed to determine the effects of fertilisation, and in some cases irrigation, on tree growth. Some of these included treatments where a deliberate attempt was made to eliminate constraints to growth caused by water and nutrients;

this was the case in the (fertiliser + irrigation) treatments applied to *E. grandis* at Gympie, in Queensland and to *P. abies* in Sweden, also the high fertility treatment applied to *P. radiata* in the Australian capital territory.

All the data sets from experiments were time series of varying lengths, except some of the *E. globulus* data from Tasmania, which consisted of stand volumes at the end of the rotation. The only time series data sets for the commercial plantations were the *P. radiata* sets and the *Pinus patula* data from Swaziland. In most cases, the plantation data were much less detailed than the experimental data, often consisting of a single set of measurements (of sometimes doubtful accuracy) made to estimate standing crop volume on the basis of conventional yield tables. The standard of management of commercial plantations was also, inevitably, far lower than the standard of management of experimental plantings.

We used, for each site and data set, weather data appropriate to the site. The average temperatures (°C) for the three summer and three winter months, total annual precipitation (mm) and total annual short-wave (global) radiant energy income (MJ yr^{-1}), are given in
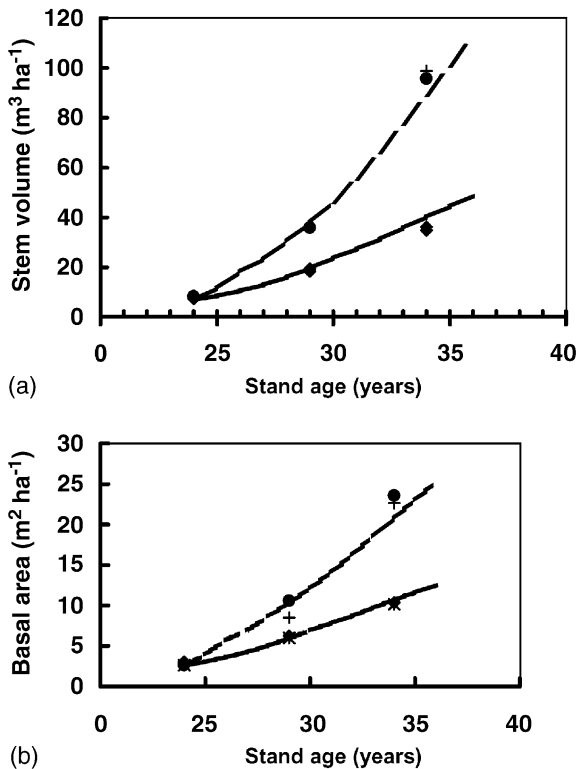
Fig. 5. (a) Calibration of 3-PG against data from a stand of Norway spruce (*P. abies*) at Flakaliden in northern Sweden. Measured (points) and simulated (dotted and solid lines) time course of stand volume (m^3 ha^{-1}) in the upper points (indistinguishable from one another) and line are for intensively fertilised, and fertilised + irrigated treatments; the lower points and line are for control and irrigated treatments (experimental data from Bergh et al., 1998). (b) Measured and simulated time of basal area in the Flakaliden stand (experimental data from Bergh et al., 1999). The parameter values obtained from the calibrations leading to Fig. 5 were used to simulate results from a similar experiment at Asa in southern Sweden (see text).

Tables 1 and 2 to show the climatic conditions experienced.

To determine parameter values for the data sets available the ASW (θ) and FR estimates were based on soil physical characteristics, chemical analyses when these were available, and the advice of the forestry officers who provided us with the growth data. Soil water holding capacity depends not only on soil type but also on the depth to which the soil is exploited by tree root systems, so there is always significant uncertainty in relation to this variable. θ values range from
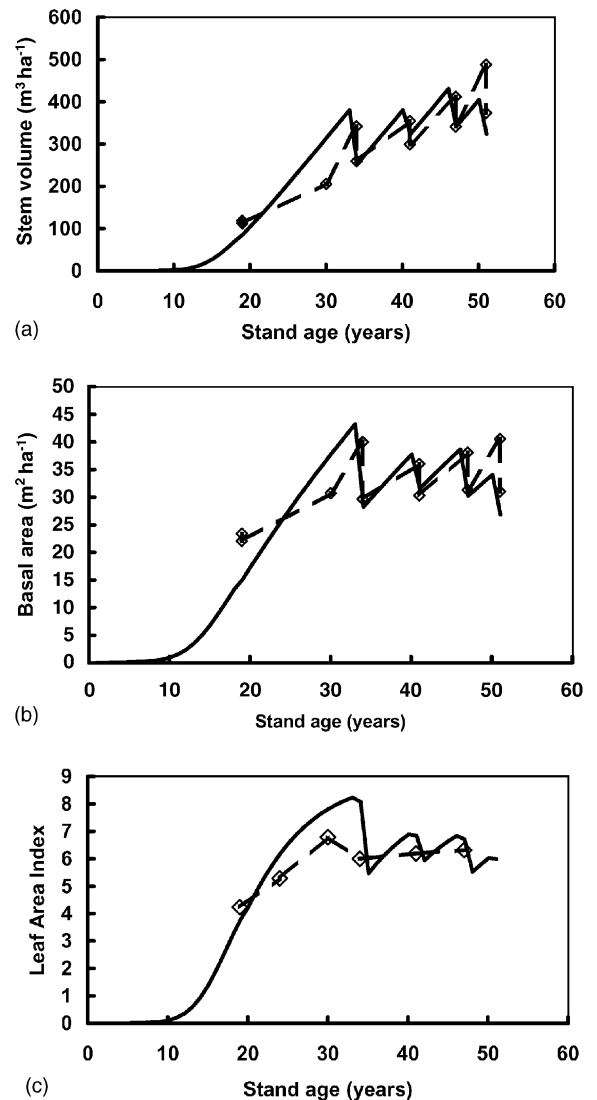

Fig. 6. (a) Calibration of 3-PG against data from a spacing × thinning experiment at Asa in southern Sweden, for the 2 m × 2 m spacing. Observed (open symbols, dashed line) and simulated (solid line) time course of stand volume. Note that the simulations were started at establishment—the model was not initialised using the first set of observational data. (b) Basal area as for (a). (c) Leaf area index (L^*) as for (a). The parameter values obtained were used to simulate the time course of stand volume, and its response to thinning in 1 m × 1 m, 1.5 m × 1.5 m and 2.5 m × 2.5 m spacings. The statistics of the comparisons are presented in Table 5.

40 to 600 mm where necessary, in fitting the model to the data, we adjusted the FR up or down from the value assumed on the basis of information available about the soil and its fertility.

Table 1

Climate data for the sites of plantation experiments analysed using the 3-PG model

Species	Location	Tav (summer) (°C)	Tav (winter) (°C)	Precipitation (mm year^{-1})	S–W radiation (MJ m^{-2} yr^{-1})
E. grandis	Kia Ora, Kwa-Zulu Natal, South Africa	21.7	14.2	844	8180
E. grandis	Kwambonambi, Kwa-Zulu Natal, South Africa	24.5	12.7	1020	6480
E. grandis	Gympie, Qld, Australia	24.4	13.2	1312	6862
E. globulus	Darkan, WA	30.5	17.2	970	6503
E. globulus	Mummbalup, WA	29.4	17	1270	6300
E. globulus	Manjimup, WA	27.7	16.6	1120	6122
E. globulus	Northcliffe, WA	26.1	17.6	1800	5937
E. globulus	ESP1, Tasmania	20.2	12.3	1052	4810
E. globulus	ESP2, Tasmania	20.2	10.8	1294	4695
E. globulus	ESP3, Tasmania	17.7	9.1	1846	4582
E. globulus	Forcett, Tasmania	20.3	12.9	1920	4995
P. radiata	ACT, Australia	22.9	9.6	784	5894
P. abies	Flakaliden, N. Sweden	16.8	−6	650	2900
P. abies	Asa, S. Sweden	21.8	−4	1327	3066
P. taeda	NC, USA	22.1	8.2	1152	5770

SLA values were obtained from various sources in the literature (see, e.g. references cited by Landsberg and Gower (1997), p. 55), or we used default values of 3.5 for eucalypts and six for conifers. Litterfall values were based on the best information available. Litterfall in 3-PG is assumed to be at a constant rate through the year, being expressed as a fraction of the total leaf mass falling in each month; e.g. if average leaf life for a species is about 3 years, this represents a loss of about 30% per year, equivalent to $0.33/12 = 0.0275$ per month. Stem numbers were available for all the experiments. If initial stem numbers were not known for the commercial plantations we used numbers that

corresponded to standard practice and adjusted the constant in the mortality ($-3/2$ power law) equation so that stand densities at the time measurements were made corresponded to those observed, or to the estimates provided by forestry officers.

Data describing the stands, for which background data are presented in Tables 1 and 2, are given in Table 3, together with the $p_{f,s}2/p_{f,s}20$ ratios used to obtain optimum results from fitting 3-PG. In all the cases, it was possible to simulate the observed data with useful accuracy, typified by Fig. 4 (see also Figs. 5 and 6).

The data available for the plantation species in NSW were limited; for each species we had a single

Table 2

Climate data for the sites of commercial plantations analysed using the 3-PG model

Species	Location	Tav (summer) (°C)	Tav (winter) (°C)	Precipitation (mm year^{-1})	S–W radiation (MJ m^{-2} yr^{-1})
E. pilularis	NSW, Australia	23.9	9.7	1200	6580
E. grandis	NSW, Australia	21.2	11.2	1160	6280
C. maculata	NSW, Australia	22.4	12.1	1170	6400
P. elliottii	NSW, Australia	22.3	14	1125	6490
Araucaria cunninghamii	NSW, Australia	22.5	11.2	1160	6500
P. radiata					
Mod. fertility sand	Sale, Vic., Australia	23.5	7.2	766	5600
Mod. fertility sand	Sale, Vic., Australia	23.5	7.2	1100	5600
High fertility loam	Sale, Vic., Australia	23.5	7.2	1134	5600
P. patula	Usutu, Swaziland	19.7	12.6	880	7832
Picea sitchensis	UK, 12 sites	12–14	0–1	790–1964	2200–4100
Pseudostuga menziesii	OR, USA, 3 sites	15–17	3.0–7.0	1042–2743	3800–4500

Table 3
Stand characteristics and ratio of carbohydrate partitioning ($p_{f,s}2/p_{f,s}20$) for a range of species growing in different locations. Ratios were obtained by fitting 3-PG to individual data sets. Standard errors indicate variation. Where they are not given a single ratio provided a good fit to all data sets or, as in the case of the last three values, there was only one data set

Species/site	Treatments	Rotation age (years)	Final stem numbers/ha	Final stem mass range (t ha^{-1})	Maximum leaf area index range	Ratio $p_{f,s}2/p_{f,s}20$
Experiments						
E. grandis, K–O, Natal	Five spacings	12	803–2089	143–163	1.3–2.6	3.84+/−0.35
E. grandis, Kw, Natal	Five spacings	12	797–2096	280–329	2.1–3	13.53+/−1.66
E. grandis, Gympie, Australia	Fertilisation, irrigation	10	1111	85–222	1.9–5.7	1.46+/−0.12
E. globulus, WA and Tas, Australia	Ecophys. observed (8)	15	430–2500	124–363	3.3–6	2.93+/−0/09
P. radiata, ACT, Australia	Fertilisation, irrigation (2)	15	700–750	69–99	5.1–6.7	4.17+/−0.20
P. abies, Asa, Sweden	Four spacings (thinning)	51	613–1094	175–219	7.1–8.4	2.00
P. abies, Asa, Sweden	Fertilisation, irrigation (2)	20	2400	42–91	5.2–8.8	2.00
P. abies, Flaka., Sweden	Fertilisation, irrigation (2)	16	2246	22–53	2.9–6.8	2.00
P. taeda, NC, USA	Fertility (2)	12	1666	20–40	2–4.3	1.51
Commercial plantations						
Plantation spp.[a]	NSW, Australia	20–40	800–1200	111–300	2–5.3	3.50
Picea sitchensis	UK, 12 sites	20	2500	100–400	4–14	2.75
P. radiata	Vic., Australia (3)	20–40	860–900	159–574	3.5–4.8	2.35+/−0.24
P. patula	Usutu, Swaziland	15	660	187	4.40	2.34
E. delagatensis	Natural forest, NSW	85	544	343	1.70	0.74
P. menziesii	Natural forest, OR, USA	100	226–870	400–700	5.7–10.6	1.17

[a] *E. pilularis*, *E. grandis*, *Corymbia maculata*, *P. elliottii*, *Araucaria cunninghamii*.

series of measurements made in forest plots in the same area. These consisted of average stem diameters and stem numbers at a specified stand age from which standing volumes had been estimated using standard relationships. Assuming wood density values, we obtained values of the coefficients of the stem allometric equations from these data. 3-PG was then fitted to the data for each species, with L^* constrained to reach maximum values of about 2.5 at 5–8 years (see Anderson, 1981). However, there was considerable variation within regions and differences between regions and species were not statistically significant. We finally used sensitivity analyses to determine the optimum parameter values presented in Table 3.

More detailed consideration of some of the simulations follows.

4. Tests against independent data

A process-based model such as 3-PG can be tested at the level of its submodels or submodel parameters, or at the level of their outputs in relation to empirical data relating to the whole system. Work to test the submodels in 3-PG is being carried out at a number of locations (e.g. Bernier et al., 1999, 2001; Law et al., 1999; Dye, 2001; A. Almeida; personal communication) and we have considerable confidence that appropriate values of most parameters are available. Fitting the model to a range of species in various locations (Table 3) has demonstrated that it can provide good descriptions of virtually any good quality forest growth data set. To test whether the model can predict stand growth when it has not been fitted to the data we require an independent set of measurements made on an identical—or very similar—stand, preferably at a different location, although that necessarily introduces some uncontrollable or unrecognised variation. The large spatial variability in forests can led to considerable variation in their physical characteristics and growth rates, even in stands regarded, for practical purposes, as homogeneous (Mäkelä et al., 2000). The testing of models on subsets of the same data set, obtained by splitting the set, does not provide a rigorous test. The data sets represented in Table 3 include three that allow tests of various severity of the predictive accuracy of 3-PG.

4.1. Test on data from the same site

3-PG was used to analyse growth data from a detailed study of the responses of loblolly pine to fertilisation and irrigation. Details can be found in Landsberg et al. (2000). We calibrated the model against the control treatment (no irrigation, no fertilisation) of that experiment, using the facility in the model that specifies the age at which canopies are assumed closed (taken as 12 years), and simulated the responses to fertilisation by increasing FR, using the parameter values established by calibration. The results are presented in Table 4 as observed and simulated values of L^*, stem mass, stem diameter and root mass. The statistics of the comparisons are given in the table. We note that the r^2 values, which indicate the proportion of the variance in the observed values accounted for by the simulated values are, with the exception of those for L^* in the fertilised treatment, all >0.9, with little loss of predictive power resulting from the fact that the model was not calibrated for the fertilised treatment. However, the mean biases (expressed as percentages: ((simulated − observed)/ observed) × 100) are relatively high, indicating that

deviations are not normally distributed, so the slope of the regression of simulated on observed values deviates from unity, or the line is displaced, i.e. the intercept deviates from unity. The reasons for these biases could be established by detailed investigations of the data and model behaviour.

4.2. Test on data from different sites

Bergh et al. (1999) provide detailed growth data from two intensive experiments carried out on Norway spruce (*P. abies*) in northern and southern Sweden. Professor S. Linder provided weather data for the two sites. The experiment in the north, at Flakaliden, which has a harsh boreal climate, consisted of untreated control plots, and treatments with irrigation (I), annual fertilisation (F) with solid fertilisers and the daily provision of tree nutrient requirements through the irrigation water (IL). Trees were 28 years at the start of the experiment. We calibrated 3-PG against 9 years' data from the control treatment of this experiment, again using the facility in the model that specifies the age at which canopies are assumed closed. For Flakaliden this was taken as 10 years from establishment.

Table 4

Comparison of observed and simulated values of stand variables from the SETRES experiment. (See Landsberg et al., 2000. Data from Tim Albaugh and Kurt Johnsen, USDA Forest Service, NC). Average bias = (observed − simulated)/observed values

	Growth year						r^2	Bias (%)
	7	8	9	10	11	12		
Control								
LAI (observed)	0.6	0.9	1.2	1.5	1.7	1.9		
LAI (simulated)	0.4	0.5	0.8	1.2	1.6	1.9	0.95	22.8
Stem mass (observed)	2.6	4.6	7	10.36	14	17.4		
Stem mass (simulated)	2.8	4.3	6.9	10.4	14.9	20.2	0.99	−3.8
B (observed)	46.1	64	78.8	93.2	110	114.2		
B (simulated)	37.3	45.9	57.1	71.5	87.6	104.5	0.95	21.2
Root mass (observed)	1.2	3.1	4.5	5.7	6.6	7.8		
Root mass (simulated)	2.2	3.5	5.5	8.1	11.3	14.7	0.92	−53.4
Fertilised								
LAI (observed)	0.6	1.8	2.4	3.1	3.2	3.5		
LAI (simulated)	0.6	0.8	1.6	2.4	3.1	3.4	0.86	19.6
Stem mass (observed)	2.6	6.5	10.9	17.2	24.9	31.6		
Stem mass (simulated)	4.1	6.7	12.3	20.5	29.5	38.3	0.997	−22.1
B (observed)	44.5	71	96.3	117.9	137	149.9		
B (simulated)	43.36	55.45	70.49	95.16	122.05	146.17	0.94	14.0
Root mass (observed)	1.5	4.5	7.1	10.2	13	15.5		
Root mass (simulated)	3.4	5.5	8.7	13.1	17.7	21.4	0.99	−45.7

Responses to fertilisation were dramatic but there were no differences between the C and I treatments and between the F and IL treatments. Standing volume in the C and IL plots at Flakaliden at the end of 1996 was 34.8 and 98.8 m³ ha⁻¹. As with the SETRES data (Table 1) it was only necessary to alter the values of the FR to simulate accurately the F and IL data; the values used were FR = 0.1 for the C and I treatments and FR = 1 for the fertilised treatments. With $f_{N_0} = 0.5$ (Eq. (2)) and $\alpha_0 = 0.055$ mol C (mol quanta)⁻¹ these give $\alpha_0 f_{N_0} = 0.03$ and 0.055 mol C (mol quanta)⁻¹ for the two treatments. The results of these calibrated simulations are shown in Fig. 5. The L^* values produced by 3-PG for the Flakaliden site (Table 3) were not as high as those observed (S. Linder, personal communication, 2001).

The southern Swedish site, at Asa, where trees were 15 years at the start of the experiment, has a milder climate and more fertile soil than Flakaliden, but at this site too the responses to fertilisation were pronounced. Irrigation also influenced growth in the later stages. We simulated the Asa data using the set of parameter values obtained from Flakaliden, except that the FR values were varied. With FR = 0.15 (hence $\alpha_0 f_{N_0} = 0.032$) and FR = 0.45 (hence $\alpha_0 f_{N_0} = 0.04$), excellent correspondence was obtained between simulated volume and basal area and measured values at Asa. Standing volume in the C and IL plots at Asa at the end of 1995 was 80.5 and 163.4 m³ ha⁻¹. The r^2 values for the relation between simulated and observed stem volumes and basal areas at Asa were 0.97 and 0.98, respectively, and the data were essentially unbiased. The L^* values generated for Asa were nearer to those observed in the experiment (Table 3; S. Linder, personal communication, 2001).

The close correspondence between observed and simulated stand volume, basal area and L^* for the *P. abies* at Asa provides strong evidence that the 3-PG model, when parameterised for a particular species can be used to predict the performance of that species and its response to conditions in other locations.

4.3. Tests against results from a spacing experiment

Professor Urban Nilsson (personal communication, 2001) provided data from a spacing × thinning experiment carried out on Norway spruce in the Asa area, at a different location to the fertilisation/irrigation

Table 5
Variance accounted for (r^2) by simulated values of stand volume and basal area before and after thinning at a range of *P. abies* stem populations. Average bias = (observed − simulated)/observed values

Spacing (m)	Stand volume (m³ ha⁻¹)		Basal area (m² ha⁻¹)	
	r^2	Average bias (%)	r^2	Average bias (%)
1.0 × 1.0	0.56	15	0.33	4
1.5 × 1.5	0.7	16	0.46	14
2.0 × 2.0	0.89	−3	0.87	−4
2.5 × 2.5	0.8	1.2	0.64	13.6

experiment. Trees were established at four spacings (1 m × 1 m; 1.5 m × 1.5 m; 2 m × 2 m and 2.5 m × 2.5 m) and were thinned after 19, 30, 34, 41, 47 and 51 years. We calibrated 3-PG against the 'standard' spacing for Norway spruce in that region (2 m × 2 m), at 19 years, and used the thinning procedure in the model to reduce stem populations to the specified numbers in the years when thinning was done. The thinning procedure in 3-PG assumes that the mass of foliage corresponding to the stems removed is also removed from the stand. The only changes necessary in relation to the parameter values used in the fertilisation/irrigation experiment were that the parameter values for stem the allometric equation, which were established using data from the spacing experiment, were not the same as those that fitted the trees in the fertilisation/irrigation experiment. The FR used was 0.8.

Results of the fitting runs, in terms of stem volume, basal area and leaf area index, are shown in Fig. 6. We then simulated the results of thinning in the other spacings without further calibration. The statistics of the comparisons between simulated and measured data are presented in Table 5. The r^2 values are generally lower than in the loblolly comparisons, but mean bias was small. This is a strong test of the model; runs were made from seedling establishment—not from the date of first thinning.

5. Discussion

The species considered in this paper grow in a wide range of environmental conditions, illustrated by the

data in Tables 1 and 2; radiant energy income ranges from 2200 to >8000 MJ m^{-2} yr^{-1}; average winter temperatures range from −6 to >17 °C, summer averages range from 12 to 29 °C and precipitation from 650 to >2700 mm yr^{-1}.

Good data sets for calibrating 3-PG should describe stand growth in terms of periodic measurements of stem diameters, observations on L^* (using, e.g. the LICOR leaf area meter), litterfall rates and stem number. Sensitivity analyses (not presented here) have shown that appropriate litterfall rates must be used if the time course of L^* is to be correctly simulated. Some (necessarily destructive) measurements of stem mass, for a range of stem sizes, to allow establishment of the stem mass/diameter relationship, are desirable. Observations and measurements on young stands are important (see Sands and Landsberg, 2001). The results presented in Figs. 4–6, show that 3-PG can be calibrated to reproduce observed stand growth accurately in terms of several variables. We have not encountered any growth and productivity data for reasonably homogeneous, even-aged forests that could not be accurately fitted by 3-PG. It can be argued, with some justification, that this is because (despite its apparent simplicity) there are enough adjustable parameters in the model to allow it to produce almost any growth pattern. It is therefore important, when calibrating the model, that as many as possible of these values are determined a priori on the basis of empirical data, or an initial calibration, rather than subsequently adjusted to improve the fit between observed and simulated data, unless the effect of that particular factor is being examined. The calibration procedure outlined in this paper is manual. It has been automated and a mathematical package is now available for this purpose (see Acknowledgements).

The data in Table 3 suggest that $p_{f,s}2/p_{f,s}20$ ratios in the range 2–3 will lead to stand dry mass—and hence volume—growth curves consistent with those observed in experiments and in production plantations. The higher values (*E. grandis* in South Africa, *P. radiata* in the ACT and plantation species in NSW) all come about because the values of the power (n_s) in the stem mass/B (allometric) equation were high—about 3 compared to the usual value of about 2.4. Variations in this values reflect differences in stem shape: foresters usually use equations involving stem height and diameter (or stand basal area) to estimate stem volume.

The 2-coefficient equation ($w_s = a_s B_s{}^n$) incorporates the effects of height and stem form in a_s and n_s.

Results of tests against data not used in calibration (Table 4, and the statistics given in relation to Figs. 5 and 6) show that the model is robust and reliable, and can be used with confidence to predict growth in areas where trees have not been grown, i.e. the model can be used to estimate site productivity. This is supported by the results obtained by Tickle et al. (2001b). They found that 3-PG provided better estimates of growth and productivity over 50,000 ha of native forest NSW than two conventional models for which (observed) site index values were provided for 22 plots. They then used 3-PG to estimate site index and re-run the better performing conventional models, leading to an improved relationship between the results produced by that model and measurements made over a number of years in 22 mensuration plots. The model can also be used to explore the influence of frost, temperature limits, drought and VPD on the distribution and productivity of tree species. An example is provided by Coops and Waring (2000). It can be used as a management tool to evaluate the probable effects of varying stocking, of thinning and—within the limits of relationships between the FR and addition of nutrients to soils—of stand fertilisation.

The widespread inadequacy of soil survey data and our poor quantitative understanding of the relationships between soil chemical properties as characterised by laboratory analysis and plant growth make it difficult to establish clear quantitative guidelines for selecting FR values. Unless there are data pertaining to the particular sites of interest, even good soil maps are only of limited value because of the immense point to point variation in soil properties and characteristics. One way forward will be through the use of a dynamic soil organic matter model, although such models will also have to be calibrated and tested in numerous locations. The relationships between canopy and soil nutritional status, and between canopy nutritional status and α_c, require considerable further research.

The question of differences among species is a matter of concern to many foresters. There is no support for the view that the central physiological process of canopy photosynthesis varies between species: there are multitudinous papers and reviews of this area—Landsberg and Gower (1997) provide a relatively detailed treatment, and Valentini et al. (1999) a

good treatment in the plant–atmosphere interaction context. Differences in radiation interception, as a result of significant differences in canopy structure, which certainly exist between species and forest types are not dealt with by 3-PG. If these are considered important then much more detailed radiation interception models will be required (see Cescatti, 1997a,b for recent developments in this area). The use of such models in a general simulation model implies much more detailed information about canopy structure, and would move 3-PG onto another plane of complexity. The analyses presented here indicate that, for tree species adapted to the environments in which they are being grown, carbon allocation patterns are not a major cause of variation in growth patterns. Parameters in 3-PG that allow the model to account for species differences, include responses to fertility (via α_c) between conifers and broad-leaved species, differences in the cardinal temperature values, differences in SLA and (possible) differences in stomatal response to water stress. Tolerance to extreme temperatures varies enormously (vide the differences in the cardinal temperature points used here for *P. abies* and *Pinus taeda*) and species are known to vary in their tolerance to drought (water availability is a major determinant of species distribution; Smith and Huston, 1989), or their ability to grow in soils of varying nutritional status—although this is less well documented.

To estimate the productivity of large areas of established forests, 3-PG can be applied through Geographic Information Systems with soil and climate layers (see Tickle et al., 2001b), or driven with satellite observations that allow assessment of seasonal changes in the capacity of the vegetative canopy to intercept radiation. The fraction of photosynthetically active radiation absorbed by the forest canopies (f_{PAR}) is calculated from the normalised difference between reflectances measured in the near-infrared and red wavelengths, termed the normalised difference vegetation index (NDVI). Stem numbers are by-passed in this version of the model and the carbohydrate allocation procedure is simplified to estimate the maximum above-ground growth at maximum L^*. This version (3-PGS) uses monthly weather data and provides spatially distributed estimates of monthly NPP. 3-PGS has been applied in Australia (Coops et al., 1998a,b; Coops, 1999), North America (Coops et al., 2001) and New Zealand (White et al., 2000).

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