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Climatic and nutritional controls on the growth of Eucalyptus grandis in South Africa

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Scientific Paper

Application of the 3-PG model to a *Eucalyptus grandis* stand subjected to varying levels of water and nutritional constraints in KwaZulu-Natal, South Africa

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SYNOPSIS

The 3-PG model has shown considerable potential as a tool for predicting forest productivity. As part of a model validation exercise, 3-PG was applied to an irrigated and fertilised *Eucalyptus grandis* stand in the KwaZulu-Natal Midlands. Simulations were run over a two-year period using appropriate initialisation data and a parameter set developed for *E. grandis* for the summer rainfall region of South Africa. The model was validated using observed leaf area index, and foliage and above-ground woody biomass, and then used to predict stand volume. Evaluation of 3-PG model outputs against field measurements indicated a generally good correlation for growth data across the control, irrigated, fertilised, and irrigated and fertilised trees. At 3.9 years, the model-predicted leaf area index over all treatments ranged from 3.8 to 5.1, similar to the observed range of 4.3 to 4.9. Stand volume at 3.9 years of age was under-predicted in the non-irrigated treatments. Actual stand volume at this age ranged from 100 to 118 m^3 ha^{-1} across all treatments, compared to model estimates of 79 to 121 m^3 ha^{-1}. Use of a dynamic fertility rating may improve model predictions and there is possible scope for improvement in the water-balance component of the model. Results from this study have shown 3-PG to be a robust model by producing accurate predictions of growth under varying levels of resource availability.

Keywords: Process-based modelling, irrigation, fertilisation, model validation, *E. grandis*

INTRODUCTION

In South Africa, estimates of growth and yield are determined using statistically-derived, empirically-based stand-level models. Such models predict plantation growth and yield as a function of stand age, site index and stand density (Kassier and Kotze, 2000). Empirical growth models provide accurate predictions of yield when applied to the conditions for which they were originally developed (Kassier and Kotze, 2000; Landsberg, 2003a). However, these models cannot simulate the results of changing environmental or management conditions (Battaglia and Sands, 1997, 1998), or predict the effects of silvicultural options such as fertilisation and irrigation (Bergh *et al.*, 1999).

In contrast to empirical models, process-based models are more flexible and can be used with greater confidence to extrapolate experimental results and investigate consequences of conditions outside the range of those experienced in the original experimentation, once adequate testing has been conducted (Landsberg, 1986). Process-based, or mechanistic models simulate stand growth in terms of the underlying physiological processes or mechanisms that govern growth, and the way stands are affected by the physical conditions to which trees are subject to, and with which they interact (Landsberg and Gower, 1997; Landsberg *et al.*, 2001). Process-based models were originally developed for research purposes, but other applications include (1) prediction of growth and yield from existing plantations, (2) site-species matching, (3) exploration of the effects of different silvicultural practices on the utilisation of site resources, (4) assessment of risks associated with plantation locations or management decisions, (5) evaluation of the effects of events such as fertilisation and thinning, (6) improved understanding of production constraints and growth potential of a site, and (7) questions for which 'real time' experiments are not feasible, such as long-term impacts of practices on sustainability (McMurtrie *et al.*, 1990; Battaglia and Sands, 1998; Landsberg, 2003a). However, few process-based productivity models are adopted for forest management systems as they are complex, poorly validated, and the details of many fundamental processes, such as carbon allocation, remain uncertain (Battaglia and Sands, 1998). In addition, these models

require large amounts of input data, and parameter values are not readily available or economically obtainable (Landsberg *et al.*, 2001; Landsberg, 2003a). More generalised and simplified process models, such as 3-PG, have been developed specifically to bridge the gap between conventional, empirical, mensuration-based growth and yield models, and process-based carbon balance models (Johnsen *et al.*, 2001; Sands and Landsberg, 2002; Landsberg, 2003a, b).

The 3-PG (Physiological Principles Predicting Growth; Landsberg and Waring, 1997) model can realistically simulate growth and water use over a wide range of rotation age and growth conditions (Dye *et al.*, 2004), and has been identified as an ideal tool to determine site constraints on growth and potential productivity over a range of sites (Esprey and Sands, 2004). This model has yielded credible predictions for a wide range of species across several countries, e.g. Australia and New Zealand (Landsberg and Waring, 1997; Coops *et al.*, 1998; Sands and Landsberg, 2002), Brazil (Almeida *et al.*, 2004a; Stape *et al.*, 2004), Chile (Rodríguez *et al.*, 2002), USA (Coops and Waring, 2001; Landsberg *et al.*, 2001), South Africa (Gush, 1999; Dye, 2001; Esprey and Smith, 2002; Dye *et al.*, 2004), and Sweden (Landsberg *et al.*, 2003). In addition to 3-PG's widespread application, this model was selected as the most appropriate for use as it was developed with the end user in mind, is robust with a simple and transparent structure, is extensively documented (see Sands, 2004), data inputs are readily obtained, outputs are of interest to the forest manager, and the model and source-code are freely available.

Model validation is important to test the performance of the model in predicting growth and productivity. Many tests against good measurements of stem growth rates, leaf area index, stand biomass, average stem diameter and sap flow data should be conducted as a means of validating model outputs (Landsberg and Waring, 1997; Sands and Landsberg, 2002; Landsberg *et al.*, 2003). Various aspects of the 3-PG model have been tested, e.g. stem diameter and volume growth (Landsberg *et al.*, 2001; Rodríguez *et al.*, 2002; Almeida *et al.*, 2004a; Stape *et al.*, 2004), leaf area index and above- and below-ground biomass (Landsberg *et al.*, 2003), stem number and available soil water (Coops and Waring, 2001; Dye, 2001), and sap flow rates (Dye *et al.*, 2004).

The principal objective of this study was to validate the 3-PG model using the parameter set developed by Esprey and Sands (2004), by applying the model to biomass data collected from an irrigation and fertilisation trial. This trial was originally initiated in an *E. grandis* stand in the KwaZulu-Natal Midlands, South Africa, to determine the influence of soil water and nutrient availability on the growth of this species under these particular climatic conditions. The 3-PG model was validated by testing both the primary outputs of the model, i.e. leaf area index and above-ground biomass partitioning, and those outputs of relevance to forestry management, such as stand volume. This study builds on the earlier work conducted by Gush (1999), Dye (2001), Esprey and Smith (2002) and Dye *et al.* (2004), who demonstrated the potential use of 3-PG as a tool for modelling South African forest productivity. The novel contribution from this trial is the application of 3-PG to trees subjected to irrigation and fertilisation treatments, which could aid in scenario analysis and planning, and the development of fertiliser recommendations.

MATERIALS AND METHODS

Site Description and Experimental Design

Eucalyptus grandis Hill ex Maiden seedlings were planted in March 1999 at a 2.0 x 3.0 m spacing at a site near New Hanover in KwaZulu-Natal (Lat. 29° 14' S, long. 30° 33' E, alt. 1113 m a.s.l.), which was previously vegetated by *Eragrostis curvula* pasture. The site has a mean annual precipitation of 919 mm, with rainfall occurring predominantly during the summer months between November and March. The mean annual temperature is 16.6 °C. The soil is derived from shale parent material and belongs to the Kranskop/Magwa

TABLE 1. Physical and chemical properties of the surface soil (0.0 – 0.4 m) prior to treatment initiation.

Particle size distribution[a]	38% clay 48% silt 14% sand
$pH_{(KCl)}$[b]	4.0
Available P[c]	22.0 mg kg^{-1}
Organic carbon[d]	4.69%
Total N[e]	0.36%

[a] Pipette method
[b] 1:2.5 suspension of soil in extractant
[c] Bray-2
[d] Walkley-Black
[e] Kjeldahl digestion
[a] Handbook of Standard Soil Testing Methods for Advisory Purposes (1990)
[b-e] Heffernan (1985); Kalra and Maynard (1991); Nicholson (1984)

soil form (Soil Classification Working Group, 1991). This highly weathered acid mineral soil has a silty clay loam texture and contained a high available phosphorus (P) concentration of 22 mg kg^{-1} and relatively high values of organic carbon (4.69%) and total nitrogen (N) (0.36%) prior to treatment implementation (**Table 1**).

The 6.5 ha plantation area comprised 16 plots, each measuring 54 x 75 m, with 675 trees in a replicate plot. The trial design consisted of a control, irrigation, fertilisation, and irrigation and fertilisation combined (C, I, F and IF, respectively), initially with four replicates per treatment, arranged in four blocks. Due to equipment constraints, the trial was laid out as a split-plot, complete block design, with irrigation as the whole plot and fertilisation as the subplot factor. The fertilisation treatment was systematically alternated within the whole plots in each of the four blocks. Many trees were badly damaged by the effects of two very severe windstorms during October and November 2001. After conducting a complete site inventory in February 2002, it was decided to eliminate one replicate of each treatment due to the extent of the damage in these plots. As such, all observed data presented are the average of three replicates per treatment. Measurements were initially conducted on 30 centrally-located trees; the number of measured trees was increased to 80 trees per plot to account for the variability following the windstorms. At the final measurement (age 3.9 years), the stocking in the C, I, F and IF treatments was 1250, 1181, 1261 and 1194 stems per hectare, respectively.

The imposed treatments aimed to eliminate both water (I and IF), and nutritional (F and IF) constraints. Water was applied on a weekly basis using drip irrigation and was aimed at replacing amounts lost through evapotranspiration, calculated using the Penman-Monteith equation (R. Mottram, personal communication, 2004). Nutrients were applied to the fertilised treatments according to the results of routine foliar analyses. Fertiliser application was aimed at maintaining foliar elements at specified target levels: N concentration at 23 mg g^{-1}, and the proportional percentage of elements relative to N at values of 7.5 (P), 33.0 (potassium, K), 2.5 (calcium, Ca), 4 (magnesium, Mg), 0.05 (manganese, Mn), 0.2 (iron, Fe), 0.05 (zinc, Zn), 0.02 (copper, Cu), and 0.05 (boron, B), based on the recommendations of Schönau and

TABLE 2. Quantities of nutrients applied to fertilised (F and IF) E. grandis *trees over the first four years of growth.*

Date	Nutrient application (kg ha^{-1}), and sources of fertiliser applied			
	N	P	K	B
	LAN[1]	Single superphosphate[2]	KCl[3]	Solubor[4]
01/07/1999	17	0	0	0
05/04/2000	50	0	0	0
08/08/2000	10	30	30	2
29/05/2001	29	11	25	2
24/01/2002	0	22	22	0
21/10/2002	0	50	0	0
Total	**106**	**113**	**77**	**4**

[1] Limestone ammonium nitrate, 28% N
[2] 10.5% P
[3] Potassium chloride, 50% K
[4] A highly soluble B fertiliser derived from sodium borates, 16.5% B

TABLE 3. Monthly water amounts (mm) received by E. grandis *trees from rainfall and irrigation over the period March 1999 to December 2002. Irrigation data were recorded from July 1999 onwards. Irrigation was terminated at the end of October 2002.*

	Jan	Feb	March	April	May	June	July	Aug	Sep	Oct	Nov	Dec	Total
1999													
Rain			90	11	6	0	2	28	15	89	34	109	**383**
Irrig.							15	66	66	63	36	12	**258**
2000													
Rain	88	79	103	50	87	4	0	0	67	67	126	172	**841**
Irrig.	36	63	48	34	24	10	23	24	17	15	0	0	**294**
2001													
Rain	75	78	47	149	13	0	0	0	78	163	117	105	**825**
Irrig.	3	3	14	19	24	42	54	15	0	38	5	0	**216**
2002													
Rain	121	66	56	49	6	12	127	81	40	32	60	61	**710**
Irrig.	25	6	15	23	22	0	0	20	48	24	0	0	**181**

Herbert (1983) and Linder (1995). The quantities of nutrients applied to the fertilised trees are presented in **Table 2**. Monthly rainfall and irrigation totals received by *E. grandis* are shown in **Table 3**.

Measurements and Sampling

Stem diameter at breast height (DBH) and tree height data were collected on a routine basis, approximately four times per year, and used to calculate stem volume to 5 cm underbark diameter, using the Schumacher-Hall equation as described in Coetzee (1992). Estimates of above-ground biomass and partitioning were obtained from destructive harvests carried out when the trees were aged 1.9, 2.8 and 3.9 years. Sample trees (n = 4, 4, and 6 trees per treatment for each of the three destructive harvests, respectively) were selected to represent the range in DBH at the time of harvesting. The representative trees were felled at ground level and separated into stem, foliage, and total branches (live and dead). Each stem was measured for total length (height) and sample disc sections were cut at 1 m intervals to determine the ratios of stemwood and stembark. The fresh mass of all material was measured in the field by weighing both the total mass and a representative sub-sample, which was returned to the laboratory for dry mass determination at 70°C. The fresh:dry mass ratios were used to estimate total dry mass of the various components. The leaf areas of foliar sub-samples were determined by scanning using a LI-3100 Area Meter (LI-COR Inc., Lincoln, Nebraska, USA). These leaf area measurements were used for the calculation of specific leaf area (*SLA*; leaf area per unit dry leaf mass) and hence leaf area index (*L*; leaf area per unit ground surface area). Allometric relationships of the form $y = ax^b$, where y = mass and x = DBH, were developed to derive biomass estimates of above-ground components for each treatment.

Routine foliar analysis was conducted on approximately 30 of the most recent, fully-developed intact leaves collected from the outer branch position of the upper third of the canopy of six trees per plot. Foliar samples were processed for nutrient concentration using methods outlined by Nicholson (1984), Heffernan (1985) and Kalra and Maynard (1991). Foliar material was analysed for total N by Kjeldahl digestion and titration. After dry ashing, P concentration was determined spectrophotometrically using the molybdenum blue method and segmented flow auto-analyser. Foliar samples were also analysed for K (flame emission spectroscopy), Ca, Mg, Mn, Cu, Fe, Zn (atomic absorption spectroscopy), and B (segmented flow autoanalyser).

The 3-PG Model

3-PG is a stand-level model of forest growth (i.e. it is not site- or species-specific, but needs to be parameterised for individual species) (Sands and Landsberg, 2002; Landsberg, 2003b). Since the initial publication of 3-PG (Landsberg and Waring, 1997), several structural modifications have been made to the model, and the manner in which various relationships between parameters are depicted has been changed to make the parameters more intuitively meaningful; these are summarised in Sands and Landsberg (2002). The most recent changes to the model are presented by Sands (2004).

The structure of the 3-PG model is comprehensively described in the literature (Landsberg and Waring, 1997; Sands and Landsberg, 2002; Landsberg *et al.*, 2003) and only a brief summary will be provided here. The 3-PG model is based on the fraction of photosynthetically active radiation absorbed by the forest canopy, and consists essentially of two sets of calculations; biomass production, and the subsequent allocation of biomass between the component parts of the tree. 3-PG also contains submodels relating to the calculation of soil water balance, evapotranspiration and tree mortality.

In the 3-PG model, the conversion of absorbed photosynthetically active radiation to gross primary production (GPP) is based on a theoretical maximum canopy quantum efficiency constrained by various environmental modifiers (atmospheric vapour pressure deficit (*D*), available soil water, temperature, frost, site nutrition and stand age; Sands and Landsberg, 2002). These modifiers are applied multiplicatively, with the most limiting of the atmospheric *D* and soil water factors being used, i.e. if soil water is more limiting than *D*, growth is assumed to be constrained by soil water during that period (Landsberg *et al.*, 2001; Sands and Landsberg, 2002). Net primary production (NPP) in 3-PG is calculated as a constant fraction of GPP (see Waring *et al.*, 1998), which is then allocated to roots, stems and foliage (Landsberg *et al.*, 2001). The proportion of NPP allocated to roots increases if nutritional status and/or available soil water are low, and allocation to stems and foliage growth are reduced such that the allometric balance of the trees is conserved (Landsberg and Waring, 1997; Landsberg *et al.*, 2001).

Mandatory inputs required by 3-PG are monthly weather data (average values of daily solar radiation and temperature, atmospheric *D*, total rainfall and the number of frost days per month), site-specific factors, initial stand conditions and species-specific parameter values. The model can be run for any number of years, using actual monthly weather data or long-term monthly averages. Using historical long-term averages is the normal procedure unless there is particular interest in specific events, such as droughts (Landsberg *et al.*, 2001). Site-specific factors in 3-PG which describe the physical properties of the site include latitude, a site fertility rating (*FR*), maximum available soil water and a general descriptor of soil texture. The fertility rating accounts for the nutrition of the site, and varies between 'poor' (*FR* = 0) and 'optimal' (*FR* = 1) nutrient status. The effects of nutrition enter the 3-PG model through influences on

canopy quantum efficiency and biomass allocation and therefore fertility is a potentially important input variable. Despite many years of worldwide research efforts on this subject, our ability to predict soil nutrient status in terms usable in quantitative models of plant growth is extremely limited (Landsberg *et al.*, 2001). Ingestad (1982, 1991) addressed the dynamic nature of the underlying relationships between nutrition and growth, which vary with climatic conditions (Negi and Sharma, 1996), soil processes which regulate nutrient quantities in soil solution, the amount and distribution of fine roots and mycorrhizae (Landsberg and Gower, 1997), the efficiency with which nutrients are absorbed from the soil, the total nutrient demand of the stand, and the growth rate of the trees (Gonçalves *et al.*, 1997). Plant analyses can be used as an indirect measure of the fertility status of soils and the efficiency of fertilisation events (Melsted *et al.*, 1969). In 3-PG, *FR* values are usually allocated on the basis of local knowledge about soil fertility (Landsberg, 2003a).

The stand initialisation data in 3-PG include the year and month of planting, the initial stand age and the age at the end of the rotation, the foliage, root and stem biomass, soil water holding capacity in the root zone, and initial stem number appropriate to the stand at the starting age. The species-specific parameter values pertain to allometric relationships, canopy structure and processes, wood and stand properties, stem mortality, litterfall and root turnover, and the various environmental modifiers.

The 3-PG model can be initialised for any stand age, although the normal procedure is to start simulations from the second year of growth (Landsberg *et al.*, 2003). In 3-PG, the state of the stand is updated at each monthly time step. The primary output variables from the model include monthly or annual values of NPP, foliage, root and stem biomass, stem number, available soil water and stand transpiration, and of value to forest managers – DBH, *L*, stand volume and mean annual increment (Sands and Landsberg, 2002). Given the appropriate geometrical relationships, 3-PG can also provide estimates of stand height (Landsberg *et al.*, 2003), although this component of the model still needs to be tested.

Model inputs

Weather data

Long-term monthly mean solar radiation data were obtained from the 1´ x 1´ latitude by longitude digital database developed by Schulze (1997). Actual monthly temperature data were collected from an automatic weather station situated at a nearby research site in the Seven Oaks district (Lat. 29° 11' S, long. 30° 40' E, alt. 1110 m a.s.l.). The distance of this station from the trial site is 12.5 km and the altitude difference is 3.0 m. A Campbell Model 207 temperature and relative humidity sensor (Campbell Scientific, Inc., 815W. 1800 N., Logan, UT 84321-1784, USA) was used to record temperature, and a Campbell 21X data logger was programmed to log the data at 20 minute intervals, which were averaged over a 12 hour period each day. The 3-PG model calculates mean air temperature and *D* from mean minimum and maximum air temperatures. Real-time monthly rainfall data were extracted from a raster database (Lynch, 2003) by selecting a rainfall station at a similar altitude and with a long continuous data record that was located closest to the site. The altitude of the selected rainfall station is 1084 m a.s.l., and the distance from the trial site is 4.9 km. Irrigation amounts were added to the rainfall in the I and IF treatments.

Initialisation data

The 3-PG model predicts growth from the time of stand establishment, but the accuracy for young trees prior to canopy closure may be significantly in error (Landsberg and Waring, 1997; Landsberg, 2003a). Therefore, 3-PG was initialised at age two, and model runs were conducted for a two-year period. The mean maximum available soil water content was determined on a per treatment basis as 151 mm (C), 128 mm (I), 112 mm (F) and 84 mm (IF), calculated as the product of soil depth and texture-derived available water capacity (Smith *et al.*, 2004; **Table 4**).

Fertility rating values of 0.6, 0.7, 0.8 and 0.9 were specified for the C, I, F and IF treatments, respectively. In this study, soil chemical characteristics at the start of the experiment were used in conjunction with foliar nutrient analyses to assign *FR* values. Prior to treatment implementation, the surface soil contained high concentrations of available P, organic carbon and total N (**Table 1**). The relative fertility of the site was the justification for setting the *FR* value of the C treatment at 0.6. Over the simulation period from two to four years of age, the foliar P:N and K:N ratios of the F and IF treatments closely approximated the target values only in February 2002 (aged 3.1 years). These P:N ratios were 7.2 (F) and 7.6 (IF), with associated K:N values of 32.7 and 33.4. A comparison across all treatments over the remainder of the

TABLE 4. Total soil depth and available soil water content of the control (C), irrigated (I), fertilised (F) and irrigated and fertilised (IF) treatments.

	C	I	F	IF
Total soil depth (mm)	950	783	683	500
Available water capacity (mm m^{-1})	160	160	160	160
Total available water (mm)	151	128	112	84

simulation indicated that P and K were potentially limiting to growth when compared with the optimum ratios of 7.5 and 33.0 for P:N and K:N, respectively. The foliar N concentration in all treatments closely approximated or was higher than the recommended value for optimal growth (23.0 mg g^{-1}). The concentrations of Ca, Mg, Mn, Fe, Zn, Cu and B relative to N exceeded the target values in all treatments and it was concluded that these elements were not limiting (data not shown). Due to the possible limitation of P and K at the site, the *FR* value of the F treatment was set at 0.8, in contrast to a value of 1.0, which would indicate optimal nutrient status. Soil nutrient availability and uptake by trees are strongly influenced by the soil moisture status (Gonçalves *et al.*, 1997), with reduced uptake under dry soil conditions (Landsberg and McMurtrie, 1985). Many studies have shown increased nutrient accumulation as a result of irrigation (Axelsson and Axelsson, 1986; Madeira and Pereira, 1990/91; Pereira *et al.*, 1994; Hunter, 2001). For this reason, the *FR* of the I and IF treatments was set at a 0.1 unit higher than their respective non-irrigated counter-parts. Fertilisation can be incorporated as a silvicultural event in 3-PG, i.e. temporal changes in *FR* can be specified. Due to our limited understanding of the complex interactions between factors and processes governing nutrient availability and uptake at this site, we used a static *FR* input into the model.

Using observed data, initial foliage and stem biomass values were assigned, with root biomass estimated as approximately 25% of total tree biomass (Shepherd, 1985). These data are presented in **Table 5**.

Parameter values used in the model simulations are listed in Esprey and Sands (2004). Based on measurements at the site, *SLA* at the initial stand age was reduced from 13 to 11. Parameters used in the calculation of mortality were adjusted to account for the reduction in stem number following the two wind storms. All other parameters remained unchanged. Model runs were made with $3PG_{PJS}$, a user-friendly interface to 3-PG, developed as Visual Basic macros using Excel spreadsheets (Sands, 2004).

Model Performance

3-PG model-performance can be evaluated through assessing the correlation between observed and simulated values (R^2) (Esprey and Smith, 2002; Landsberg *et al.*, 2003; Almeida *et al.*, 2004b; Stape *et al.*, 2004). In this trial, however, it is unlikely that the small number of data points (n = 4) at any one sampling period would generate a realistic estimate of the correlation between observed and simulated values. Therefore, model predictions of above-ground biomass and *L* were assessed in terms of percent bias, calculated as ((observed – simulated) / simulated)*100, with negative values indicating model over-prediction.

RESULTS AND DISCUSSION

Using the appropriate weather and initialisation data, site factors, and parameter values as inputs into 3-PG, simulations were carried out for a two-year period and outputs compared against observed above-ground biomass and *L* values (**Figure 1**).

The 3-PG model accurately predicted foliage (W_F) and above-ground woody (W_S) biomass, and *L* across all treatments at 2.8 and 3.9 years. The correspondence between observed and simulated values in the irrigated (I and IF) trees was excellent, particularly at 3.9 years. Above-ground woody biomass was consistently under-predicted in the non-irrigated (C and F) treatments. The highest bias values were calculated for W_S in the C and F treatments at both time periods (**Table 6**). In general, the model predictions for these non-irrigated trees were poorer than for irrigated trees. The 3-PG model produced under-predicted values for all variables at both time periods in the F treatment, indicated by the positive bias.

Leaf area index determines radiation interception, which drives carbon assimilation and stand growth, as well as transpiration rates (Landsberg *et al.*, 2001). It is therefore essential to ensure that maximum *L* produced by a stand, and the time course of this variable are consistent with observations (Landsberg *et al.*, 2001). Unfortunately, only two data points for each treatment could be used to compare observed and simulated *L* values, but the close agreement between these increases our confidence that the 3-PG model predictions of growth and biomass data are correct for the right reasons.

Encouraged by the close correspondence between observed and simulated above-ground biomass and *L* values, we used the 3-PG model to predict stand volume (**Figure 2**).

TABLE 5. Biomass values of E. grandis *entered as input data into the 3-PG model. C = control, I = irrigated, F = fertilised and IF = irrigated and fertilised; W_F, W_R, and W_S refer to the foliage, root and above-ground woody biomass (stem wood plus bark and branches), respectively. W_R was estimated as approximately 25% of total tree biomass (Shepherd, 1985).*

Treatment	W_F (t ha^{-1})	W_R (t ha^{-1})	W_S (t ha^{-1})
C	3.0	4.7	11.1
I	3.4	5.9	14.4
F	3.7	6.1	14.7
IF	4.3	7.9	19.4

In general, there is good agreement between observed and simulated stand volume growth across all treatments. The 3-PG model tends to under-predict stand volume in the non-irrigated treatments at the end of the second simulation year. At this age (3.9 years), simulated stand volume in the C and F trees was 78.9 and 89.6 m^3 ha^{-1}, respectively, compared to observed values of 100.0 and 106.5 m^3 ha^{-1}. In the I treatment, stand volume was slightly under-estimated (105.5 and 113.8 m^3 ha^{-1} for predicted and observed data, respectively), but in the IF treatment, the predicted value (120.8 m^3 ha^{-1}) very closely approximated observed stand volume (118.0 m^3 ha^{-1}).

There are three plausible explanations as to why the 3-PG model under-predicted stand volume in the non-irrigated treatments at age 3.9 years. Firstly, it is

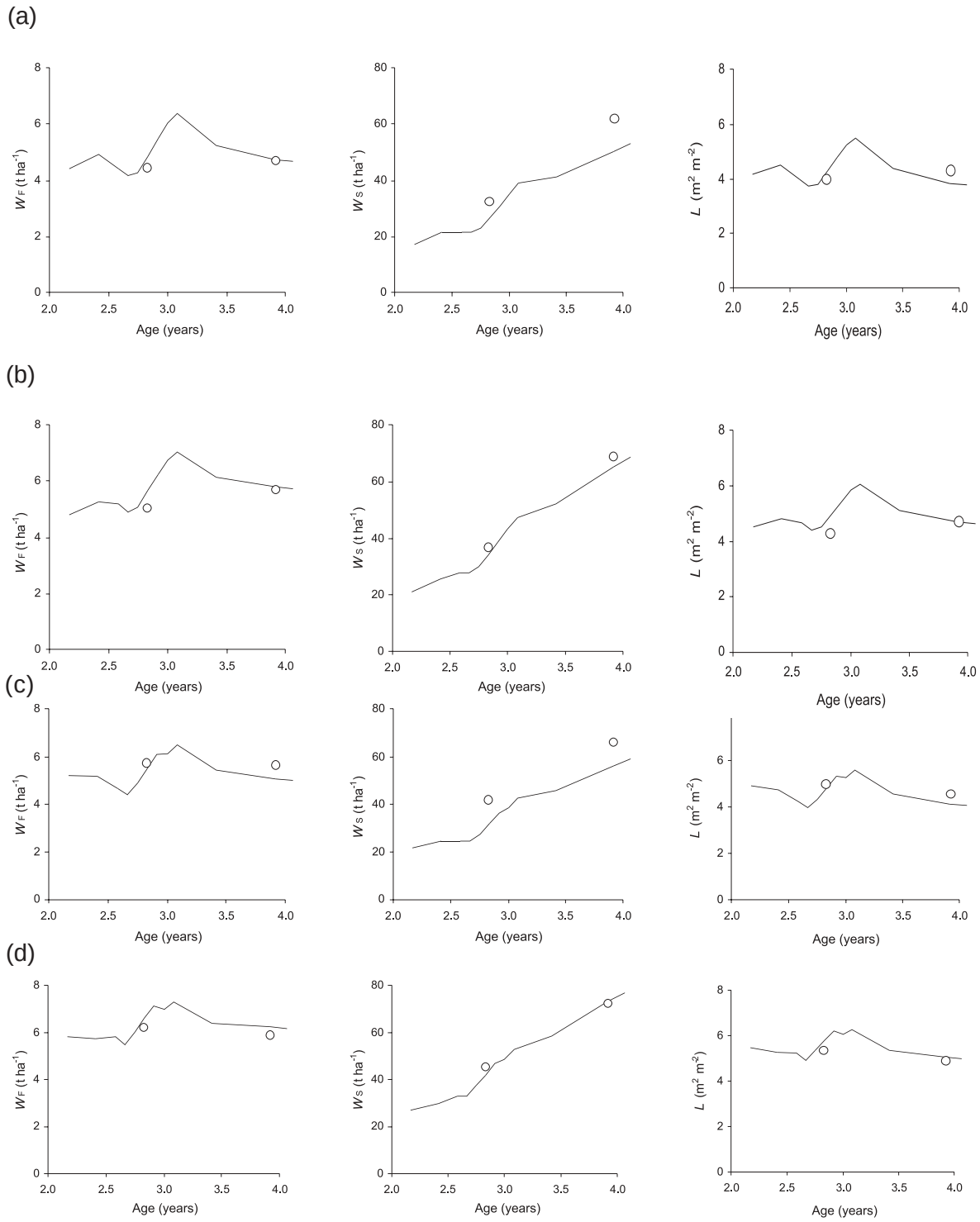


FIGURE 1. Time series of observed (o) and 3-PG model-simulated (—) foliage (W_F) and above-ground woody (stem wood plus bark and branches) (W_S) biomass, and leaf area index (L) in (a) control, (b) irrigated, (c) fertilised and (d) irrigated and fertilised E. grandis *trees.*

TABLE 6. Percentage bias of model predictions for E. grandis *trees subjected to various treatments. C = control, I = irrigated, F = fertilised and IF = irrigated and fertilised; W_F and W_S refer to the foliage and above-ground woody (stem wood plus bark and branches) biomass, respectively. L represents the leaf area index.*

Output variable	2.8 years	3.9 years
	C	
W_F	-8.4	-0.6
W_S	21.8	23.7
L	-7.3	12.3
	I	
W_F	-11.1	-1.6
W_S	8.0	6.1
L	-14.1	0.4
	F	
W_F	4.3	11.1
W_S	31.1	17.5
L	2.9	10.8
	IF	
W_F	-5.8	-5.4
W_S	8.1	-1.2
L	-8.1	-2.9

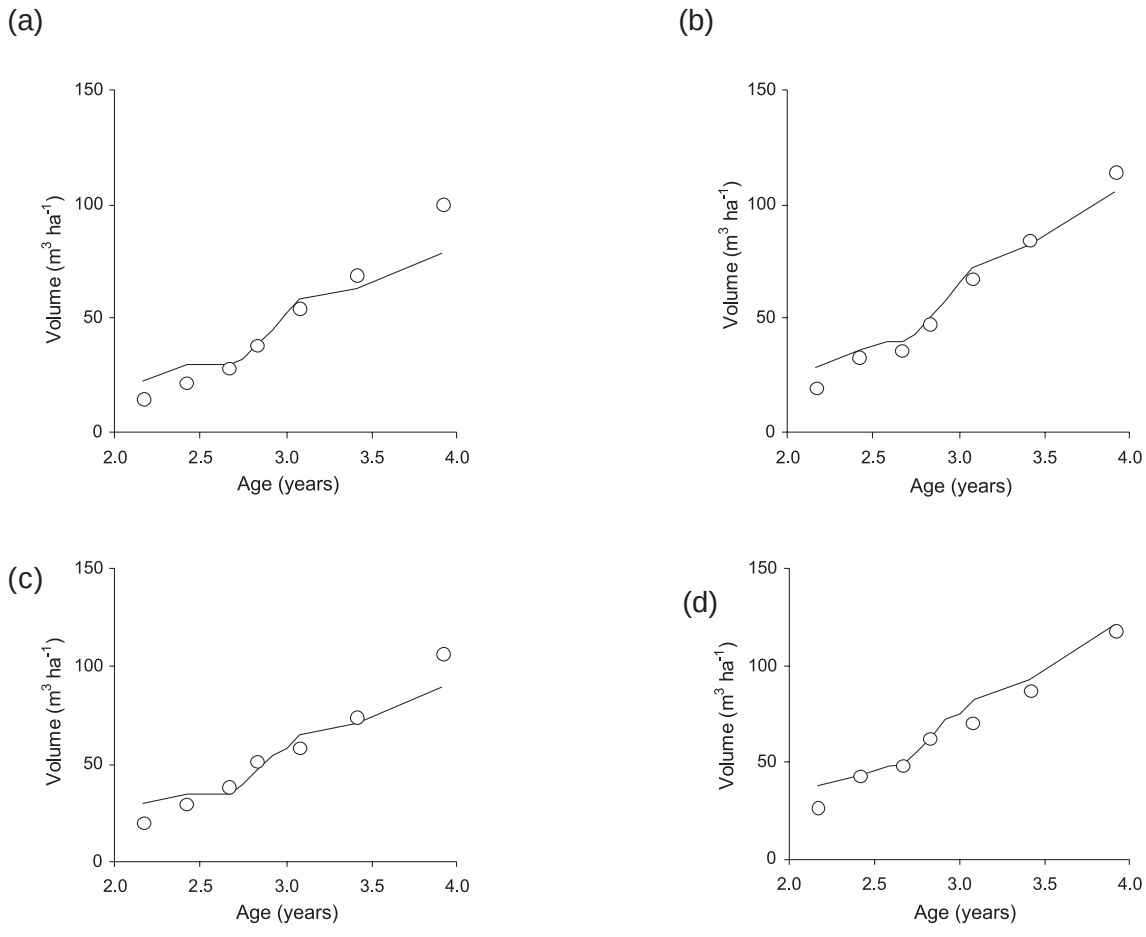


FIGURE 2. Time series of observed (o) and 3-PG model-simulated (—) stand volume in (a) control, (b) irrigated, (c) fertilised and (d) irrigated and fertilised E. grandis *trees.*

possible that the C and F trees had access to more water than was estimated. A simulation conducted under the assumption of additional water (approximately 50% of that received by irrigated trees) increased growth to provide a closer approximation to measured values. These predicted stand volumes were 89.8 and 100.6 m^3 ha^{-1} in the C and F treatments, respectively. In a review provided by Knight (1999), it emerged that *Eucalyptus* trees have dimorphic root systems, consisting of wide-spreading lateral roots just below the soil surface, with deep tap roots in young trees and deep vertical sinker roots in mature trees. During dry periods, deep-rooted eucalypts are able to maintain transpiration at rates which enable the trees to function, by accessing water stored in the soil profile (Knight, 1999). The failure of four-year-old *E. grandis* trees to respond to an imposed soil water deficit in Mpumalanga was attributed to their ability to abstract soil water to a depth of at least 8 m (Dye, 1996; Dye *et al.*, 1997). Alternatively, trees could access water by means of a vertical water flux: Dye *et al.* (1997) suggested the possibility of an upward movement of water during dry weather, which could supplement soil water availability within the rooting zone. This type of water movement was quantified by Soares and Almeida (2001) to approximate 1 mm day^{-1} at a site in Brazil. This upward flux from the water table into the root zone helped prevent complete stomatal closure and maintained *E. grandis* functioning at approximately 30% of its potential at the end of a long dry season (Soares and Almeida, 2001). If these types of processes occur in our trial, it is unlikely that they will operate to the same extent as the studies mentioned here, due to the lower porosity of the saprolite at this site.

Secondly, the stand volume may have been under-estimated in the non-irrigated treatments if the workings of the soil water module of the model are problematic. Dye *et al.* (2004) checked 3-PG-simulated transpiration rates with observed sap flow data collected from stands of *E. grandis* x *camaldulensis* in the Zululand region. These authors observed a good correspondence between the highest simulated transpiration rates and the measured median daily sap flow rates. However, almost all of the minimum simulated transpiration data points were lower than the observed lowest sap flow rates; Dye *et al.* (2004) attributed this discrepancy to the simple manner in which 3-PG calculates soil water availability. The soil water balance component in 3-PG is a simple, single-layer model obtained as the difference between monthly precipitation and monthly evapotranspiration, calculated using the Penman-Monteith equation (Landsberg and Waring, 1997). The use of a monthly water balance in 3-PG assumes that rainfall is evenly distributed over the month, which obviously does not occur, so that soil depletion and recharge patterns are distorted (Landsberg and Waring, 1997). These authors suggested using a daily water balance model to solve this problem, but also stated that this would increase model complexity and data requirements.

The discrepancy between observed and predicted stand volume in the non-irrigated treatments could also be related to an under-estimation of NPP and/or an under-estimation of NPP allocation to stemwood, which may be attributed to errors in the calculation of soil water or atmospheric *D*, or could result from the assigned *FR* values. In the 3-PG model, adjustments to *FR* influence above-ground biomass production by altering the canopy quantum efficiency and carbohydrate allocation to roots (Landsberg *et al.*, 2003). If the nutritional status at 3.9 years was higher than the *FR* values of 0.6 and 0.8 specified for the C and F treatments, respectively, allocation to below-ground components would be lower, and as suggested by Binkley (1986), could result in more carbohydrates for stem growth. Esprey *et al.* (2004) showed the moderate sensitivity of stand volume to site fertility. Over- or under-estimation of this variable at particular points in a time series may indicate that the nutritional status was respectively lower, or higher than the static *FR* used as an input into the model. Litterfall N or N mineralisation rates, as well as conventional analyses of soil P content can be used as measures of fertility (Landsberg and Waring, 1997). The development of satisfactory and dependable relationships between *FR* values and conventional measures of soil fertility will probably result from understanding and quantifying foliage response (in terms of mass dynamics and nutrient concentrations) to site fertility and nutrient availability (Landsberg *et al.*, 2001). These authors also suggested using dynamic soil organic matter models which may aid in solving the problem of modelling site nutrition and tree nutrient uptake. Stape *et al.* (2004) recommended the use of paired plots with and without fertiliser in a plantation inventory network over a regional area as an effective tool for estimating *FR* for 3-PG and other process-based models.

Given suitable data, a model intended for management should be recalibrated for local conditions (Sands *et al.*, 2000). Some studies have calibrated the 3-PG model for a particular site (Landsberg *et al.*, 2001, 2003; Almeida *et al.*, 2004a; Stape *et al.*, 2004). At this stage, we do not have the necessary information for calibration of the model to this site. However, we are certain that if adequate data were available, the 3-PG model outputs would have provided an even closer fit to observed values.

CONCLUSIONS

Model testing is imperative to build user confidence in the accuracy of a model. In this study, validation of the 3-PG model was performed using the parameter set developed by Esprey and Sands (2004). Although the observed data from this trial are independent of those used to develop the parameter set, this study does not constitute a complete validation of 3-PG, which would require consideration of the temporal variation of all above- and below-ground biomass pools, and of available soil water (Esprey *et al.*, 2004).

Outputs from the 3-PG model have highlighted the

need to focus our understanding on how *FR* varies seasonally and with silvicultural regime to provide an objective method for estimating *FR* values. Dynamic allocation patterns between above- and below-ground components in response to site resource availability deserve further investigation. The results have shown 3-PG to be a robust model, producing accurate predictions of tree growth under varying levels of resource availability, using a single parameter set. It is encouraging that the model can predict canopy response (in terms of leaf area) to changes in resource availability, as this is the tree component that ultimately drives growth and water use.

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