



Testing the utility of the 3-PG model for growth of *Eucalyptus grandis* × *urophylla* with natural and manipulated supplies of water and nutrients

Jose Luiz Stape^{a,*}, Michael G. Ryan^{b,c}, Dan Binkley^c

^aDepartment of Forest Science, University of São Paulo, Piracicaba, SP CNPq 13418-970, Brazil

^bUSDA Forest Service, Rocky Mountain Research Station, 240 W. Prospect, Ft. Collins, CO 80523, USA

^cDepartment of Forest, Rangeland and Watershed Stewardship Sciences, Graduate Degree Program in Ecology and Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins, CO 80523, USA

Abstract

The productivity of fast-growing tropical plantations depends, in part, on the ability of trees to obtain and utilize site resources, and the allocation of fixed carbon (C) to wood production. Simulation models can represent these processes and interactions, but the value of these models depends on their ability to improve predictions of stand growth relative to simpler empirical approaches. We evaluated the 3-PG process-based model for simulating the response of *Eucalyptus grandis* × *urophylla* to changes in soil fertility and climate. This was done by calibrating the model with a complete C budget from an irrigated plantation, and then validating the model using independent data based on 2 years of growth from 40 pairs of fertilized and unfertilized stands. The 3-PG predictions were tested against actual production, and against a classic, empirical approach to estimating stand yield. The 3-PG parameter for site fertility was based on an objective fertilization response from the paired-plots. The 3-PG model responded well to the range of soil and climatic conditions during calibration, and was particularly sensitive to estimates of leaf area index. Actual wood production for the 40 validation stands ranged from 2 to 51 Mg ha⁻¹ per year, compared with model estimates of 10–42 Mg ha⁻¹ per year ($r^2 = 0.78$). Both 3-PG and the empirical model provided good estimates of wood production for average conditions, but 3-PG successfully represented the wet years and dry years that were not differentiated in the empirical model. This sensitivity of 3-PG to climate may be very useful for the prediction of wood production during short rotations, where a few years of unusual weather may strongly influence yield. Process-based models can play an important role in improving the management of these almost-agricultural forests, especially in regions with high rainfall variability.

© 2004 Elsevier B.V. All rights reserved.

Keywords: *Eucalyptus grandis* × *urophylla*; Forest carbon; Forest productivity; Forest simulation model; Gross primary production

1. Introduction

Eucalyptus is the dominant and most productive planted forest in Brazil, with mean annual increments

of 9–39 Mg ha⁻¹ per year (Stape, 2002). These plantations cover more than 3.0 million ha, and are managed intensively for charcoal, pulpwood and sawtimber products (Simoes et al., 1981; FAO, 1999; Neilson, 2000). Growth and yield models based on stand attributes are the current tools for predicting wood increments and wood supplies (Campos et al., 1988; Scolforo and Machado, 1988). Site index is still

* Corresponding author. Tel.: +55-19-3436-8679;

fax: +55-19-3436-8601.

E-mail address: stape@esalq.usp.br (J.L. Stape).

the central concept embodying the average environmental quality that sites may have on tree growth (Scolforo and Machado, 1988; Burkhart, 1997; Reed, 1997). Classic growth and yield models, however, have limitations when used to estimate forest production that include: (i) they cannot be used to estimate productivity on non-forested landscapes; (ii) in the short term, they are insensitive to inter-annual climatic variations; unusual growing conditions can dramatically affect final production of short-rotation forests; and (iii) changes in management practices between rotations can alter empirical relationships (Gonçalves et al., 2000; Eldridge et al., 1994; Seixas et al., 1995).

Empirical growth and yield models do not allow forest production to be integrated into a broader ecosystem framework of resource use (Running and Gower, 1991; Kimmins, 1997; Landsberg and Gower, 1997) and the forest-soil feedback throughout the detritus C and nutrient cycling (Parton et al., 1994; Burger and Kelting, 1998). These issues of wood production and soil changes also have increasing economical and social relevance (Brown et al., 1997).

Process-based models describe forest productivity based on plant physiological processes that control growth (i.e., photosynthesis, allocation, respiration, transpiration, nutrition and litterfall), and many have been developed (see summary in Landsberg and Gower, 1997). Despite the appeal of mechanistic simulations of growth and resource use under different environmental conditions, process-based models were rarely used in the last century as management tools (Kimmins, 1997; Landsberg and Waring, 1997). Recent reviews of process-based models suggest that simple approaches based on absorbed photosynthetically active radiation (APAR, a measure of the amount of incident light intercepted by the canopy) (Battaglia and Sands, 1998; Mäkelä et al., 2000) may overcome these difficulties. Models based on APAR calculate photosynthesis by first estimating the amount of photosynthetically active radiation (PAR) absorbed by the canopy, and the canopy's ability to fix C based on a light-use efficiency parameter (Monteith, 1977) that changes with environmental factors that affect stomatal conductance or the activity of the photosynthetic pathway (Jarvis and Leverenz, 1983; Sands, 1996; Goetz, 1997). This "top-down" approach to the physiology of forest growth reduces the number of model parameters and eliminates many of the non-

linearities of these processes at finer scales (Medlyn, 1998). Submodels for water flux and C allocation can be coupled with canopy processes (McMurtrie et al., 1990; Landsberg and Gower, 1997), and nutrient-soil dynamics can be lumped into fertility-rating scaling factors (Landsberg and Waring, 1997; Battaglia and Sands, 1997).

The use of process-based models as management tools by the large and expanding forest sector in the tropics may allow: (i) assessments of the risks of climatic variation on forest productivity and profitability, (ii) estimation of potential productivity for the planning of regional afforestation, (iii) identification of environmental factors limiting growth and resource use, (iv) a framework for management and breeding programs, and (v) evaluation of the long-term forest productivity when coupled with soil models. As a step in this direction, we evaluated the 3-PG model (Landsberg and Waring, 1997) for *Eucalyptus* plantations in Brazil. The model was selected due to its concise structure, dynamic regulation of carbon allocation, sensitivity to environmental factors and site management practices, successful parameterization and validation for other forest systems (Law et al., 2000; Coops et al., 1998; Landsberg et al., 2001; Sands and Landsberg, 2002), and adequate documentation (Sands, 2001).

Our test of the utility of the 3-PG model had two components. The model was calibrated for an irrigation and fertilizer trial with *E. grandis* × *urophylla* in northeastern Brazil, and then the model's performance was validated against independent growth data from 40 pairs of control and fertilized inventory plots monitored for 2 years. The performance of the model was judged in comparison to a locally developed empirical model of wood production.

2. Methods

2.1. 3-PG model

3-PG is a monthly time-step process-based forest model (Landsberg and Waring, 1997; Sands and Landsberg, 2002) of the APAR family (after Monteith, 1977). It has a biophysical submodel which estimates monthly evaporation and canopy transpiration using the Penman–Monteith model and standard weather data. Canopy conductance in the Penman–Monteith

model is controlled by the more restrictive factor controlling stomatal aperture, either vapor pressure deficit or soil water limitation. The vapor pressure deficit modifier (f_D) is negatively and exponentially related to average monthly vapor pressure deficit through the coefficient of stomatal response to vapor pressure deficit (k_g). Soil water balance is the difference between precipitation and evapotranspiration. Water is drained if water holding capacity in the rooting zone is exceeded. The soil water modifier (f_{ASW}) is inversely related to soil moisture and depends on soil texture.

The forest production submodel estimates gross primary production (GPP) based on the monthly APAR times a theoretical maximum canopy quantum efficiency (α_{Cx}) reduced by physiological (age, vapor pressure deficit or soil water) or environmental modifiers (temperature, soil fertility and frost). Soil fertility is expressed as a simple rating factor (FR), with a subjective approach. APAR is calculated based on the Beer–Lambert law, and leaf area index (LAI) is calculated from the foliage biomass and specific leaf area. Net primary production (NPP) is calculated as GPP times a NPP:GPP ratio (0.45 ± 0.05) to account for respiration. Allocation of NPP to the below-ground biomass is inversely proportional to the harshness of the environment (defined as the minimum of f_D and f_{ASW}) and soil fertility, within maximum and minimum allocation limits defined for the species. The fraction of NPP allocated above-ground is partitioned between stem and foliage growth in a proportion that varies with tree size. The establishment of this proportion can be based on species- and site-specific allometrics for foliage and stem biomass and is represented in 3-PG by two partitioning parameters. Litterfall rate increases with age up to a maximum defined value. No mortality rate was employed (as mortality is commonly negligible in these silvicultural systems), and the effect of age-related decline on growth (Ryan et al., 1997) was not implemented. For this study, we coded the 3-PG model in Visual Basic (based on Landsberg and Waring, 1997; Sands, 2001; Sands and Landsberg, 2002).

2.2. 3-PG calibration

We parameterized the 3-PG model for an experiment with *Eucalyptus saligna* in Hawaii (Stape, 2002),

and then recalibrated the model for *Eucalyptus grandis* × *urophylla* in Brazil. The calibration in Hawaii yielded reasonable estimates of growth and leaf area over a 6-year period, but the Hawaii parameters performed poorly for the irrigated clonal *E. grandis* × *urophylla* treatment in Brazil (data not shown; Stape, 2002), including the wrong directions over time in C fluxes and LAI. The calibration for Brazil required changes in the foliage–stem partitioning parameters (based on empirical relationships from 24 sampled trees in the Brazil trial). After this modification, GPP remained low, so a tuning process was carried out for k_g (the response to vapor pressure deficit) and maximum canopy quantum efficiency, after altering the species-specific parameters based on local data. From the 38 parameters needed in 3-PG, we calibrated a maximum of three for each calibration step. Maximum canopy quantum efficiency, foliage–stem partitioning parameters and stomatal response to vapor pressure deficit (or the maximum stomatal conductance) were the key parameters adjusted in this study, and are recognized as the most influential ones through sensitivity analyses performed in other studies (Landsberg and Waring, 1997; Law et al., 2000; Waring and McDowell, 2002; Landsberg et al., 2001).

An irrigation and fertilizer experiment in Brazil was used to calibrate 3-PG with 2 years of a complete C budget (both above- and below-ground). The experiment was located on the northeastern coast of Brazil, about 20 km SW of Entre-Rios ($11^\circ 58'S$, $38^\circ 07'W$) with a mean annual temperature of $25.5^\circ C$ and an average rainfall of 1040 mm per year. The slopes were gentle (<3%), with deep (>3 m), excessively drained sandy isohyperthermic Typic Haplustox soil. The stand was established in June 1996 by planting an *E. grandis* × *urophylla* clone at 3.0 m × 3.0 m spacing, and treatments were installed when the plantation was 3 years old. A 2 × 2 factorial with four replicates was used with two levels each of nutrient and water supply. High fertilizer and irrigation regimes (rainfall + irrigation > 2100 mm per year) were designed to eliminate any nutrient or water limitation on growth. No effect of fertilizer was observed in this experiment, so we analyzed results as averages across irrigation regimes (rainfed and irrigated treatments), and fertility rating was considered to be 1.0 (not limiting). A monthly meteorolo-

gical file with maximum and minimum temperatures, vapor pressure deficit and photosynthetically active radiation were derived based on weather data from two nearby meteorological stations (Stape, 2002). The 3-PG biophysical water submodel had already been shown to adequately estimate the water balance of this clonal *Eucalyptus* trial (Stape, 2002) as well as other *Eucalyptus* plantations in Brazil (Soares et al., 1997).

Above-ground woody biomass (AWB) and LAI were measured every 6 months along with yearly estimates of above-ground net primary production (ANPP), total below-ground carbon allocation (TBCA) and gross primary production for each plot and year. Above-ground woody biomass was calculated by tree diameters and regression equations determined by destructive harvesting within this stand but

outside the experimental plots. Leaf area index was estimated by light interception (Ceptometer-AccuPAR Model 80, Decagon Devices, Pullman, USA) in combination with leaf mass measured in the destructive sampling. Total below-ground C allocation was determined by the mass-balance technique (Giardina and Ryan, 2002) and represents all C allocated to the roots, while GPP was obtained as the sum of ANPP, TBCA and above-ground autotrophic respiration (Ryan, 1991).

The number of parameters adjusted was minimized by keeping constant all possible site- or species-specific parameters that were locally determined or derived from the literature (Table 1). The chosen outputs to evaluate the model during the calibration phase were the yearly estimates of GPP, ANPP, TBCA,

Table 1

Main parameter values of 3-PG model after calibration for the irrigation and fertilization experiment

Parameter	Brazil	Unit	Source	Symbol
NPP/GPP ratio	0.50	–	Landsberg and Waring (1997)	Y
Canopy quantum efficiency	0.080	mol C mol PAR ⁻¹	Stape (2002)	α_{Cx}
Specific leaf area	8.5 or 11.0	m ² kg ⁻¹	Stape (2002)	σ
PAR extinction coefficient	0.4	–	Stape (2002)	k
Age canopy cover	1.5	Year	Stape (2002)	
Proportion of intercepted rainfall evaporated	0.15	–	Lima (1993)	I_x
Canopy albedo	0.2	–	Landsberg and Waring (1997)	
Maximum stomatal conductance	0.008	m s ⁻¹	Mielke et al. (1999)	
Maximum canopy conductance	0.02	m s ⁻¹	Landsberg and Waring (1997)	
Coefficient of stomatal response to vapor pressure deficit	0.324	kPa ⁻¹	Tuning	k_g
Canopy boundary layer conductance	0.2	m s ⁻¹	Landsberg and Waring (1997)	g_B
Maximum litterfall rate	0.070	g per month	Stape (2002)	γ_{Fx}
Age at which litterfall rate has median value	4	month	Stape (2002)	t_{yF}
Foliage/stem partitioning DAP = 2	0.096	–	Stape (2002)	
Foliage/stem partitioning DAP = 20	0.034	–	Stape (2002)	
Constant coefficient at stem mass/DAP equation	0.065	–	Stape (2002)	
Power coefficient at stem mass/DAP equation	2.68	–	Stape (2002)	
Maximum fraction of NPP to roots	0.8	–	Landsberg and Waring (1997)	
Minimum fraction of NPP to roots	0.20	–	Landsberg and Waring (1997)	
Fertility parameter	1.00–0.60	–	Tuning	FR
Maximum available soil water	80/160	mm	Stape (2002)	
Texture coefficient for soil water modifier	0.3/0.5	mm	Landsberg and Waring (1997)	
Power coefficient for soil water modifier	4/7	mm	Landsberg and Waring (1997)	
Maximum growing temperature	40	°C	Sands and Landsberg (2002)	T_{max}
Optimum growing temperature	25	°C	Specific	T_{opt}
Minimum growing temperature	8	°C	Sands and Landsberg (2002)	T_{min}

Table 2

Characterization of the genetics, location, soil taxonomy, soil clay content and total carbon (0–0.3 m) of the 40 stands of *E. grandis* × *urophylla*, grouped by area

Area	Number of plots	Number of clones	Latitude	Longitude	Elevation (m)	Main soil order	Clay (%) (1 S.D.)	Soil carbon (kg m ⁻²) (1 S.D.)
1	5	2	12°02'S	38°28'W	301	Quartzpsament	13 (7)	3.1 (0.7)
2	20	4	11°47'S	37°55'W	166	Ultisol	29 (10)	3.7 (0.8)
3	3	3	11°50'S	38°28'W	250	Oxisol	22 (3)	3.4 (0.3)
4	7	2	11°53'S	38°30'W	296	Oxisol	16 (3)	2.3 (0.4)
5	5	1	11°55'S	38°31'W	256	Quartzpsament	8 (3)	1.4 (0.3)

average LAI and the AWB at the end of each year. These variables capture three crucial processes: (i) the total amount of C fixed, (ii) the C allocation pattern (TBCA and ANPP), and (iii) the above-ground partitioning between woody and foliage biomass (AWB and LAI). We estimated TBCA from the model as two times the below-ground NPP, assuming that respiration equals production (Binkley and Ryan, 1998; Law et al., 2000). The calibration process was conducted to simultaneously match predicted and observed values of GPP, ANPP, AWB and LAI (TBCA was not incorporated because it was a linear combination of GPP and ANPP), using a weighted sum of squares to normalize the sum of squares of each variable to its absolute magnitude:

$$WSS = \sum_{i=1}^v \frac{n_i \sum_{j=1}^{n_i} (P_j - O_j)^2}{\left(\sum_{j=1}^{n_i} O_j \right)^2} \quad (1)$$

where WSS is the weighted sum of squares, v the number of variables ($v = 4$), n_i the number of predicted–observed pairs for the variable i ($n = 2$), and P_j and O_j are the predicted and observed values. The calibration process used an automated optimization procedure in Visual Basic to minimize WSS with constraints to limit the search within feasible values of the parameters. The optimization routine was initialized several times with different combinations of initial values for the parameters, and the final parameterization was based on the visual inspection of plotted observed and simulated outputs. As criteria for the goodness of fit of the model, we expected the simulated line to pass within one or two standard deviations about the observed data points. In all cases, the model was initialized with observed data at 3.5 years of age and run for 2 years.

2.3. 3-PG validation: site descriptions and measurements

The performance of 3-PG was evaluated on its ability to predict 2 years of independent above-ground woody biomass increment measured in 40 inventory plots located in five areas of commercial plantations (Table 2) in northeastern Brazil (within a 60 km radius of Entre-Rios, 11°58'S, 38°07'W). The final parameterization obtained for the irrigation experiment was used. The utility of the 3-PG simulations was evaluated by a comparison with an empirical model that predicts wood growth based on age, site index and basal area.

The forty 6-year-old, first-rotation stands were chosen to capture regional differences in soil and productivity (mean annual increment at age 6 ranged from 7 to 20 Mg ha⁻¹ per year). All sites were located on the flat or modest slopes (<3%) and site preparation included slash-and-burning of the initial vegetation (pasture, secondary forest or savanna), disking and harrowing. Forests were planted in July 1993 at 3.5 m × 2.6 m or 3.0 m × 3.0 m spacings and fertilized with 22 kg N ha⁻¹, 36 kg P ha⁻¹ and 19 kg K ha⁻¹. Four-month-old clonal cuttings were produced in a shade-house and selected for uniform size (25–35 cm in height) (Stape et al., 2001). Chemicals were applied yearly to control leaf-cutting ants (sulfuramid) and during the first 2 years to control weeds (glyphosate). All stands consisted of monoclonal plantings of *E. grandis* × *urophylla* (Clones COP-0204, 0321, 0477, 0670, 1341 or 2361). In each stand, a circular inventory plot of 471 m² had been measured yearly since 2 years of age. The diameters at breast height (DBH at 1.30 m) were measured for all trees, as well as the first 20 heights (based on consecutive numbers of trees in the plots) and the heights of the

Table 3

Rainfall, estimated transpiration and average available soil water (ASW, 0–2.0 m) during the two study periods (wet and normal years) for the 40 stands of *E. grandis* × *urophylla*, grouped by area^a

Area number	Rainfall (mm)		Transpiration ^b (mm)		Available soil water ^b (mm)	
	Wet	Normal	Wet	Normal	Wet	Normal
1	1691	1112	1211	886	65	49
2	2114	1518	1284	1091	116	76
3	1524	1028	1185	883	73	54
4	1520	1001	1180	833	70	52
5	1569	1051	1117	850	58	43
Mean (1 S.D.)	1845 a (274)	1287 b (234)	1230 a (60)	971 b (122)	92 a (25)	64 b (13)

Average vapor pressure deficit wet year = 1.08 kPa, normal year = 1.20 kPa. Rainfall, transpiration: area 2 > area 1 > areas (3–5) ($P < 0.001$). ASW: area 2 > areas (1 and 3–5) ($P < 0.001$).

^a Values followed by different letters between years differ at $P = 0.05$.

^b Transpiration and ASW based on measured and interpolated LAI.

four dominant trees. A paired-plot with the same form and dimension was installed in July 1999 in each of the stands within 30 m of the original inventory plot (control plots). This plot was fertilized to eliminate any nutrient deficiency and evaluate the effect of fertilizer on growth. Fertilizers were applied at high rates of: 600 kg Ca ha⁻¹ and 300 kg Mg ha⁻¹ (as lime); 4 kg B ha⁻¹, 2 kg Cu ha⁻¹ and 2 kg Zn ha⁻¹ (as FTE micronutrient fertilizer) in September 1999, followed by quarterly additions of 126 kg N ha⁻¹ (as ammonium sulfate), 21 kg P ha⁻¹ (as superphosphate) and 79 kg K ha⁻¹ (as KCl). All fertilizers were broadcast applied for 2 years. Trenches (0.25 m wide and 0.80 m deep) between adjacent plots minimized any fertilizer effect on the control plots. From July 1999 to August 2001, all paired-plots were measured every 6 months.

For the control plot, above-ground woody biomass (stem wood plus bark and branches) was calculated between age 2 and 4 years using a general allometric equation. For measurement at age 5 years or older local equations were used. For the paired-plots after fertilizer was applied, annual above-ground woody biomass production was the summed growth of individual trees between July 1999 and June 2000, and between July 2000 and June 2001. The site index (height of the largest 100 trees/ha at age 5 years) was measured as the average of the four dominant trees in each plot at that age. Leaf area index was calculated for each plot in July 1999 and June 2000 with the regional allometrics and an average SLA of 8.5 m² kg⁻¹, and interpolated monthly between the

annual estimates based on the seasonal changes observed in the plantation used to calibrate 3-PG. In March 2001, LAI was measured directly in each plot using the ceptometer and used to estimate LAI in June 2001. For each validation site, an interpolated meteorological file was created with monthly PAR, vapor pressure deficit, rainfall and temperatures based on daily weather data from nine local meteorological stations (Stape, 2002). Light-use efficiency (LUE) was calculated for each year and plot as the ratio between wood increment and APAR. Water holding capacity for each site (a 2 m profile was used for each water budget) was estimated by a general equation developed for the region based on soil texture (Stape, 2002).

The two growing periods (1999/2000 and 2000/2001) used to validate 3-PG for the fertilized plots (FR = 1.0), had very distinct rainfall totals (a wet year with 1845 mm rainfall, and normal year with 1287 mm rainfall, Table 3). The model was provided with the initial stand and soil conditions at age 6 years, together with the respective monthly meteorological files for the two growing years. The monthly growth estimates were summed to obtain the yearly estimates. A complete soil and stand characterization was prepared for each site, and a total of 38 soil, 8 bioassay and 16 stand indices (Table 4) were obtained for the control plots. The sampling and laboratory procedures for soil (van Raij et al., 1987), bioassay and canopy indices are fully described in Stape (2002).

Based on the validation results of wood increments, LAI, and water balance for the first 3-PG application, a slight re-parameterization was implemented by

Table 4

Variables used on stepwise regression procedures having fertilization response as the dependent variable and the independent variables organized by soil and stand-canopy categories

Category	Variables
Soil-physical	Sand, silt, clay, bulk density
Soil fertility	Soil C, soil N, extractable nutrients (P, K, Ca, Mg), sum of bases, H + Al, CEC, pH
Soil-lab incubations	N resin bag, N boiling water, N anaerobic, N aerobic fresh soil, N aerobic dried soil
Soil-bioassay	Seedlings dry matter, and N, P, K, Ca and Mg contents
Stand-canopy	Site index, LAI, leaf nutrient content (N, P, K, Ca and Mg), canopy nutrient content (N, P, K, Ca and Mg)

manually changing the SLA parameter (from 8.5 to 11.0 m² kg⁻¹, Table 1). A second 3-PG application was developed; statistics calculated, and results compared with the first application.

Site-specific fertility-rating factors were needed to obtain 3-PG simulated values for the control plots using the second parameterization. For that purpose, we investigated fertilizer response as an objective index for FR. Fertilizer response (FER, in Mg ha⁻¹ per year) was defined as

$$FER = \left(\frac{WNPP_F}{IWB_F} - \frac{WNPP_C}{IWB_C} \right) \left(\frac{IWB_F + IWB_C}{2} \right) \quad (2)$$

where WNPP is the wood increment, IWB the initial wood biomass (at age 6 years), and the subscripts C and F are for control and fertilized plots, respectively. This adjusted fertilizer response did not differ from the non-adjusted response due to the paired-plot design. Fertilizer responses were evaluated for the wet year only because the differences in growth due to fertilization among sites are clearest when water is not a limiting factor. Fertilizer response did not relate with initial biomass (data not shown), and no covariate adjustment was needed. A completely independent validation of the fertility rating would require application of values derived from this set of 40 inventory plots to predict growth in a different set of plots.

To test if the fertility-rating parameter in 3-PG was in line with fertilizer responses, we selected the three

sites with the highest fertilizer responses (29.0, 22.9 and 19.0 Mg ha⁻¹ per year) and three sites with no response (-3.3, -2.3 and -0.8 Mg ha⁻¹ per year). For each, FR was adjusted to match the wood increment during the wet year. For the high fertilizer response sites, FR was 0.61, 0.72 and 0.78, while for the non-responsive sites, FR was 0.88, 1.01 and 1.10. Due to the coherent directional trend of the FR values (higher for non-responsive sites), we estimated all FRs by scaling between 0.6 (maximum fertilization response, arbitrarily chosen based on highest responsive plot) and 1.0 (no fertilization response), during the wet year $FR = [0.4(29 - FER)/29] + 0.6$, where 29 Mg ha⁻¹ per year was the highest observed fertilizer response. With the site-specific fertility ratings, 3-PG was used to estimate wood increment for the control plots.

2.4. 3-PG validation: comparison with empirical yield model

The empirical yield model used was the Sullivan and Clutter (SC) model (Sullivan and Clutter, 1972; Clutter et al., 1983). This model has been successfully and routinely applied in Brazil for *Eucalyptus* (Campos et al., 1988; Scolforo, 2002) and is derived from two production equations, one for basal area and one for above-ground woody biomass based on age and site index, which are mathematically manipulated to obtain the biomass yield equation:

$$\ln(AWB_2) = \alpha_0 + \alpha_1 S + \frac{\alpha_2}{A_2} + \frac{\alpha_3 \ln(BA_1) A_1}{A_2} + \alpha_4 \left(1 - \frac{A_1}{A_2} \right) + \alpha_5 S \left(1 - \frac{A_1}{A_2} \right) \quad (3)$$

where BA is the basal area (m² ha⁻¹), S the site index (m), A the stand age (months), AWB above-ground woody biomass (Mg ha⁻¹), and α_i are the coefficients to be estimated, and the subscripts 1 and 2 on AWB and BA stand for their values at ages A₁ and A₂. The available data from ages 2 to 6 years for the 40 control inventory plots were used to estimate the parameters of the SC model using ordinary least-squares procedures in SAS 8.1 (SAS Institute, Carry, NC, 2001).

After estimating these parameters, basal area at age 6 years and site index of the control plots were used to estimate wood biomass at ages 7 and 8 years.

2.5. Statistical analysis

For each set of simulated and observed values of above-ground woody biomass production, the following statistics were obtained to help evaluate model performance: model efficiency (EF), root mean square error (RMSE), the a and b coefficients of the linear relation between predicted (P_i) and observed (O_i) data, and the coefficient of determination (r^2) (Loague and Green, 1991):

$$EF = \frac{\sum_{i=1}^n (O_i - \bar{O})^2 - \sum_{i=1}^n (P_i - O_i)^2}{\sum_{i=1}^n (O_i - \bar{O})^2} \quad (4)$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (P_i - O_i)^2}{n}} \quad (5)$$

The best model should have EF and r^2 close to the unity, RMSE close to zero, and a and b not significantly different from 0 and 1, respectively. As we were interested in yearly production estimates, all analyses were done considering a total of 80 observed–simulated pairs ($n = 2$ years \times 40 plots).

Analyses of variance considered fertilization and site (block) as the main effects, with year as a repeated measurement factor for variables estimated for both the wet and normal years: wood increment, LAI, canopy N, canopy P, APAR and LUE. The initial woody biomass of the stands and its interaction with fertilization were tested as potential covariates for the wood increment analysis, but both were shown to be non-significant ($P = 0.51$ and 0.33 , respectively) due to the blocking. For variables evaluated just once, or analyzed independently at the beginning or end of the study period, an ANOVA having fertilization and block as the main effects was used: total soil C, total soil N, and biometric stand attributes. Year and block were the main effects for meteorological data analysis.

We used multiple regressions to investigate the relationship between fertilizer response and soil or stand-canopy indices, with fertilizer response as the dependent variable and the indices as independent variables. The minimal inclusion significance of a variable was set at $P = 0.10$. Due to the large number of soil independent variables we utilized the following steps to avoid overparameterization: (i) independent variables were classified into soil-physical, soil-lab

incubations, soil fertility and soil-bioassay groups (Table 4); (ii) fertilizer responses were regressed against the independent variables of each group, separately; and (iii) groups were aggregated by taking, at most, the best three variables of each group during the isolated analysis. Residual analysis checked for normality and homocedasticity. For the stand indices no grouping was necessary.

All analyses were performed on SAS 8.1 with multiple comparisons with a significant level of 0.05 to protect against type I error.

3. Results

3.1. Calibration

Canopy quantum efficiency was between 0.060 (maximum observed value in an irrigated stand; Stape, 2002) and $0.080 \text{ mol C mol}^{-1}$ APAR. The highest value was used (Table 1) to represent the maximum efficiency. Calibrating the coefficient of stomatal response to vapor pressure deficit (k_g , which affects canopy quantum efficiency and allocation to roots) and to the foliage–stem partitioning parameters (which influence wood biomass and LAI estimates) resulted in an adequate time series simulation of the C budget fluxes (GPP, ANPP and TBCA) and the wood biomass and LAI state variables (Fig. 1). The performance of the model for the rainfed treatment was also satisfactorily achieved by using the actual rainfall of the site, which reduced canopy quantum efficiency and increased allocation to roots, providing a good simulation of the C fluxes and state variables, except for a slight underestimation of LAI (Fig. 1). Overall, we considered the calibration to be satisfactory despite the slight underestimation of LAI (Fig. 1).

3.2. Validation

Woody biomass of the 40 stands varied by threefold at age 6 years ($42\text{--}118 \text{ Mg ha}^{-1}$), owing to different locations (climate), soil groups and clonal genotypes (Tables 2 and 3). The two measurement years had distinct rainfall regimes (1845 versus 1287 mm, for the wet and normal years), leading to higher transpiration rates and available soil water in the root zones for

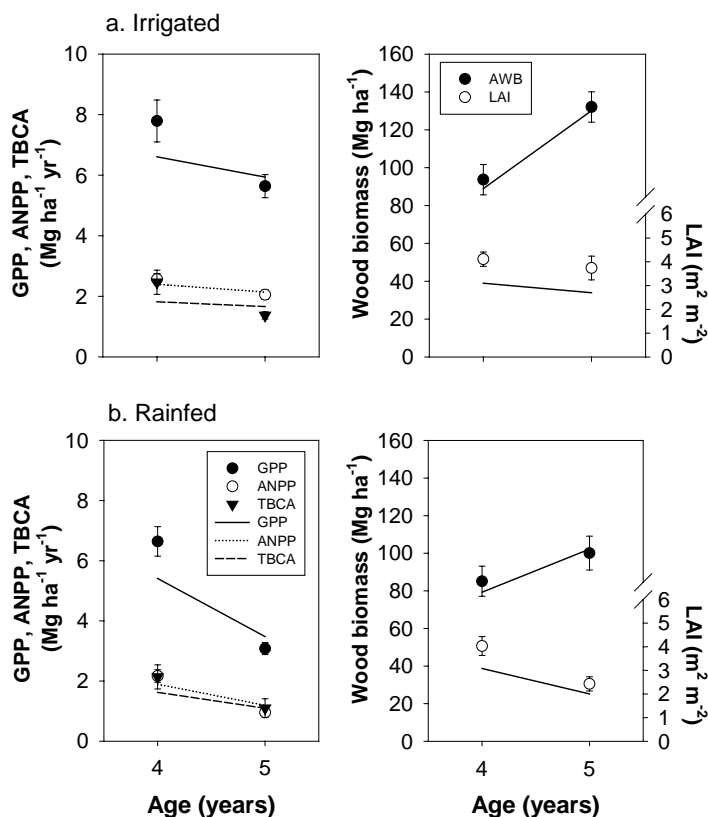


Fig. 1. Observed (symbols) and 3-PG simulated (lines) values of GPP, ANPP, TBCA, woody biomass and LAI for *E. grandis* × *urophylla* for irrigated treatment (fertility rating = 1.0) after calibration (a), and for the rainfed treatment using the previous parameterization (b).

the wet year (Fig. 2 and Table 3). The paired control and fertilized plots did not differ initially for any soil or biometric attributes (Fig. 2). Wood increments were affected by both fertilizer and year, leading to a fertilizer × year interaction (Fig. 3). Increments for both control and fertilized plots were higher for the wet (29.3 and 37.9 Mg ha⁻¹ per year, respectively) than for the normal year (15.1 and 17.3 Mg ha⁻¹ per year; Figs. 2 and 3). Fertilizer response was also higher for the wet year (8.6 versus 2.2 Mg ha⁻¹ per year; Table 5), and did not correlate with initial biomass ($r^2 = 0.01$).

For the fertilized plots, the first application of 3-PG indicated a strong correlation between observed and simulated values ($r^2 = 0.81$, Fig. 4a), although the slope of the linear regression line (0.48) differed significantly from 1, mainly due to an overestimation of wood production for the normal year (25.2 versus

17.3 Mg ha⁻¹ per year). The wet year had satisfactory estimates (36.2 versus 37.9 Mg ha⁻¹ per year).

A re-parameterization of 3-PG was implemented for the validation exercise because the overestimate of wood production during the normal year was also associated with both a very low simulated LAI compared with observed values (1.7 versus 2.5 m² m⁻², Fig. 1) and with no soil water deficit (data not shown), despite the low soil available water (Table 3). Among the parameters that could affect LAI, model sensitivity was high for the specific leaf area (SLA). This was changed from 8.5 to 11.5 m² kg⁻¹, the upper limit observed for the species (Stape, 2002), resulting in a better simulation ($r^2 = 0.83$, higher slope, Table 6 and Fig. 4b). This second 3-PG application for the fertilized plots adequately predicted wood increments (36 Mg ha⁻¹ per year) and LAI (3.3 m² m⁻²) for the wet year, and improved estimates for the normal

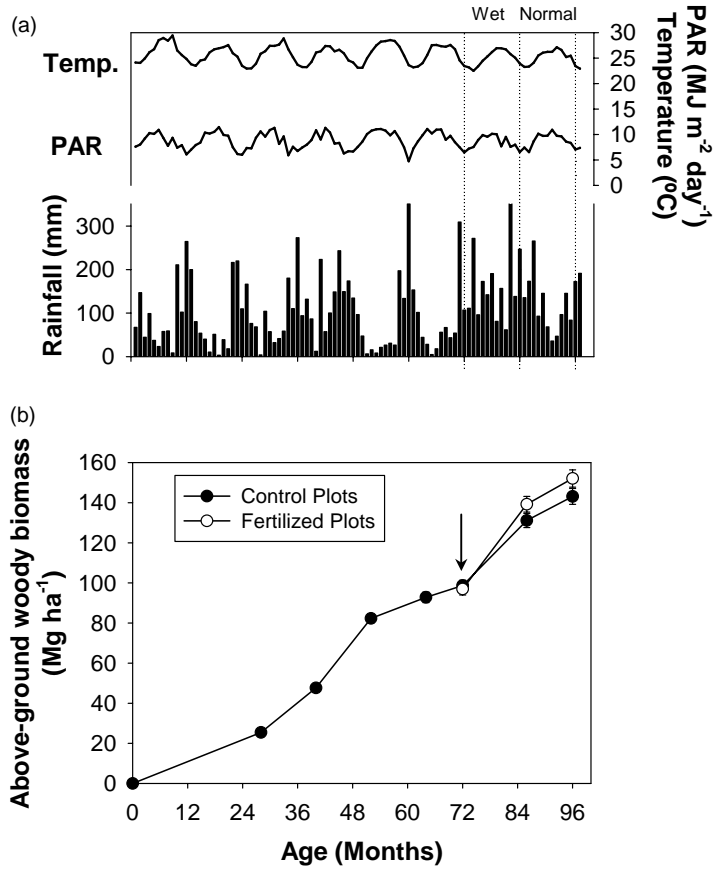


Fig. 2. Average monthly meteorological variables (rainfall, PAR and temperature) for the complete rotation of the 40 studied sites indicating the last two wet and normal years (a). Average biomass accumulation (and standard error bars) for the control and fertilized plots (b). The arrow indicates the initiation of quarterly fertilization.

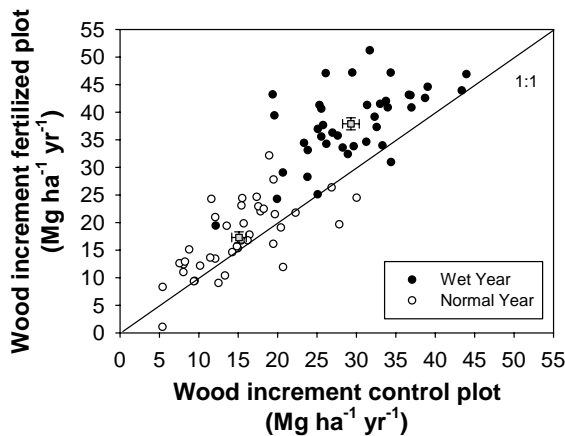


Fig. 3. Wood (stem + bark + branch) increments during wet and normal years of the 40 paired-plots. Gray squares represent the average growth for the years with standard error bars.

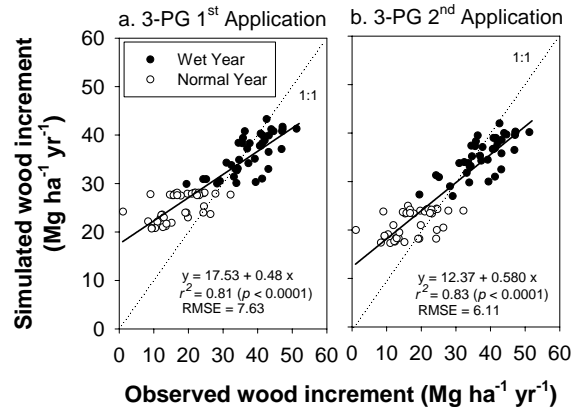


Fig. 4. Observed and simulated wood (stem + bark + branch) increments for the wet and normal years for 3-PG model on fertilized plots before (a) and after re-parameterization (b).

Table 5

Average canopy attributes, absorbed light, wood increment and light-use efficiency by treatment (control and fertilized) and year (wet and normal), and the respective fertilization response^a

Variable	Year	Control	Fertilized	Response
Leaf area index (m ² m ⁻²)	Wet	3.2 A	3.3	–
	Normal	2.8 Bb	3.2 a	0.4
Foliage N concentration (g kg ⁻¹)	Wet	18.5 Ab	20.0 Ba	1.5
	Normal	17.6 Bb	23.0 Aa	5.4
Canopy N content (g m ⁻²)	Wet	7.1 Ab	8.0 a	0.9
	Normal	5.2 Bb	8.6 a	3.4
Foliage P concentration (g kg ⁻¹)	Wet	1.12	1.17 B	–
	Normal	1.10 b	1.72 Aa	0.62
Canopy P content (g m ⁻²)	Wet	0.43 A	0.48 B	–
	Normal	0.32 Bb	0.62 Aa	0.30
APAR (TJ ha ⁻¹ per year)	Wet	20.7 A	21.1	–
	Normal	19.7 Bb	21.4 a	1.70
Wood increment (Mg ha ⁻¹ per year)	Wet	29.3 Ab	37.9 Aa	8.6
	Normal	15.1 Bb	17.3 Ba	2.2
Light-use efficiency (g MJ ⁻¹)	Wet	1.41 Ab	1.79 Aa	0.38
	Normal	0.77 B	0.80 B	–

^a Values followed by different small letters (between treatments) or capital letters (between years) differ at $P = 0.05$. All significant fertilization responses are presented.

year, increasing LAI (from 1.7 to 2.3 m² m⁻²) and soil water deficits (data not shown), and decreasing production (from 25.2 to 21.0 Mg ha⁻¹ per year). The slope of the prediction line in Fig. 4b differs from 1:1, even after recalibration; observed increments in the dry year were lower than predicted, whereas observed increments were somewhat higher than predicted in the normal year. This pattern indicates that the 3-PG representation did not capture the full responsiveness of the plantations to changes in water supply and vapor pressure deficit. We expect that further calibration and

validation of the model would likely move the slope of the relationship in Fig. 4 toward 1:1.

This final parameterization of 3-PG was used to simulate wood increments of the control plots (Fig. 5a) after scaling FR for each site. The observed and simulated results were strongly correlated ($r^2 = 0.71$), with a high slope coefficient (0.63) and small RMSE (Table 6). Across the 40 sites, the observed and simulated wood increments and LAI for the wet year were similar (29.3 versus 30.3 Mg ha⁻¹ per year, 3.1 versus 3.1 m² m⁻²), but small differences persisted for

Table 6

Summary of the statistics between observed and simulated wood increment values for both years ($n = 80$)

	Model (plots)			
	SC (control)	3-PG first application (fertilized)	3-PG second application (fertilized)	3-PG (control)
Intercept, a	24.79 (1.87)	17.53 (0.79)	12.37 (0.91)	10.35 (1.08)
Slope, b	–0.10 (0.08)	0.48 (0.03)	0.58 (0.03)	0.63 (0.04)
r^2	0.02	0.81**	0.83**	0.71**
RMSE	12.30	7.63	6.11	5.60
Model efficiency	–0.68	0.61	0.75	0.65

** $P < 0.001$.

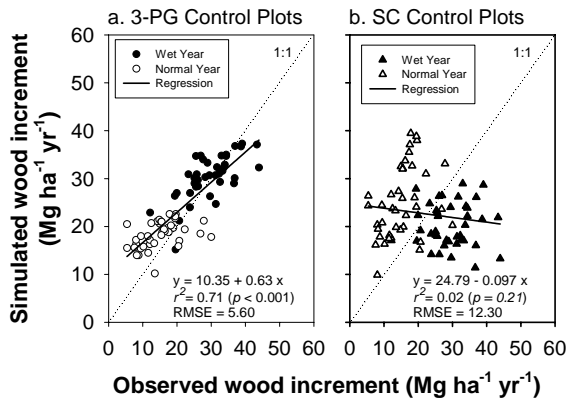


Fig. 5. Observed and simulated wood (stem + bark + branch) increments for the wet and normal years for 3-PG model on control plots (a) and for the SC empirical model on control plots (b).

the normal year (15.1 versus 18.3 Mg ha⁻¹ per year, 2.8 versus 2.0 m² m⁻²).

The Sullivan–Clutter empirical model adequately described the growth of the stands between age 2 and 6 years ($n = 200$, $r^2 = 0.94$, $P < 0.0001$; data not shown):

$$\ln(\text{AWB}_2) = 2.32 + \frac{0.015S - 44.51}{A_2} + \frac{0.88 \ln(\text{BA}_1)A_1}{A_2} - 0.22 \left(1 - \frac{A_1}{A_2}\right) + 0.17S \left(1 - \frac{A_1}{A_2}\right)$$

However, predictions were poor for the subsequent wet and normal years (Fig. 5b). The empirical model underestimated wood production for the wet year by almost one third (20.2 versus 29.3 Mg ha⁻¹ per year), and overestimated wood production for the normal year by two thirds (25.0 versus 15.1 Mg ha⁻¹ per year). The superior predictive ability of 3-PG for estimating wood increment of the control plot relative to the Sullivan–Clutter model was clear (Fig. 5 and Table 6).

3.3. Fertility indices

Very few of the fertility indices (Table 4) correlated with the fertilization response in the wet year (data not shown; Stape, 2002). No physical or bioassay indices presented a correlation with fertilizer response, while eight fertility indices showed a negative correlation (mineral N extracted with boiling salt solution, extractable P, extractable K, extractable Mg and cation exchange capacity from 0 to 15 or 0 to 30 cm depth).

The majority of the fertility indices correlated negatively (although not all were significant) with the fertilization response (data not shown), indicating stronger responses to fertilization on less fertile soils. Using the stepwise procedure, extractable potassium at 0–0.15 m, phosphorus at 0–0.30 m and cation exchange capacity at 0–0.15 m explained 56% of the variation of the fertilizer response. We developed a soil fertilizer response index (SFRI) with the linear combination of these soil attributes (Fig. 6a). Among the stand properties, only canopy N and canopy P (Table 4) presented a slightly negative correlation with fertilizer response. Fertilizer response tended to decrease as the content of N in the canopy increased, which we termed canopy fertilization response index (CFRI, Fig. 6b).

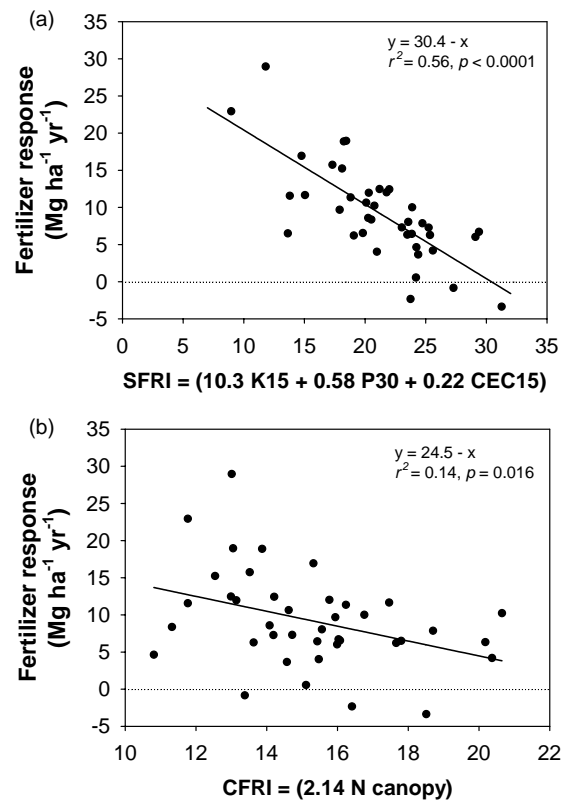


Fig. 6. Relationship between fertilization response (FER) of the 40 stands during the wet year, and soil fertilization response index (a) and canopy fertilization response index. K15: K in mmol_c kg⁻¹ at 0–0.15 m; P30: P in mg kg⁻¹ at 0–0.30 m; CEC: CEC in mmol_c kg⁻¹ at 0–0.15 m; N canopy: N in the canopy in g m⁻². Fertility rating is estimated as FR = [0.4(29 – FER)/29] + 0.6.

4. Discussion

The complete C budgets from the fertilizer and irrigation experiments were critical for the calibration of the 3-PG model and the partial evaluation of its descriptive structure of C fixation, and above- and below-ground C allocation. The calibration using the treatments with the highest supplies of nutrients and water set the fertility and soil moisture modifiers to 1.0 (not limiting to production), and let the vapor pressure deficit be the primary modifier controlling both C fixation (by affecting canopy quantum efficiency) and allocation (by affecting root partitioning). Under these circumstances, calibration of the model was satisfactory. Simulated GPP was 6.3 kg C m^{-2} per year (28% allocated below-ground), well within the 95% confidence interval for estimated GPP of 6.7 kg C m^{-2} per year (and 28% allocated below-ground; Fig. 1).

After these calibrations, 3-PG simulations of the rainfed treatment estimated average GPP as 4.4 kg C m^{-2} per year ($\sim 8.8 \text{ kg dry mass m}^{-2}$ per year, 31% allocated below-ground), well within the 95% confidence interval for estimated GPP of 4.8 kg C m^{-2} per year ($\sim 9.6 \text{ kg dry mass m}^{-2}$ per year, 32% allocated below-ground) (Fig. 3). These results support the model's description of both water (Brazil site) and nutrient (observed on Hawaii study; Stape, 2002) effects on C gain and allocation.

The empirical structure of the Sullivan–Clutter model made it naturally insensitive to inter-annual climatic variations (Clutter et al., 1983; Kimmins, 1997). In contrast, 3-PG, even for the first application (Fig. 4), was responsive to distinct sites and weather conditions. The diversity of clones among the sites probably contributed to reduced performance of the model.

In the first attempt to validate 3-PG, LAI was underestimated (Fig. 1). LAI is the most important state variable in models that are based on APAR because it integrates C and water fluxes (Law et al., 2000). The second validation with an increased SLA resulted in higher LAI but lower wood production, because higher transpiration rates induced water deficits that counteracted the potential increase in C fixation. SLA was the only parameter adjusted, other parameters that directly affect LAI (litterfall, foliage:stem partitioning parameters) or water balance

(rainfall interception, available soil water) still require investigation. Moreover, shedding of leaves by *Eucalyptus* in response to drought is common in the region (Stape, 2002) and should be added explicitly to the model (Landsberg and Waring, 1997; Sands and Landsberg, 2002).

The description of root C allocation in 3-PG as a function of both soil fertility and environmental stress indicates that the effects of high fertility will increase with water supply (Stape et al., 1997; Fisher and Binkley, 2000; Soares and Leite, 2000). Indeed, 3-PG simulated fertilization responses of 5.1 and 2.7 Mg ha^{-1} per year for the wet and normal year, respectively, in line with the observed values of 8.6 and 2.2 Mg ha^{-1} per year. Furthermore, the model correctly estimated a higher light-use efficiency for the fertilized plots during the wet year, and a lower during the normal year (Table 5). An adequate description of the C allocation process is crucial for the correct yearly estimates of wood production for *Eucalyptus* in areas with large inter-annual climatic variability and intense silvicultural practices.

Predictions by 3-PG of wood increment and LAI were reasonable for control plots, indicating that the fertility-rating scheme (based on fertilization responses) was adequate. The absence of a correlation between fertilizer responses and mean annual increment (MAI) or site index ($r^2 < 0.04$) showed that soil fertility should be considered as an independent concept in forest modeling. In this region, MAI and site index correlate well with water supply (Stape, 2002), and the adequate evaluation of the effects of soil fertility among stands depends on the occurrence of high rainfall or the use of a paired-plot design (Hart and Binkley, 1985). Fertilizer responses as a function of soil properties are species-, region- and management-specific (Hart et al., 1986; Gale et al., 1991). In this study that was based on the same basic genotype, management and geology, the soil fertilization response index was satisfactory (Fig. 6a) to predict the fertility-rating parameter. In the same direction, N in the canopy seems to be a potential index, because it is in line with the observed increase in LAI and leaf nutrient content on fertilized plots (Fig. 6b). The use of paired-plots with and without fertilizer in a plantation inventory network over a regional area is an effective tool for estimating FR for 3-PG and other process-based models.

In Brazil, LAI is not assessed during inventory surveys on a regular basis (Campos et al., 1988; Scolforo, 2002), but this could be implemented easily using light meters (Cutini et al., 1998), and would provide essential information for process-based APAR model evaluations for tropical plantations.

5. Conclusions

Empirical yield models typically describe growth adequately for average environmental conditions, but they may perform poorly during dry and wet years, or when silvicultural treatments are not consistent across sites. The adaptation of the 3-PG process-based model for tropical *Eucalyptus* plantations was relatively easy given the model calibration and testing that was facilitated by the complete C budget from the irrigation and fertilization experiment. The calibrated model represented the effects of soil water deficit and soil fertility on C gain and allocation very effectively.

The soil fertility rating is a key feature of 3-PG. Our use of the paired control and fertilized inventory plots allowed both the validation 3-PG for fertilized stands and the identification of a protocol to scale fertility among sites based on the response to fertilizer. We hope that our approach to using the response of production to heavy fertilization will be tested as a means to develop objective fertility ratings for other stands; this approach might be particularly useful for applications of 3-PG in a management context.

The simulated growth of between 10 and 42 Mg ha⁻¹ per year (average 26 Mg ha⁻¹ per year) for all plots and years was highly correlated ($r^2 = 0.78$, $n = 160$, $P < 0.0001$) with the observed values of between 2 and 51 Mg ha⁻¹ per year (average 25 Mg ha⁻¹ per year). These results indicate that species- and site-specific parameters that affect LAI must be adequately estimated. Further consideration of parameter values is required to improve the model's case-specific usefulness.

Overall, 3-PG required a reasonable level of localized calibration, and was able to predict yearly growth better than an empirical model. The superiority of 3-PG was especially evident in capturing the effects of inter-annual variations in precipitation and fertilizer addition in northeastern Brazil. We concluded that

3-PG is highly suitable as a management tool for *Eucalyptus* plantations, but this will require assessment of LAI as part of inventory surveys.

Acknowledgements

This research was supported by the National Science Council of Brazil (CNPq), the University of São Paulo, Piracicaba, the USDA Forest Service Rocky Mountain Station, and McIntire-Stennis appropriations to Colorado State University. We thank Reinoldo Poernbacher, Jose Augusto Ribeiro, Jacyr M. Alves and the people of Copener Florestal Ltd. for the use of their forests and the SETEC sector for all the fieldwork they contributed. Stape has a special thanks to his wife, Luceni, for support given to realize this work. Finally, we thank two anonymous reviewers for comments that helped improve our paper.

References

- Battaglia, M., Sands, P.J., 1997. Modelling site productivity of *Eucalyptus globulus* in response to climate and site factors. *Aust. J. Plant Physiol.* 24, 831–850.
- Battaglia, M., Sands, P.J., 1998. Process-based forest productivity models and their application in forest management. *For. Ecol. Manage.* 102, 13–32.
- Binkley, D., Ryan, M.G., 1998. Net primary production and nutrient cycling in replicated stands of *Eucalyptus saligna* and *Albizia facaltaria*. *For. Ecol. Manage.* 112, 79–85.
- Brown, A.G., Nambiar, E.K.S., Cossalter, C., 1997. Plantations for the tropics—their role, extent and nature. In: Nambiar, E.K.S., Brown, A. (Eds.), *Management of Soil, Water, and Nutrients in Tropical Plantation Forests*. ACIAR Monograph No. 43, Canberra, pp. 1–24.
- Burger, J.A., Kelting, D.L., 1998. Soil quality monitoring for assessing sustainable forest management. In: Bigham, J.M. (Ed.), *The Contribution of Soil Science to the Development of and Implementation of Criteria and Indicators of Sustainable Forest Management*. SSSA Special Publication No. 53, Madison, USA, pp. 17–52.
- Burkhart, H.E., 1997. Development of empirical growth and yield models. In: Amaro, A., Tome, M. (Eds.), *Empirical and Process-based Models for Forest Tree and Stand Growth Simulation*. Edicoes Salamandra, Oeiras, pp. 53–60.
- Campos, J.C.C., Campos, A.L.A.S., Leite, H.G., 1988. Decisao silvicultural empregando um sistema de predicao do crescimento e da producao. *Rev. Arvore* 12, 100–110.
- Clutter, J.L., Fortson, J.C., Piennar, L.V., Brister, R.G.H., Bailey, R.L., 1983. *Timber Management: A Quantitative Approach*. Wiley, New York, 333 pp.

- Coops, N.C., Waring, R.H., Landsberg, J.J., 1998. Assessing forest productivity in Australia and New Zealand using a physiological-based model driven with average monthly weather data and satellite-derived estimates of canopy photosynthetic capacity. *For. Ecol. Manage.* 104, 113–127.
- Cutini, A., Matteucci, G., Mugnozza, S., 1998. Estimation of leaf area index with the LI-COR LAI 2000 in deciduous forests. *For. Ecol. Manage.* 105, 55–65.
- Eldridge, K.G., Davidson, J., Harwood, C., van Wyk, G., 1994. *Eucalypt Domestication and Breeding*. Clarendon Press, Oxford, 288 pp.
- FAO, 1999. State of the world's forests. Food and Agriculture Organization of the United Nations, Rome, 146 pp.
- Fisher, R.F., Binkley, D., 2000. *Ecology and Management of Forest Soils*. Wiley, New York, 489 pp.
- Gale, M.R., Grigal, D.F., Harding, R.B., 1991. Soil productivity index: predictions of site quality for white spruce plantations. *Soil Sci. Soc. Am. J.* 55, 1701–1708.
- Giardina, C.P., Ryan, M.G., 2002. Total belowground carbon allocation in a fast growing *Eucalyptus* plantation estimated using a carbon approach. *Ecosystems* 5, 487–499.
- Goetz, S.J., 1997. Modeling carbon fluxes, net primary production, and light utilization in boreal forest stands. Ph.D. Dissertation. University of Maryland, USA.
- Gonçalves, J.L.M., Stape, J.L., Benedetti, V., 2000. Reflexos do cultivo mínimo e intensivo do solo em sua fertilidade e nutrição das árvores. In: Gonçalves, J.L.M., Benedetti, V. (Eds.), *Nutrição e Fertilização Florestal*. IPEF, Piracicaba, pp. 1–57.
- Hart, S.C., Binkley, D., 1985. Correlations among indices of forest soil nutrient availability in fertilized and unfertilized loblolly pine plantations. *Plant Soil* 85, 11–21.
- Hart, S.C., Binkley, D., Campbell, R.G., 1986. Predicting current growth and N + P fertilization growth response of loblolly pine stands in the Coastal Plain of North Carolina. *Soil Sci. Soc. Am. J.* 50, 230–233.
- Jarvis, P.G., Leverenz, J.W., 1983. Productivity of temperate, deciduous and evergreen forests. In: Lange, O.L., Nobel, P.S., Osmund, C.B., Ziegler, H. (Eds.), *Encyclopedia of Plant Physiology*, vol. 12D. *Physiological Plant Ecology*, vol. IV. Springer-Verlag, Berlin, pp. 233–280.
- Kimmins, J.P., 1997. *Forest Ecology—A Foundation for Sustainable Management*. Prentice-Hall, New Jersey, 596 pp.
- Landsberg, J.J., Gower, S.T., 1997. *Applications of Physiological Ecology to Forest Management*. Academic Press, San Diego, 354 pp.
- Landsberg, J.J., Johnson, K.H., Albaugh, T.J., Allen, H.L., McKeand, S.E., 2001. Applying 3-PG, a simple process-based model designed to produce practical results, to data from loblolly pine experiments. *For. Sci.* 47, 43–51.
- Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manage.* 95, 209–228.
- Law, B.E., Waring, R.H., Anthoni, P.M., Aber, J.D., 2000. Measurement of gross and net ecosystem productivity and water vapor exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Glob. Change Biol.* 6, 155–168.
- Lima, W.P., 1993. *Impacto ambiental do eucalipto*. Edusp, Sao Paulo, 301 pp.
- Loague, K., Green, R.E., 1991. Statistical and graphical methods for evaluating transport models: overview and application. *J. Contam. Hydrol.* 7, 51–73.
- Mäkelä, A., Landsberg, J.J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Ågren, G.I., Oliver, C.D., Puttonen, P., 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. *Tree Physiol.* 20, 289–298.
- McMurtrie, R.E., Benson, M.L., Linder, S., Running, S.W., Talsma, T., Crane, W.J.B., Myers, B.J., 1990. Water/nutrient interactions affecting the productivity of stands of *Pinus radiata*. *For. Ecol. Manage.* 30, 415–423.
- Medlyn, B.E., 1998. Physiological basis of the light use efficiency model. *Tree Physiol.* 18, 167–176.
- Mielke, M.S., Oliva, M.A., Barros, N.F., Penchel, R.M., Martinez, C.A., Almeida, A.C., 1999. Stomatal control of transpiration in the canopy of a clonal *Eucalyptus grandis* plantation. *Trees* 13, 152–160.
- Monteith, J.L., 1977. Climate and the efficiency of crop production in Britain. *Phil. Trans. R. Soc. London, Ser. B* 281, 277–294.
- Neilson, D., 2000. The global *Eucalyptus* resource and some solidwood-panel product development issues. In: Proceedings of the IUFRO Conference on the Future of Eucalypts for Wood Production, Launceston, Australia. http://oak.arch.utas.edu.au/test_area/iufro/program.htm.
- Parton, W.J., Woerner, P.L., Martin, A., 1994. Modelling soil organic matter dynamics and plant productivity in tropical ecosystems. In: Woerner, P.L., Swift, M.J. (Eds.), *The Biological Management of Tropical Soil Fertility*. Wiley/Sayce Publication, New York, pp. 171–188.
- Reed, D.D., 1997. Evaluating empirical and process-based forest growth models. In: Amaro, A., Tome, M. (Eds.), *Empirical and Process-based Models for Forest Tree and Stand Growth Simulation*. Edicoes Salamandra, Oeiras, pp. 499–505.
- Running, S.W., Gower, S.T., 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiol.* 9, 147–160.
- Ryan, M.G., 1991. A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. *Tree Physiol.* 9, 255–266.
- Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: pattern and process. *Adv. Ecol. Res.* 27, 213–262.
- Sands, P.J., 1996. Modelling canopy production. III. Canopy light-utilisation efficiency and its sensitivity to physiological and environmental variables. *Aust. J. Plant. Physiol.* 23, 103–114.
- Sands, P.J., 2001. 3PGpjs—a user-friendly interface to 3-PG, the Landsberg and Waring model of forest productivity. Technical Report No. 29. CRC for Sustainable Production Forestry and CSIRO Forestry and Forest Products, Hobart, Australia, 22 pp.
- Sands, P.J., Landsberg, J.J., 2002. Parameterisation of 3-PG for plantation grown *Eucalyptus globulus*. *For. Ecol. Manage.* 163, 273–292.
- Scolforo, J.R.S., 2002. *Biometria florestal: manejo florestal avançado*. UFLA, Lavras, 322 pp.

- Scolforo, J.R.S., Machado, S.A., 1988. Curvas de índice de sitio para plantações de *Pinus taeda* nos Estados do Paraná e Santa Catarina. *Floresta* 18 (1–2), 159–173.
- Seixas, F., Stokes, B.J., Rummer, B., McDonald, T.P., 1995. Harvesting soil impacts for selected silvicultural prescriptions. In: Proceedings of the Post-congress of the IUFRO P3.07 Meeting, vol. 20. World Congress of the IUFRO, Tampere, 1995, pp. 230–238.
- Simoes, J.W., Leite, N.B., Brandi, G., 1981. Formação, manejo e exploração de florestas com espécies de rápido crescimento. IBDF, Brasília, 131 pp.
- Soares, C.P.B., Leite, H.G., 2000. Predição da produção de madeira de eucalipto em região com alta variabilidade pluviométrica. *Sci. For.* 58, 41–48.
- Soares, J.V., Almeida, A.C., Penchel, R.M., 1997. Balanço hídrico de plantações de eucalipto a partir da estimativa de transpiração pelo método de Penman–Monteith. In: Proceedings of the IUFRO Conference on Silviculture and Improvement of Eucalypts. EMBRAPA/CNPQ, Salvador, 1997.
- Stape, J.L., 2002. Production ecology of clonal *Eucalyptus* plantations in northeastern Brazil. Ph.D. Dissertation. Colorado State University, Ft. Collins, 225 pp. <http://www.cnr.colostate.edu/~dan/papers/stape.pdf>.
- Stape, J.L., Gomes, A.N., Assis, T.F., 1997. Estimativa da produtividade de povoamentos monoclonais de *Eucalyptus grandis* × *urophylla* no Nordeste do Estado da Bahia-Brasil em função das variabilidades pluviométrica e edáfica. In: Proceedings of the IUFRO Conference on Silviculture and Improvement of Eucalypts. EMBRAPA/CNPQ, Salvador, 1997, pp. 192–198.
- Stape, J.L., Gonçalves, J.L.M., Gonçalves, A.N., 2001. Relationships between nursery practices and field performance for *Eucalyptus* plantations in Brazil: a historical overview and its increasing importance. *New For.* 22, 19–41.
- Sullivan, A.D., Clutter, J.L., 1972. A simultaneous growth and yield model for loblolly pine. *For. Sci.* 18, 76–86.
- van Raij, B., Quaggio, J.A., Cantarella, H., Ferrerira, M., Lopes, A.S., Bataglia, O., 1987. Análise química do solo para fins de fertilidade. IAC FCAVJ/CARGILL, 170 pp.
- Waring, R.H., McDowell, N., 2002. Use of a physiological process model with forestry yield tables to set limits on annual carbon balances. *Tree Physiol.* 22, 179–188.