

## Parameterisation of 3-PG for plantation grown *Eucalyptus globulus*

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### Abstract

A set of parameter values for the forest growth model 3-PG was determined. These permit the modelling of the time-course of growth and development of even-aged, intensively-managed, fertilised stands of *Eucalyptus globulus*. The parameters were determined by fitting output from 3-PG to observed stem biomass data (i.e. total above-ground woody biomass) and canopy leaf area index (LAI). To fit these data, it was necessary to modify 3-PG by making specific leaf area and the fraction of stem biomass in branch and bark explicitly age-dependent, and to include effects of temperature on canopy quantum efficiency.

With these parameter values, 3-PG gave a good description of growth at seven of nine disparate sites in Tasmania and Western Australia. A partial explanation for its failure at one site in Western Australia is that this site was subject to a prolonged drought not reflected in the long-term mean climatic data used in this study. At the other, a high altitude site in Tasmania, 3-PG predicted significant growth although extensive frost damage had prevented establishment of a viable canopy. The model was also applied to non-fertilised stands in northern Tasmania for which only basic growth and site data were available. 3-PG adequately predicted the observed peak MAI of the better sites, but over-estimated peak MAI at poor or high-altitude sites.

The following conclusions are drawn: 3-PG can provide a good simulation of future growth of intensively-managed, fertilised stands of *E. globulus* if the model is initialised with observed biomass data at some age around or following canopy closure. If the model is initialised with typical seedling biomass at planting, 3-PG adequately predicts stem growth rate but not canopy LAI. Further development of 3-PG should take into account possible environmental effects on litterfall, the effects of partial canopy closure during early canopy development, and the prediction of mortality prior to the onset of self-thinning.

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**Keywords:** *Eucalyptus globulus*; 3-PG model; Leaf area index; Model parameterisation; Biomass production

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### 1. Introduction

The model called 3-PG (Physiological Principles Predicting Growth), developed by Landsberg and Waring (1997), is a simple process-based, stand-level

model of forest growth. It requires few parameter values and only readily available site and climatic data as inputs. The 3-PG model predicts the time-course of stand development, water use, and available soil water. Its primary output variables are net primary production, the standing biomass in foliage, stem (i.e. all above-ground woody tissue) and roots, stem number, available soil water, and transpiration. However, it

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also infers variables familiar to the forest manager or of use as inputs into management programs, e.g. leaf area index, mean stem diameter at breast height, main stem volume, and mean annual increment.

The model has found numerous applications for various species (Coops and Waring, 2000; Landsberg et al., 2000; Law et al., 2000; Waring, 2000). A modified version, 3-PG Spatial (Coops et al., 1998a), has been applied to study forest productivity across landscape areas (Coops et al., 1998a,b; Coops and Waring, 2000).

The 3-PG model is a deliberate attempt to bridge the gap between conventional empirical, mensuration-based growth and yield models, and process-based, carbon-balance models. It can be applied to plantations, or to even-aged, relatively homogeneous forests. It is a generic stand model, in the sense that its structure is not site or species-specific. However, it must be parameterised for individual species.

This paper reports the parameterisation of 3-PG for plantation grown *Eucalyptus globulus* across a range of sites in south-western Western Australia and in Tasmania, Australia. Parameterisation entailed fitting model output to observed time-series of stem biomass and canopy leaf area index (LAI). No root data were available, and no attempt was made to test or fit the water balance submodel. The objective was a set of parameter values that provide good fits to stem biomass, leaf area index and litterfall across a diverse range of stands. The process also entailed a critical examination of 3-PG, and resulted in a strengthening of the model and of its implementation. The procedure we followed parameterising 3-PG for *E. globulus* should facilitate rapid parameterisation for other species.

## 2. Overview of 3-PG

A full description of the original 3-PG is provided by Landsberg and Waring (1997). The following provides an overview of the model, and reference should be made to Landsberg and Waring (1997) for justification of the relationships used. This section also includes structural modifications we made as a result of this study. The manner in which various relationships are parameterised has been changed (but not their form) to make parameters intuitively

meaningful. This greatly aided the parameterisation process.

The 3-PG model consists of five simple submodels: the assimilation of carbohydrates, the distribution of biomass between foliage, roots and stems, the determination of stem number, soil water balance, and conversion of biomass values into variables of interest to forest managers. The state of the stand is updated each month. The following description builds on Landsberg and Waring (1997). Mathematical details are given in the Appendix. A summary of all parameters and their units is given in Table 1, along with their values for *E. globulus*. This table classifies parameters according to whether they are likely to be site- or species-specific, and indicates whether the value given was obtained directly from observed data, was estimated by fitting output from the model to observed data, or was some generic default (e.g. from Landsberg and Waring, 1997).

### 2.1. Data inputs

The 3-PG model requires as climatic inputs monthly average values of solar radiation ( $Q$  ( $\text{MJ m}^{-2} \text{d}^{-1}$ )), mean air temperature ( $T_a$  ( $^{\circ}\text{C}$ )), atmospheric vapour pressure deficit ( $D$  (mbar)), rainfall ( $R$  (mm per month)), and frost days ( $d_F$  (days per month)). If mean maximum and minimum air temperatures ( $T_x$  and  $T_n$  ( $^{\circ}\text{C}$ )) are known,  $T_a = 1/2(T_x + T_n)$ . Vapour pressure deficit can also be estimated from  $T_x$  and  $T_n$ , e.g. as half the difference between the saturated vapour pressure at  $T_x$  and  $T_n$ . The 3-PG model can be run for any number of years, using either actual monthly weather data or long-term monthly averages. Using averages is the normal procedure unless there is particular interest in specific events, such as droughts. Other inputs are factors describing the physical properties of the site: latitude, a site fertility rating (FR), maximum available soil water ( $\theta_{Sx}$  (mm)), and a general descriptor of soil texture.

### 2.2. 3-PG outputs

Outputs from 3-PG can be either monthly or annual values. They include stem, root and foliage biomass ( $W_S$ ,  $W_R$  and  $W_F$  ( $\text{t ha}^{-1}$ )), available soil water ( $\theta_S$  (mm)), and stand transpiration ( $E_T$  (mm)). Stand-level outputs include canopy leaf area index ( $L$ ), main-stem

Table 1  
Description of 3-PG parameters and default values for *E. globulus*

Meaning/comments	3-PG symbol	Site or species specific	Default, fitted or observed	Value	Units
<b>Allometric relationships and partitioning</b>					
Ratio of foliage:stem partitioning at $B = 2$ cm	$p_2$	Species	Fitted	1	–
Ratio of foliage:stem partitioning at $B = 20$ cm	$p_{20}$	Species	Fitted	0.15	–
Constant in stem mass and diameter relationship	$a_S$	Species	Observed	0.095	–
Power in stem mass and diameter relationship	$n_S$	Species	Observed	2.4	–
Maximum fraction of NPP to roots	$\eta_{R_x}$	Species	Default	0.8	–
Minimum fraction of NPP to roots	$\eta_{R_n}$	Species	Default	0.25	–
<b>Temperature and frost modifier</b>					
Minimum temperature for growth	$T_{\min}$	Species	Fitted	8	°C
Optimum temperature for growth	$T_{\text{opt}}$	Species	Fitted	16	°C
Maximum temperature for growth	$T_{\max}$	Species	Fitted	40	°C
Number of days of production lost for each frost day	$d_F$	Species	–	0	days
<b>Litterfall and root turnover</b>					
Maximum litterfall rate	$\gamma_{F_x}$	Both	Observed	0.027	per month
Litterfall rate for very young stands	$\gamma_{F0}$	Both	Default	0.001	per month
Age at which litterfall rate = $\frac{1}{2}(\gamma_{F0} + \gamma_{F_x})$	$t_{\gamma F}$	Both	Fitted	12	month
Average monthly root turnover rate	$\gamma_R$	Both	Default	0.015	per month
<b>Conductance</b>					
Maximum canopy conductance	$g_{C_x}$	Species	Default	0.02	$\text{m s}^{-1}$
Maximum stomatal conductance	$g_{S_x}$	Species	Default	0.006	$\text{m s}^{-1}$
Defines stomatal response to VPD	$k_g$	Species	Default	0.05	$\text{kPa}^{-1}$
Canopy boundary layer conductance	$g_B$	Both	Default	0.2	$\text{m s}^{-1}$
<b>Fertility effects</b>					
Value of $m$ when FR = 0	$m_0$	Species	Default	0	–
Value of $f_N$ when FR = 0	$f_{N0}$	Species	Default	1	–
<b>Soil water modifier</b>					
Moisture ratio deficit which gives $f_\theta = 0.5$	$c_\theta$	Site	Determined by soil texture (Landsberg and Waring, 1997)		
Power of moisture ratio deficit in $f_\theta$	$n_\theta$	Site			
<b>Stem number</b>					
Maximum tree stem mass for 1000 trees $\text{ha}^{-1}$	$w_{S_x,1000}$	Both	Default	300	kg per tree
<b>Age modifier</b>					
Maximum stand age used to define relative age	–	Species	Default	50	years
Power of relative age in $f_{\text{age}}$	$n_{\text{age}}$	Species	Default	4	–
Relative age to give $f_{\text{age}} = \frac{1}{2}$	$r_{\text{age}}$	Species	Default	0.95	–
<b>Specific leaf area and branch+bark fraction</b>					
Specific leaf area at stand age 0	$\sigma_0$	Species	Observed	11	$\text{m}^2 \text{kg}^{-1}$
Specific leaf area for mature aged stands	$\sigma_1$	Species	Observed	4	$\text{m}^2 \text{kg}^{-1}$
Age at which leaf area = $\frac{1}{2}(\sigma_0 + \sigma_1)$	$t_\sigma$	Species	Observed	2.5	years
Branch+bark fraction at stand age 0	$p_{B0}$	Species	Observed	0.75	–
Branch+bark fraction for mature aged stands	$p_{B1}$	Species	Observed	0.15	–
Age at which branch+bark fraction = $\frac{1}{2}(p_{B0} + p_{B1})$	$t_{pB}$	Species	Observed	2	years
<b>Various</b>					
Extinction coefficient for absorption of PAR by canopy	$k$	Species	Default	0.5	–
Maximum canopy quantum efficiency	$\alpha_{C_x}$	Species	Fitted	0.07	$\text{mol mol}^{-1}$
Ratio NPP/GPP	$Y$	No	Default	0.47	–
Basic density	$\rho$	Both	Default	0.5	$\text{t m}^{-3}$
Fraction of intercepted rainfall evaporated from canopy	–	Species	Default	0.15	–

volume ( $V$  ( $\text{m}^3 \text{ha}^{-1}$ )), average stem diameter at breast height ( $B$  (cm)), mean annual stem-volume increment (MAI ( $\text{m}^3 \text{ha}^{-1}$  per year)), and stem number ( $N$  (trees  $\text{ha}^{-1}$ )).

### 2.3. Gross and net primary production

The photosynthetically active radiation (PAR or  $\phi_p$  ( $\text{mol m}^{-2}$ )) incident on the canopy is determined from  $Q$ , assuming 1 MJ of solar radiation is equivalent to 2.3 mol PAR. The PAR absorbed by the canopy ( $\phi_{pa}$  ( $\text{mol m}^{-2}$ )) is determined from  $L$  and  $\phi_p$  through Beer's law. Gross primary production (GPP or  $P_G$  ( $\text{t}_{\text{DM}} \text{ha}^{-1}$ )) is proportional to  $\phi_{pa}$ , with 1 mol C equivalent to 24  $\text{g}_{\text{DM}}$ . The proportionality factor is called the canopy quantum efficiency ( $\alpha_C$  ( $\text{mol mol}^{-1}$ )), and takes into account environmental modifiers  $f_x$  ( $0 \leq f_x \leq 1$ ) based on atmospheric vapour pressure deficit ( $f_{\text{VPD}}$ ), available soil water ( $f_{\text{SW}}$ ), mean air temperature ( $f_T$ ), frost days per month ( $f_F$ ), site nutrition ( $f_N$ ), and stand age ( $f_{\text{age}}$ ). Only the most limiting of  $f_{\text{VPD}}$  and  $f_{\text{SW}}$  (i.e. the smaller value) is used, but the factors  $f_T$ ,  $f_F$ ,  $f_N$  and  $f_{\text{age}}$  are applied multiplicatively (see Appendix A). The current study was the original impetus for the inclusion of the modifiers  $f_T$  and  $f_N$  reported elsewhere (e.g., Waring, 2000). Net primary production (NPP or  $P_N$  ( $\text{t}_{\text{DM}} \text{ha}^{-1}$ )) is a constant fraction  $Y$  ( $= 0.47$ ) of GPP (Waring et al., 1998).

### 2.4. Biomass allocation

Allocation of NPP to roots is determined by growing conditions, as expressed by available soil water, vapour pressure deficit and site nutrition, in accordance with well established principles (e.g. Beets and Whitehead, 1996; Landsberg and Gower, 1997, p.150). Thus, the proportion ( $\eta_R$ ) of NPP allocated to roots increases when nutritional status and/or available soil water are low. Biomass allocation to foliage ( $\eta_F$ ) and to stems ( $\eta_S$ ) also varies with growing conditions, but allocation also depends on average tree size in such a manner that  $\eta_F$  declines and  $\eta_S$  increases as stands age.

Landsberg and Waring (1997) originally determined  $\eta_F$  and  $\eta_S$  from the ratio of the derivatives of allometric functions for mean single-tree foliage and stem biomass ( $w_F$  and  $w_S$  ( $\text{kg}_{\text{DM}}$  per tree)) in terms of

mean stem diameter at breast height ( $B$  (cm)).  $B$  is determined from the stand-level stem biomass ( $W_S$ ) by dividing by the current stem number and then inverting the allometric relationship between  $w_S$  and  $B$ . Their key result was that the ratio  $p_{\text{FS}}$  ( $= \eta_F/\eta_S$ ) of foliage to stem biomass partitioning is also an allometric function of  $B$ . Any relationship between  $w_F$  and  $B$  determined before canopy closure breaks down following canopy closure as  $B$  continues to increase whereas  $w_F$  is in a quasi steady-state. Accordingly, we used the observed allometric relationship between  $w_S$  and  $B$ , but assumed an allometric relationship between  $p_{\text{FS}}$  and  $B$  (see Appendix A) and estimated parameters in the latter.

### 2.5. Stem mortality

Changes in stem populations are calculated using the  $-3/2$  self-thinning law to estimate an upper limit ( $w_{Sx}$  ( $\text{kg}_{\text{DM}}$  per tree)) to the mean single-tree stem mass ( $w_S$ ), given the stem population  $N$ . The self-thinning law is parameterised by an estimate of  $w_{Sx}$  for stands with low stem populations (see Appendix A). If the current mean single-tree stem mass is greater than the current  $w_{Sx}$ , the population is reduced to a level consistent with the current  $w_{Sx}$ . Because mortality entails changes to both stem number and biomass, an iterative application of the self-thinning law may be required to ensure the self-thinning law is satisfied for the new state. When stems are removed, it is assumed that each stem removed has approximately 20% of the biomass of the average stem, and that no foliage biomass is lost. This simulates the fact that trees that die are often the smaller trees with low stem biomass and little or no foliage.

### 2.6. Soil water balance

The 3-PG model includes a simple, single-layer soil-water-balance model working on a monthly time step. Monthly rainfall (plus irrigation) is balanced against monthly evapotranspiration computed using the Penman–Monteith equation (Landsberg and Gower, 1997, p. 76). Canopy interception is a fixed percentage of rainfall. Soil water in excess of  $\theta_{Sx}$  is lost as runoff.

Vapour pressure deficit, available soil water and stand age are assumed to affect stomatal conductance.

Canopy conductance ( $g_C$  ( $\text{m s}^{-1}$ )) is determined from a nominal stomatal conductance scaled by  $f_{\text{age}}$  and by the lesser of the environmental modifiers  $f_{\text{SW}}$  and  $f_{\text{VPD}}$ , and increases with increasing canopy LAI up to a maximum canopy conductance ( $g_{C_x}$  ( $\text{m s}^{-1}$ )).

### 3. Data sources

Parameterisation of 3-PG was achieved by adjusting the values of selected parameters of the model to give good fits of model output to observed time-series of stem biomass and canopy leaf area index. The biomass and stand growth data used to parameterise 3-PG came from fertilised stands of *E. globulus* grown for research purposes. The stands were at contrasting sites in south-western Western Australia (Hingston, 1994), at an irrigated and fertilised site at Forcett, south-east Tasmania (Honeysett et al., 1996), and at four fertilised sites in the Esperance valley, southern Tasmania (Turnbull et al., 1993). The Esperance sites form an altitudinal sequence (50, 200, 430 and 640 m) where annual mean temperature declines from 12 to 8 °C (Turnbull et al., 1993). These sites are separately called the WA sites, the Forcett site, and the Esperance sites 1–4 (in increasing altitude), but are collectively referred to as the research sites. Data from these sites were used to develop the productivity model PROMOD, and full details are given in Battaglia and Sands (1997). Additional data from various sources were used to provide values for individual parameters.

All the research stands had been fertilised, and as nutrient availability was assumed non-limiting, fertility rating FR was set to 1. Water availability and high VPD potentially limit growth at the WA sites. Growth at the Forcett site is not limited by water, but may be constrained to some extent by low temperatures. Temperature strongly affects growth at the Esperance sites, especially at the 650 m site where persistent frosts prevented establishment of a viable canopy. This site is probably beyond the limit for survival of *E. globulus*.

Above-ground woody biomass rather than stem volume was used so that it was not necessary to account in 3-PG for possible temporal variation of basic density ( $\rho$  ( $\text{t m}^{-3}$ )) or of the fraction ( $p_B$ ) of stem biomass as branches and bark. The original version

of 3-PG inferred main-stem volume  $V$  ( $\text{m}^3$ ) from predicted stem biomass  $W_S$  and stem number  $N$ , using a nominal basic density of  $0.5 \text{ t m}^{-3}$  and a branch and bark to stem biomass ratio of  $p_B = 0.17$ . Because these parameters can be site- and species-specific, we used observed  $\rho$  and  $p_B$  to convert observed data on  $V$  to  $W_S$ . In cases where observed  $p_B$  was not available, the empirical age-related relationship based on other data sets and developed below was applied. This relationship was subsequently incorporated into 3-PG.

Data of a lesser quality were also available from a further 19 sites in northern Tasmania (Battaglia and Sands, 1997). These sites were in commercial plantations and not fertilised. Although detailed growth data were not available, the peak MAI reported by Battaglia and Sands enabled a weak validation of the parameterisation of 3-PG.

#### 3.1. Stem biomass

Observed data were either main-stem, branch and bark biomass data, obtained from destructive harvests, or main-stem volume data (excluding bark and branches) determined from stem height and diameter data using a volume formula. In the latter case, stem volume was converted into main-stem biomass using observed basic density, and branch and bark biomass were inferred from an empirical, age-dependent relationship for  $p_B$ . In both cases, main-stem, branch and bark biomass were combined to give stem biomass, i.e. total above-ground woody biomass.

A relationship for  $p_B$  was based on data from 1–4-year-old *E. globulus* at the Esperance sites (C. Beadle, personal communication), and fitted biomass partitioning coefficients obtained for 5–9-year old stands in Western Australia (Hingston, 1994). These data suggest  $p_B$  declines with age to 0.15–0.18 (Fig. 1a), and were fitted to an exponential decay to a non-zero asymptote

$$p_B(t) = p_{B1} + (p_{B1} - p_{B0}) e^{-(\ln 2)t/t_{pB}} \quad (1)$$

where  $p_{B0} = 0.75$ ,  $p_{B1} = 0.15$  and  $t_{pB} = 2$  years. This relationship reproduces the observed  $p_B$  with  $r^2 = 0.81$ , and predicts  $p_B$  to have a value of  $0.16 \pm 0.01$  for stands aged 6–10 years (Fig. 1a). Additional data from Gippsland, Victoria (Cromer and Williams, 1982) in Fig. 1a show how  $p_B$  can be site specific.

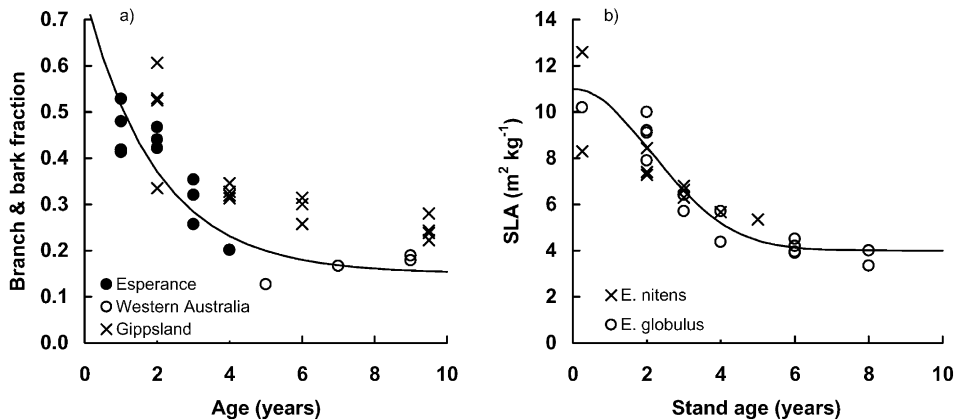


Fig. 1. Age dependence of (a) branch and bark fraction  $p_B$  and (b) specific leaf area  $\sigma$ . The lines (—) are fitted curves used when compiling observed stem and foliage biomass data, and when applying 3-PG, i.e. Eqs. (1) and (2).

### 3.2. Foliage biomass

3-PG predicts foliage biomass  $W_F$  ( $\text{t ha}^{-1}$ ) and infers canopy leaf area index  $L$  from  $L = 0.1\sigma W_F$ , where  $\sigma$  ( $\text{m}^2 \text{kg}^{-1}$ ) is specific leaf area and the 0.1 is a conversion factor. The only data on foliage biomass were from stands aged 1–3 years at the Esperance sites (C. Beadle, personal communications). However, observed  $L$  were available for stands aged 1–4 years at these sites (Beadle et al., 1995), 2–6 years at Forcett (M. Cherry, personal communications), and 4–8 years in Western Australia (Hingston, 1994). Accordingly, these data were compared with corresponding LAI predicted using 3-PG.

Data on  $\sigma$  for both *E. globulus* and *E. nitens* were available from seedlings prior to planting (Close, personal communications), from 2–4-year-old stands at Esperance (C. Beadle, personal communications), from 2–3 year old irrigated and un-irrigated stands at Forcett (White, 1996). Data for *E. globulus* were available from 6-year-old stands in Gippsland (Bennett et al., 1997), and 4–8 year-old stands in Western Australia (Hingston, 1994). Data for both species were fitted to a Gaussian function with non-zero asymptote

$$\sigma(t) = \sigma_1 + (\sigma_0 - \sigma_1) e^{-(\ln 2)(t/t_\sigma)^2} \quad (2)$$

where  $\sigma_0 = 11 \text{ m}^2 \text{kg}^{-1}$ ,  $\sigma_1 = 4 \text{ m}^2 \text{kg}^{-1}$  and  $t_\sigma = 2.5$  year, with  $r^2 = 0.92$  (Fig. 1b). This relationship is assumed to apply for all *E. globulus* and *E. nitens* stands, and was included in 3-PG because assimilation is sensitive to  $L$ , especially during early canopy growth

when  $L$  is low, and because  $\sigma$  is involved in the calculation of  $L$  ( $0.1\sigma W_F$ ). Fig. 1b shows that  $\sigma$  declines from  $9 \pm 1.0$  for stands aged 2 years, to  $4 \pm 0.7$  for stands aged 4–10 years.

### 3.3. Litterfall data

3-PG calculates monthly leaf litterfall  $\Delta W_{FL}$  ( $\text{t ha}^{-1}$  per month) as  $\Delta W_{FL} = \gamma_F W_F$  where the litterfall rate  $\gamma_F$  (per month) is age-dependent, decreasing from a low value ( $\gamma_{F0}$ ) for young stands, to a maximum value ( $\gamma_{Fx}$ ) for stands of age about 3 years and above. Data on observed total annual litterfall  $\Delta_T W_{FL}$  ( $\text{t ha}^{-1}$  per year) were available from the Forcett (D. Worledge, personal communications) and WA stands (Hingston, 1994). Given observed  $\Delta_T W_{FL}$ , leaf area index  $L$  and specific leaf area  $\sigma$ , monthly leaf litterfall rate can be approximated by  $\gamma_F = (0.1\sigma/12L)\Delta_T W_{FL}$  and  $\gamma_F$  was estimated for the various stands for which litterfall data were available. At Forcett  $\gamma_F = 0.038 \pm 0.014$ , and for the four WA stands  $\gamma_F = 0.014, 0.03, 0.026, 0.02$ . Clearly,  $\gamma_F$  varies from stand to stand in response to local conditions. 3-PG does not include a submodel for site or environmental variation of  $\gamma_F$ , so a mean value of 0.027 was assumed.

### 3.4. Allometric relationships

Biomass partitioning assumes that mean single-tree stem biomass ( $w_S = W_S/N$ ) and the ratio of foliage to stem biomass partitioning ( $p_{FS}$ ) have an allometric

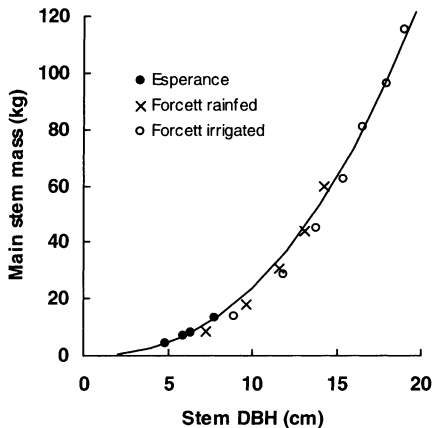


Fig. 2. Allometric relationship between single-tree above-ground woody biomass  $w_S$  and stem diameter  $B$  at breast height obtained from the Tasmanian study sites. The line (—) is the fitted relationship used in 3-PG ( $a_S = 0.095$ ,  $n_S = 2.4$ ).

relationship to mean stem diameter ( $B$ ). The allometric relationship for  $p_{FS}$  is not amenable to direct observation and its parameters can only be determined by adjusting their values when fitting 3-PG output to observed data. However, very similar allometric relationships of the form  $w_S = a_S B^{n_S}$  apply under a wide range of conditions for a given species, so 3-PG regards the allometric parameters  $a_S$  and  $n_S$  as universal for a species. Fig. 2 shows  $w_S$  as a function of  $B$  for 3–4-year-old *E. globulus* at the Esperance sites (C. Beadle, personal communications), and for 3–9 year-old irrigated and rain-fed stands at Forcett (C. Beadle, personal communications). These data were pooled, and the allometric parameters  $a_S = 0.095$  and  $n_S = 2.4$  gave an excellent fit ( $r^2 = 0.99$ ). These values were assumed to apply for all stands in this study.

#### 4. Parameterisation for *Eucalyptus globulus*

Parameterisation of 3-PG to observed *E. globulus* biomass data was a step-wise process. The goal was a set of parameter values that would provide good fits to all available observations of stem biomass, foliage biomass or leaf area index, and litterfall. If it was not possible to reproduce observed data at a site using a common set of parameters, a set of parameters for that site was found which best reproduced the observed

data. No root data were available to parameterise or validate partitioning to roots, and no attempt was made to parameterise the water balance submodel.

All runs started from the earliest observation and terminated after the last observation. Stem number and biomass were initialised with their values for the earliest observation. Foliage biomass was either assigned the initial observed value, or a value that reproduced the first observed canopy LAI. Root biomass was given some value commensurate with expected root biomass partitioning and stem biomass (since 3-PG has no internal feedback loops involving root biomass and there were no observed root biomass data, this value is actually irrelevant to this study). As there was no mortality in these stands,  $w_{Sx}$  was assigned a value so that no mortality occurred.

Parameter estimation was by hand, and all runs were made with 3PGPJS (Sands, 2000), a simple and flexible implementation of 3-PG as Visual Basic macros using Excel spreadsheets for the user interface, data input, and all output. Various errors and inconsistencies in an earlier implementation were corrected, and all modifications to 3-PG introduced in this study were included in 3PGpjs.

##### 4.1. Application of the original 3-PG

The first step was to parameterise the original model published by Landsberg and Waring (1997). In this version there was no effect of temperature or nutrition on canopy quantum efficiency  $\alpha_C$ , and specific leaf area was constant. The model was fitted to data from the four WA stands by varying the  $\alpha_C$  and the coefficients in the allometric expression for  $p_{FS}(B)$  (through the values  $p_2$  and  $p_{20}$  of  $p_{FS}$  for  $B = 2$  and 20 cm, respectively; see Appendix A). The allometric coefficients  $a_S = 0.095$  and  $n_S = 2.4$  in  $w_S(B)$ , the specific leaf area  $\sigma = 4$ , and the monthly litter fall rate  $\gamma_F = 0.027$  were given values appropriate to *E. globulus* based on data analysed above. All other 3-PG parameters were assumed to have standard values from Landsberg and Waring (1997); see Table 1. All runs were initialised so that 3-PG reproduced the first observed stem biomass and LAI.

A common set of parameters with  $\alpha_C = 0.05$  mol/mol,  $p_2 = 1$  and  $p_{20} = 0.15$  gave a good fit (Fig. 3) to three of the four WA sites. Minor adjustment of  $\gamma_F$  at each site was required to properly reproduce observed

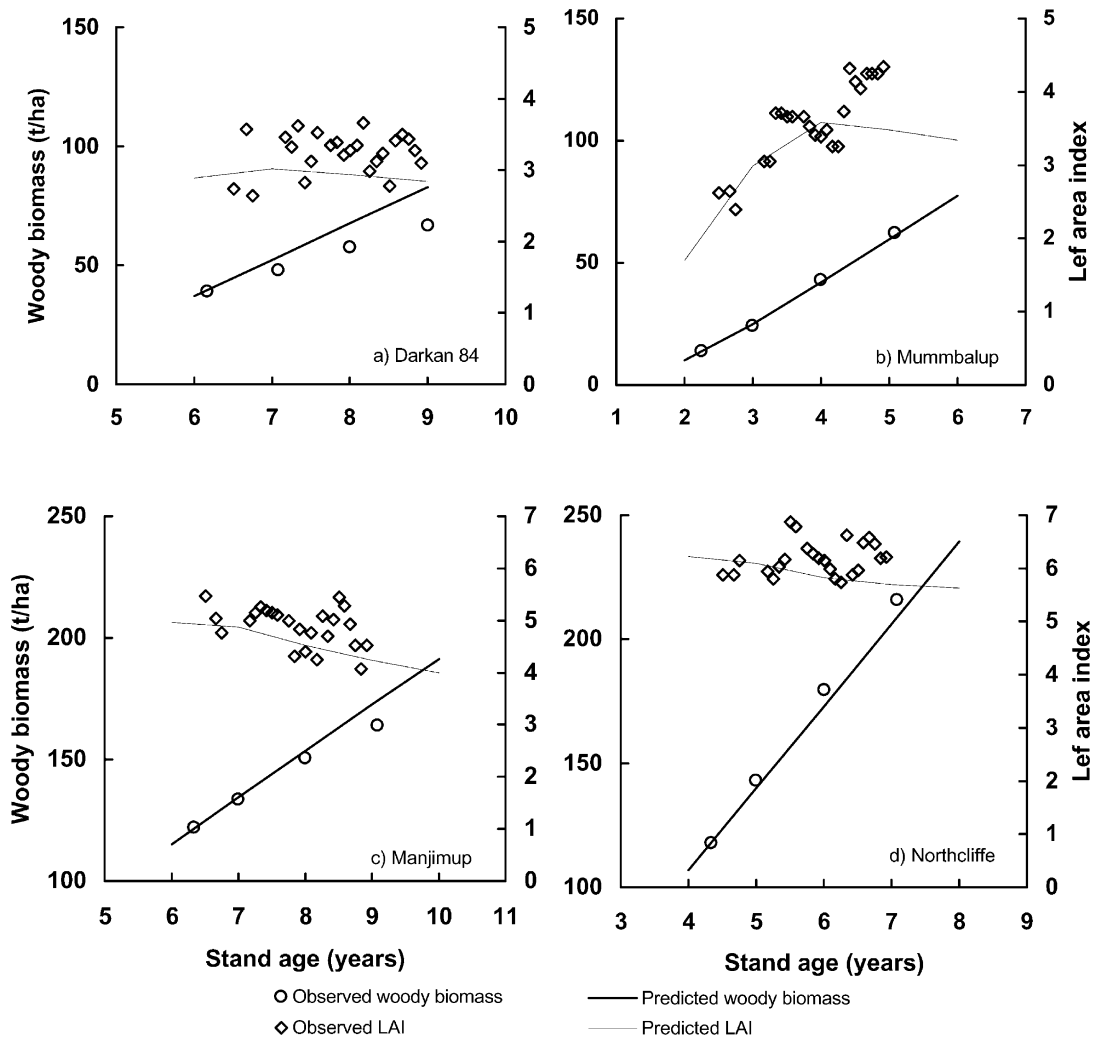


Fig. 3. Comparison of observed and predicted leaf area index  $L$  ( $\diamond$  and —) and woody biomass  $W_s$  ( $\circ$  and —). Predictions were from an application of the original 3-PG to four Western Australian sites with a common set of parameters.

leaf litter as well as stem and foliage biomass. However, at Darkan 84 these parameters lead to a 55% over-prediction of stem biomass and a 50% over-prediction of litterfall.

The parameters developed for the WA stands were now applied at the Forcett and Esperance sites, with all runs starting with the observed stem and foliage biomass at a stand age of 1 year. It was impossible to reproduce early canopy growth unless the observed age-dependence of specific leaf area (Eq. (2)) was taken into account. This is illustrated in Fig. 4 for the Esperance 1 site. When the observed age dependence

of  $\sigma$  was taken into account, an optimal fit also required a reduction in the  $\alpha_C$  obtained for the WA stands.

The Tasmanian sites are markedly cooler than the WA sites, and were subject to frequent mild or severe frosts, especially during winter months. In the original 3-PG frost affected production through a multiplier  $f_F$  that reduced monthly production in proportion to the number of frost days. However, even if this was taken into account, production at Tasmanian sites was overestimated. The value of  $\alpha_C$  which resulted in the best fit of 3-PG output to observed stem biomass data was obtained separately for each Tasmanian site. These



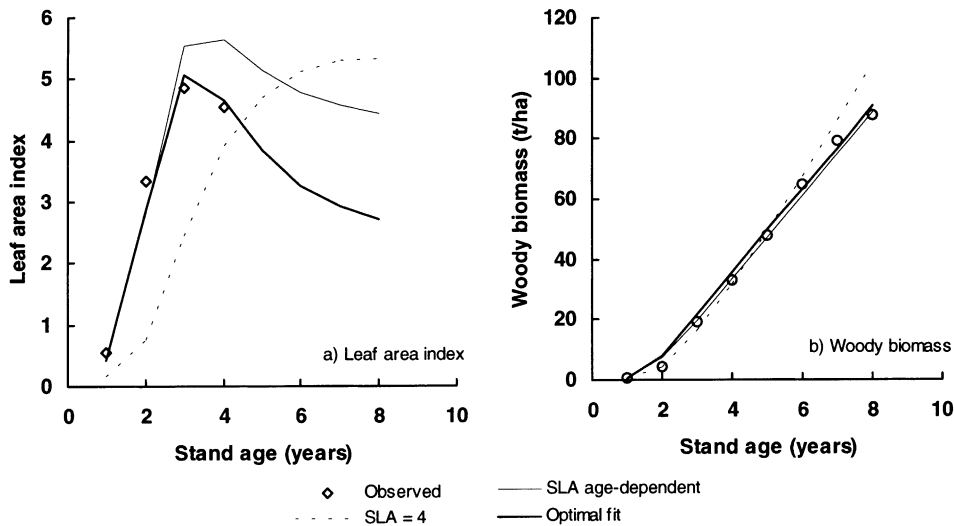


Fig. 4. Application of 3-PG to the Esperance 1 site comparing the use of a constant SLA ( $= 4 \text{ m}^2 \text{ kg}^{-1}$ ) (---), the observed age dependent SLA (—), and the litterfall rate adjusted to optimise the fit to observed  $L$  (—). In each case  $\alpha$  was adjusted to optimise the fit to observed woody biomass.

were significantly less than the value ( $\alpha_C = 0.05$ ) needed for the Western Australia sites (see below).

#### 4.2. Modification of 3-PG

When the best-fit values of  $\alpha_C$  for each site were plotted against annual mean temperature, a clear relationship was obtained (Fig. 5). It is known that photosynthetic rate in *E. globulus* declines with declining ambient temperature below an optimum of about  $20^\circ\text{C}$  (Battaglia et al., 1996; Sands, 1996). These findings suggest  $\alpha_C$  is related to monthly mean temperature ( $T_a$  ( $^\circ\text{C}$ )), so an additional environmental modifier  $f_T(T_a)$  was introduced to take into account effects of temperature on quantum efficiency. The relationship shown in Fig. 5 is well fitted by a function of the form

$$f_T(T_a) = \left( \frac{T_a - T_{\min}}{T_{\text{opt}} - T_{\min}} \right) \times \left( \frac{T_{\max} - T_a}{T_{\max} - T_{\text{opt}}} \right)^{(T_{\max} - T_{\text{opt}})/(T_{\text{opt}} - T_{\min})} \quad (3)$$

with  $f_T = 0$  if  $T_a \leq T_{\min}$  or  $T_{\max} \leq T_a$ . The parameters  $T_{\min}$ ,  $T_{\text{opt}}$  and  $T_{\max}$  are minimum, optimum, and maximum, or cardinal, temperatures for net photosynthetic production. Fig. 5 suggests  $T_{\min} \approx 7.5$  and

$T_{\text{opt}} \approx 15^\circ\text{C}$ .  $T_{\max}$  was set  $\approx 35^\circ\text{C}$  because *E. globulus* does not grow under high temperatures, but its value affects  $f_T$  at all  $T$ , not just at high temperatures. Fig. 5 also suggests maximum canopy quantum efficiency  $\alpha_{Cx} \approx 0.05$ . How the various modifiers are applied is detailed in the Appendix A. Since  $f_F$  and  $f_T$  occur as the product  $f_F f_T$ , and the number of frost days is strongly correlated with daily temperatures, the frost factor may

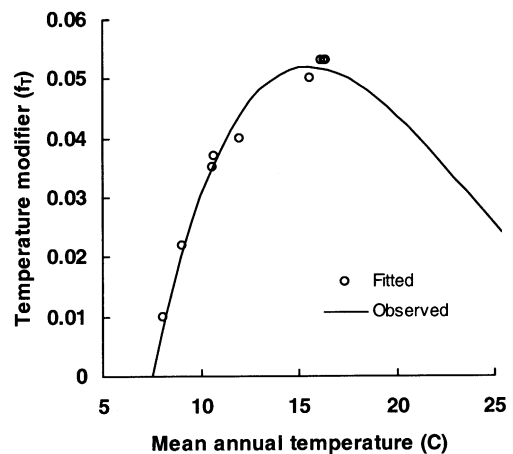


Fig. 5. Form of the temperature modifier  $f_T$ . Points fitted ( $\circ$ ) were determined by fitting 3-PG to data from sites in Tasmania and Western Australia, and the line observed (—) is a fit of these data to Eq. (3) in the text.

in fact prove redundant with frost effects effectively subsumed in  $f_T$ . In this study, the frost modifier was generally ignored.

Further modifications to 3-PG were to make the bark and branch fraction  $p_B$ , and the specific leaf area  $\sigma$ , depend explicitly on stand age through Eqs. (1) and (2), respectively. In the case of *E. globulus*, the parameters determining  $p_B$  and  $\sigma$  were those given above.

#### 4.3. Application of modified 3-PG

The modified 3-PG was applied at all nine research sites. Productivity was under-estimated, and it was necessary to increase  $\alpha_{C_x}$  to 0.06. This was because Fig. 5 was based on annual mean temperature, whereas in 3-PG monthly mean temperature affects production, and this varies from month to month. Since  $f_T$  is a convex function of  $T_a$ , the use of monthly  $T_a$  will give smaller values of  $f_T$  and hence  $\alpha_{C_x}$  must be increased. Adjustments were also required to  $T_{\min}$ ,  $T_{\text{opt}}$  and  $T_{\max}$  to optimise performance across all sites. The final parameter values were  $T_{\min} = 8.5$ ,  $T_{\text{opt}} = 16$ ,  $T_{\max} = 40$  (all °C), and  $\alpha_{C_x} = 0.06 \text{ mol mol}^{-1}$ . Note that monthly temperatures span a range on both sides of  $T_{\text{opt}}$ . No other changes in parameter values were made. In this process the parameter adjustments were manual, and judgement was based on the objective fit across all sites.

The performance of the modified 3-PG across all nine sites with a common parameter set was as good as was obtained when fitting each site independently; see Figs. 6 and 7. Further improvement for individual sites is possible by adjusting the maximum litterfall rate  $\gamma_{F_x}$ , or by minor adjustments to partitioning. Darkan 84 remains a problem, LAI is over estimated at the Esperance sites, and growth is still predicted at the 650 m Esperance site (not shown—but see Fig. 10). These issues are discussed later.

## 5. Sensitivity to stand initialisation

All 3-PG runs performed during parameter estimation were initialised using data from the first set of available observations to which the model was fitted. This is appropriate when fitting output to observed data. However, for predictive purposes, the model must be initialised to a nominal stand condition at an

early age, e.g. using typical seedling biomass data at age 0. The sensitivity of 3-PG output to initial stand conditions is therefore important.

### 5.1. Sensitivity to initial stand data

The sensitivity of the predicted time-course of LAI and stem biomass to data used to initialise the model was studied for several sites. Initial foliage and stem biomass were separately increased or reduced by factors of about 5, and 3-PG run to a stand age of 20 years. The output was compared with that obtained when initialising the stand with the actual earliest observations. The results in Fig. 8 for the Forcett site are typical of those at other sites. Large differences occur in predicted LAI in the early years of growth, but LAI converges to common values beyond age 10. The peak LAI is strongly affected, and its timing to a lesser extent. Stem biomass growth rates are similar in all runs, but the initial conditions affect the age at which stem biomass attains a particular value.

### 5.2. Sensitivity to seedling biomass data

If 3-PG is applied to predict production on sites for which there are no observed data, each run must be initialised at some early stage, e.g. at planting. Stand-level biomass data at planting were assigned on the basis of seedling biomass and stem number. It was assumed that foliage, stem and root biomass of seedlings at planting were 0.5, 0.25 and 0.25 g<sub>DM</sub>, respectively, typical of values observed by Close (Close, personal communications). Fig. 9 compares predicted time-course of stand development from planting with growth predicted when the simulation was initialised with the first biomass observation. It is clear that stem growth rate can be predicted consistently, but not canopy development. In particular, peak LAI is overestimated. This suggests further work is required on the prediction of canopy establishment, perhaps potential site variations in the age-dependence of specific leaf area.

## 6. Discussion

This study established a set of parameter values to use with 3-PG when predicting stand growth and

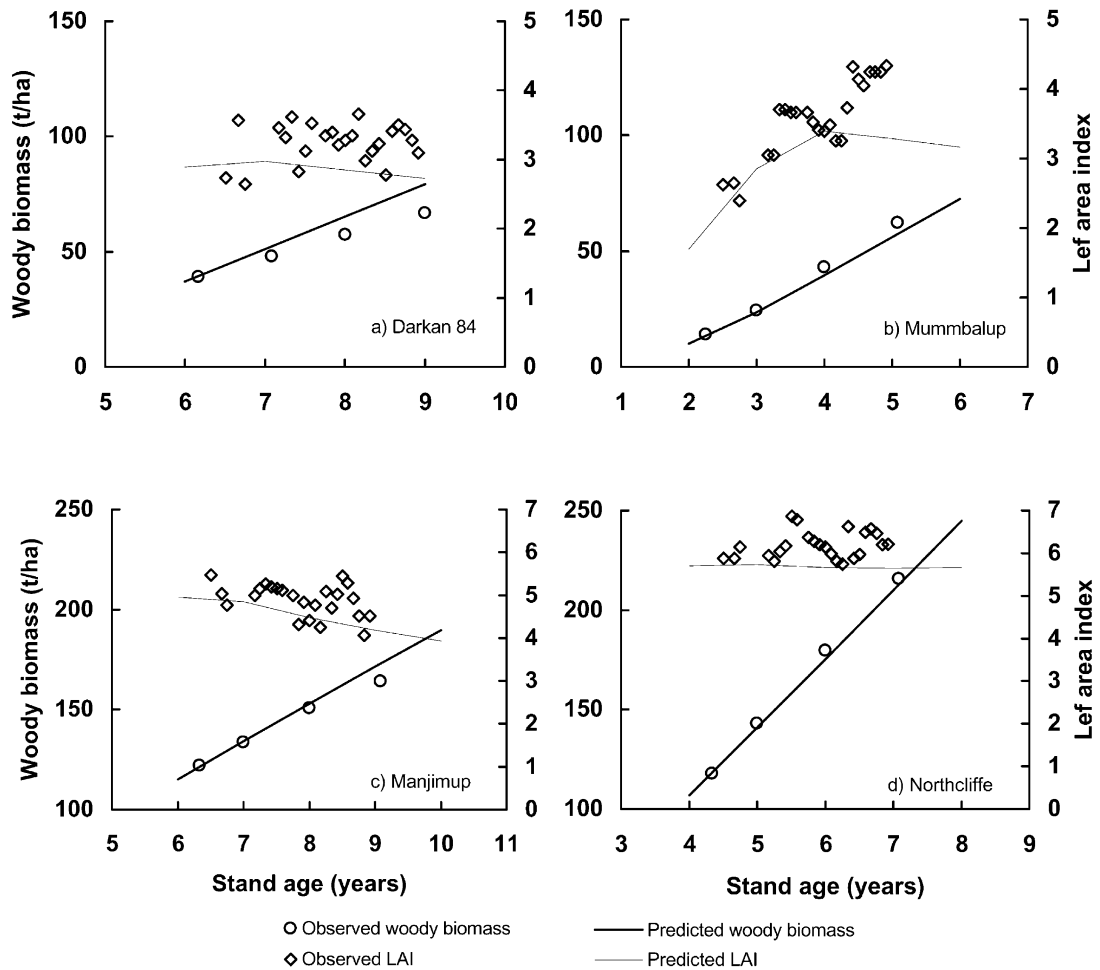


Fig. 6. Comparison of observed and predicted leaf area index  $L$  ( $\diamond$  and —) and woody biomass  $W_S$  ( $\circ$  and —). Predictions were from an application of the modified 3-PG to four Western Australian sites with a common set of parameters.

development of *E. globulus* plantations. When the simulations of the nine sites used to parameterise the model were initialised with data from the first observation at each site, the time-course of stem biomass was accurately predicted at seven of the nine sites, and the time-course of canopy LAI was accurately predicted at all Western Australian sites, but only at the low altitude sites (Forcett and Esperance 1) in Tasmania (Figs. 6 and 7).

One of the aberrant sites was Darkan 84, and two distinct approaches to fit the model here were tried. In the first, a reduced  $\gamma_F$  together with either a reduced  $\alpha_{Cx}$  or an increase in biomass partitioning to roots (i.e. an increase in the parameter  $\eta_{Rn}$ )

resulted in a good fit. A reduction in quantum efficiency cannot be distinguished from an increase in partitioning to roots unless observed root biomass data are available. This highlights a need for observed root data for proper approach annual rainfall was reduced, because Darkan 84 experienced below-average rainfall for several years during the growth period. However, reduced rainfall alone did not reproduce the full loss in production, the observed reduction in rainfall did not apply throughout the growth period, and the other three Western Australian sites also experienced varying degrees of reduced rainfall which did not affect predicted productivity.

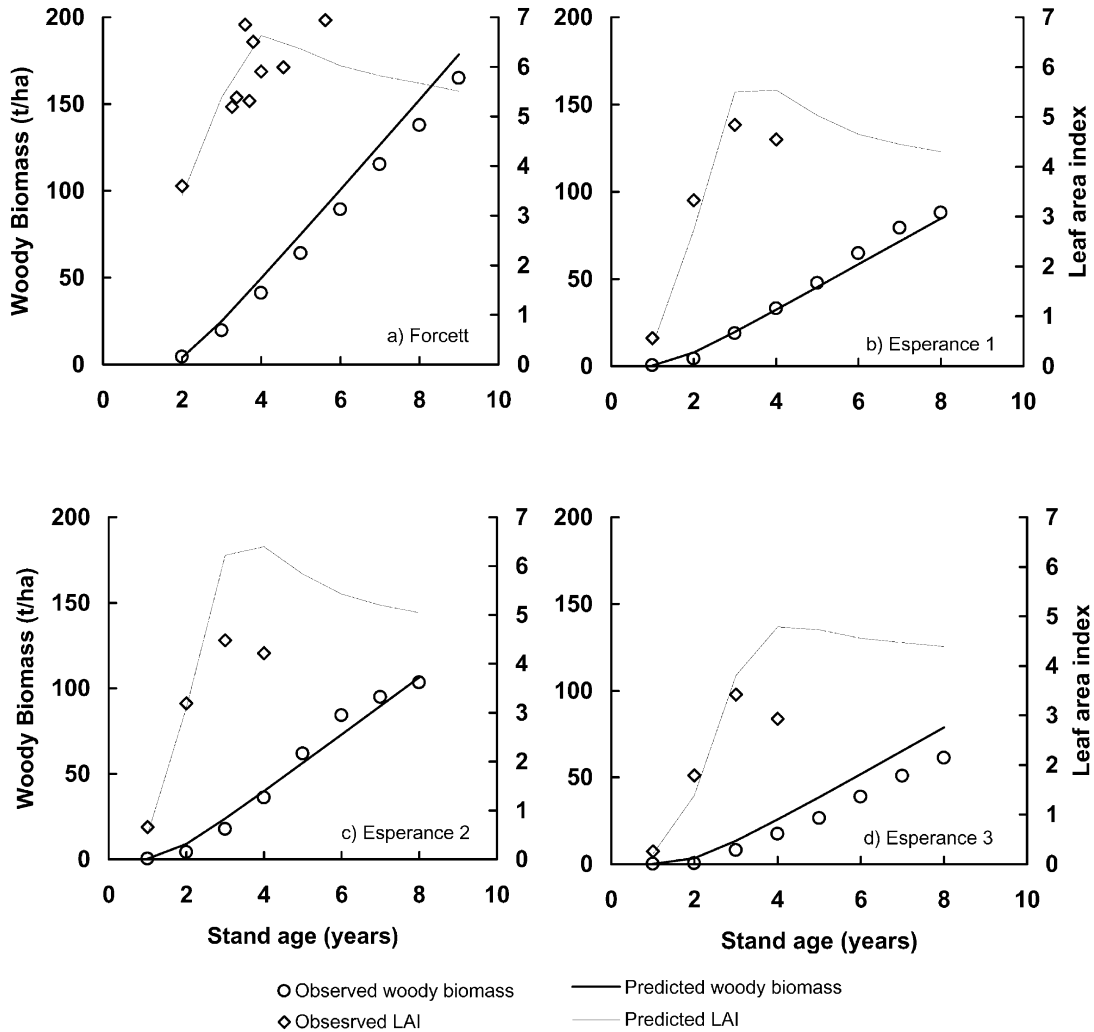


Fig. 7. Comparison of observed and predicted leaf area index  $L$  ( $\diamond$  and —) and woody biomass  $W_s$  ( $\circ$  and —). Predictions were from an application of the modified 3-PG to four Tasmanian sites with the same parameter values used for the Western Australian sites in Fig. 6.

The other aberrant site was the high altitude (650 m) site Esperance 4. 3-PG predicted sustained growth at this site, and use of the frost modifier  $f_F$  did not further reduce predicted growth. This is because  $f_T$  and  $f_F$  are non-zero during summer months and hence 3-PG predicts growth during summer. However, trees failed to establish at this site, almost certainly because frost damage to their canopies greatly increased leaf litterfall and hence reduced canopy LAI (Turnbull et al., 1993). Accordingly, 3-PG was run at this site with leaf litterfall increased to  $\gamma_F = 0.1$  and  $\gamma_F = 0.2$  per month, irrespective of stand age. The results in

Fig. 10 show large reductions in LAI and biomass were obtained, and the stand failed to establish with  $\gamma_F = 0.2$ .

Enhanced litterfall is also indicated at the lower Esperance sites because predicted LAI is high and peaks late (Fig. 7). Increasing  $\gamma_{Fx}$  from 0.027 to 0.05 per month improved the simulations of LAI (not shown). Unfortunately, there are no litterfall data from Esperance. Battaglia et al. (1998) showed that a simple model for canopy LAI in response to water and temperature stress required enhanced litterfall to predict LAI correctly at these high altitude sites. It

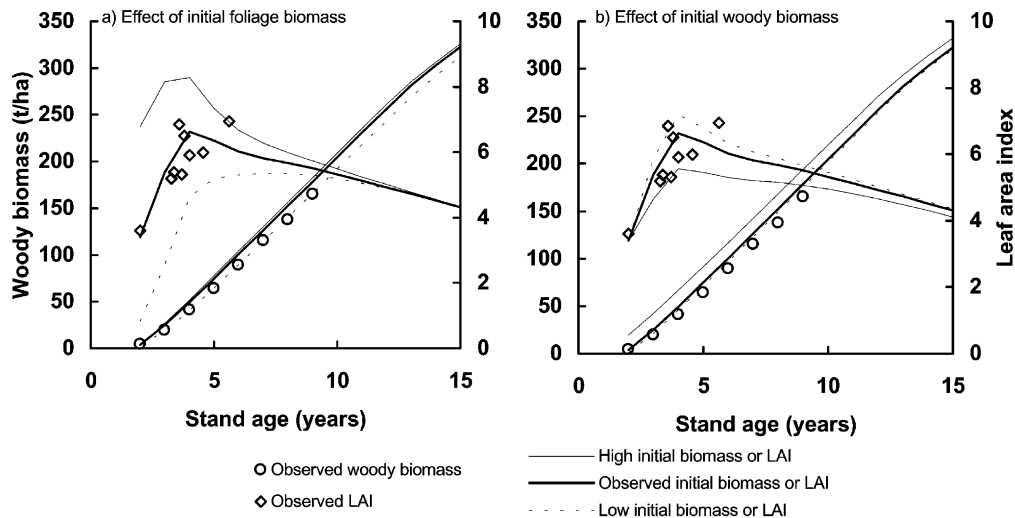


Fig. 8. Effects of varying initial (a) foliage  $W_F$  and (b) woody biomass  $W_B$  on the predicted time-course of stand development at Forcett. Symbols are observed leaf area index  $L$  ( $\diamond$ ) and woody biomass ( $\circ$ ), lines are predictions with observed (—), decreased (---), or increased (-.-) initial biomass data.

is clear that 3-PG requires a submodel for environmental effects on litterfall.

Limited data were also available from a further 19 sites in northern Tasmania. Although detailed growth data were not available, peak MAI had been estimated using several empirical growth models to project inventory data (Battaglia and Sands, 1997). These sites were not fertilised, but FR was assigned for each on the basis of the nutrient classifications given by Battaglia and Sands (1997). These data were used to provide a weak validation of 3-PG using the parameters given in Table 1. Growth from planting was simulated at these 19 sites and at the nine research sites. Predicted values of peak MAI for each site were inferred from these runs and compared with the corresponding observed peak MAI. Fig. 11 shows that about 70% of the variation in peak MAI was explained by 3-PG. However, a proper validation requires the application of 3-PG to simulate the time-course of stand growth at independent, commercial *E. globulus* stands.

The 3-PG mortality submodel predicts that mortality commences suddenly (Fig. 12), once average stem mass exceeds the value given by the self-thinning law. Fig. 12 was based on data from a Tasmanian site at which stem number was observed up to age 45 years. As the detailed site data were poor, a fertility rating

was assigned to give reasonable agreement between predicted and observed stem volumes. Setting  $w_{Sx1000} = 400$  stems per hectare ensured observed and predicted stem number agreed late in the rotation. As Fig. 12 shows, 3-PG failed to predict the gradual onset of mortality early in the stand. This example is typical, and illustrates a general failing of 3-PG.

During parameter estimation, all runs were initialised with data from the first set of observed biomass data. An analysis of the sensitivity of predicted stand development to the initial biomass data showed that the time-course of LAI was sensitive to initial conditions, but the time-course of stem biomass was less so (Fig. 8). When 3-PG is used as a predictive tool, there may not be observed data with which to initialise the model. This is especially the case for analyses of productivity across a landscape (e.g. Coops et al., 1998a,b; Coops and Waring, 2000). Typically, growth will be simulated from assumed standard seedling stock at age 0. A second sensitivity analysis showed that when 3-PG is used to predict growth from planting, early canopy development, and especially peak LAI, is sensitive to seedling mass (Fig. 9). Although stem biomass growth rate is insensitive to initial seedling mass, the age at which a particular stem biomass is attained varies 1–2 years over a wide range of initial conditions. However, it appears that after 10–15

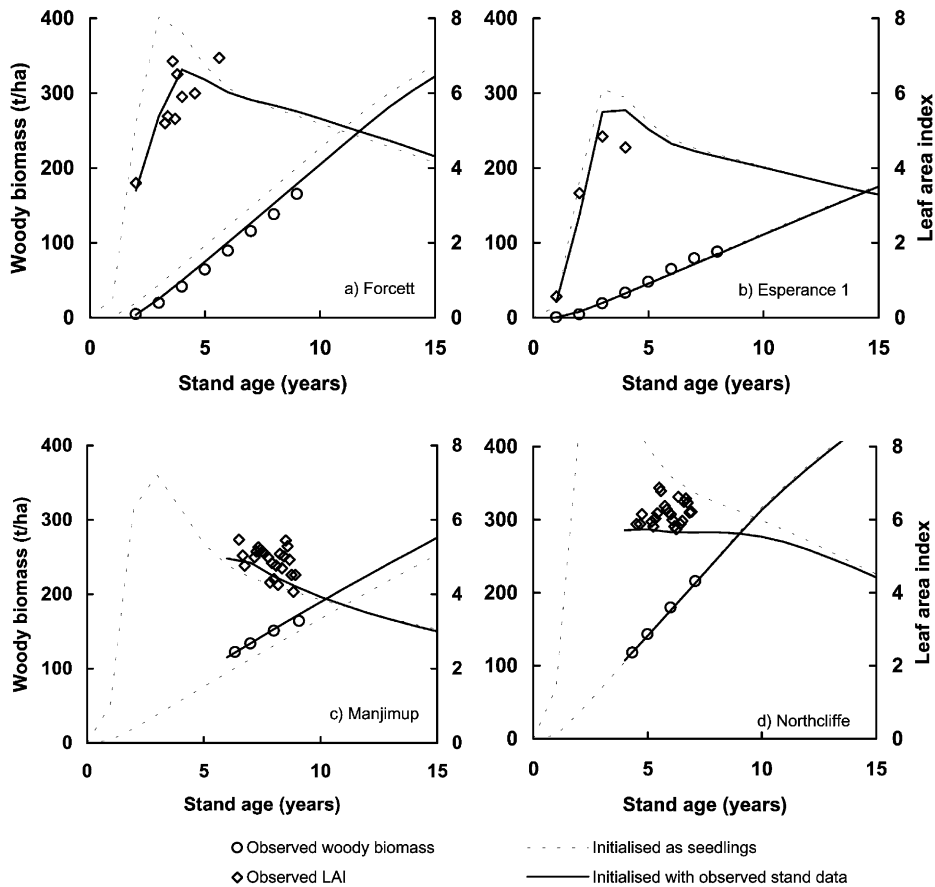


Fig. 9. The effects of initialising the stand with typical seedling data at four sites: (a) Forcett; (b) Esperance 1; (c) Manjimup and (d) Northcliffe. Symbols are observed leaf area index  $L$  ( $\diamond$ ) and woody biomass  $W_S$  ( $\circ$ ), lines are predicted time-course of stand development where stands are initialised with observed stand data (—), and at planting with typical seedling data (---). The predicted peak  $L$  for Northcliffe when the stand was initialised as seedlings at planting was 10.4.

years LAI and stem biomass converge to common values, irrespective of initial conditions (Figs. 8 and 9)

Successful parameterisation of 3-PG required careful attention to the data, and was aided by reasonable time-series of stem biomass and stand LAI. Emphasis was placed on making sure that stem biomass data were sound, and if derived from volume data, this required estimates of basic density and of the age-dependent ratio of branch and bark biomass to total stem biomass. Similarly, conversion between foliage biomass data and stand leaf area index required an accurate knowledge of the possibly age-dependent specific leaf area index.

Data from an *E. globulus* fertiliser trial in Gippsland (Cromer and Williams, 1982) suggest that the branch

and bark fraction  $p_B$  is greater than 0.25 for stands aged up to 10 years. This is greater than the corresponding value (0.16) observed for the trials considered here (Fig. 1a), and emphasises the importance of parameterising 3-PG against observed stem biomass rather than stem volumes. It also emphasises that sound additional information, or empirical relationships, are required to convert basic biomass data predicted by 3-PG into data of practical interest to forest managers. On the other hand, data on specific leaf area (Fig. 1b) suggested that site effects might be small.

There is some evidence in Fig. 2 that different allometric relationships apply to the three data sets. If so, this would be significant for older stands, and

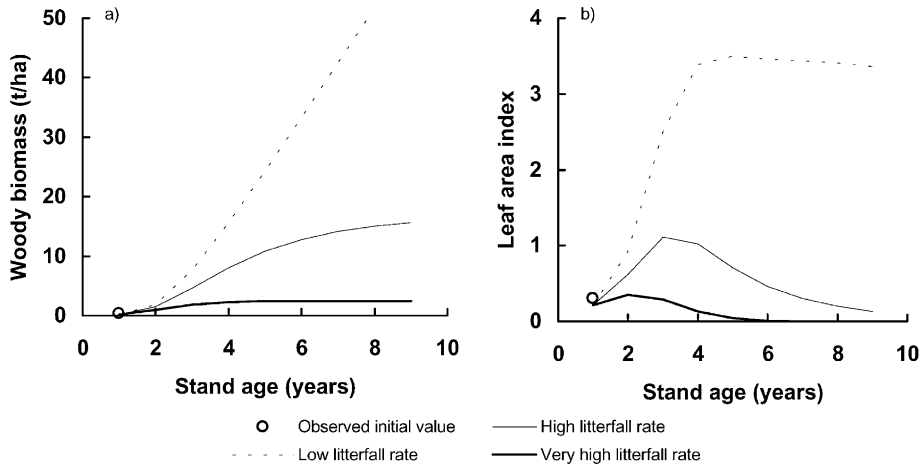


Fig. 10. Effect of litterfall rate on predictions of (a) woody biomass  $W_S$  and (b) leaf area index  $L$  at Esperance 4 (650 m). Predictions using the parameter values developed for *E. globulus* are shown as (- - -) for low litterfall rate ( $\gamma_F = 0.027$ ), (—) for high litterfall rate ( $\gamma_F = 0.1$ ), and (—) for very high litterfall rate ( $\gamma_F = 0.2$ ).

have implications for the determination of outputs of interest to managers, e.g. mean stem diameter. Reed and Tomé (1998) found allometric relations in stands of *E. globulus* in Portugal were affected by irrigation, but not by fertilisation: irrigation increased  $w_S$  by 5% for the larger trees. More importantly, for the same stem diameter, their stems had about 90% the mass of those in this study. This may be a regional difference,

or due to differences between *E. globulus* provenances (which are unknown), but emphasises that basic parameters should be tested between distinct regions or material.

3-PG applies the allometric relationship between stem mass and diameter directly to the stand-based means of tree biomass and stem diameter. However, the data available for determining this relationship are

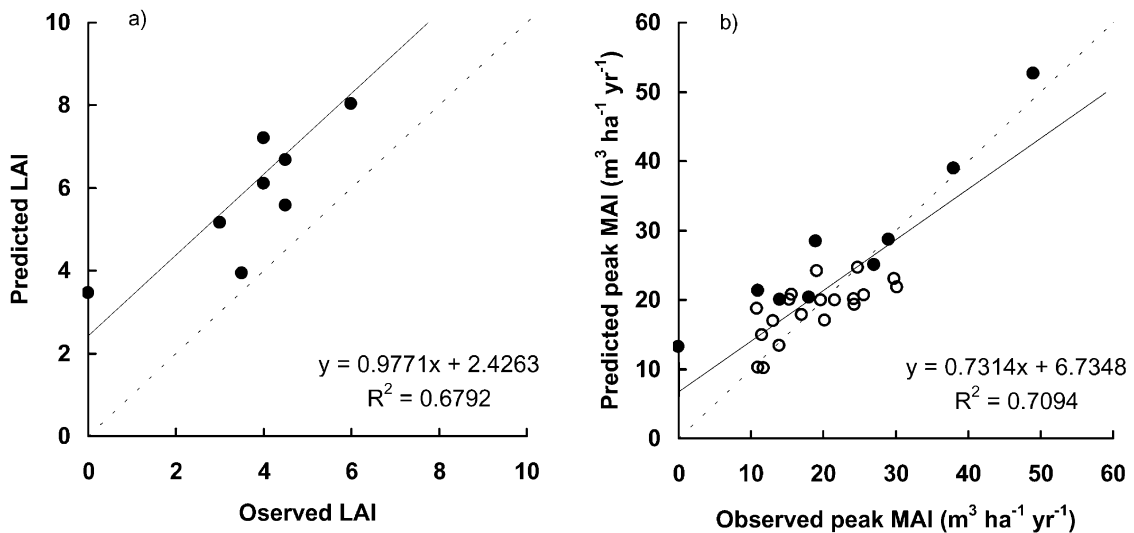


Fig. 11. Comparison of observed and predicted (a) closed canopy LAI, and (b) peak mean annual increment MAI over a 25-year rotation at 28 *E. globulus* sites in Tasmania and Western Australia. Data from calibration sites are shown as (●), and from validation sites as (○). One-to-one lines are shown as (- - -), and (—) are regression lines.

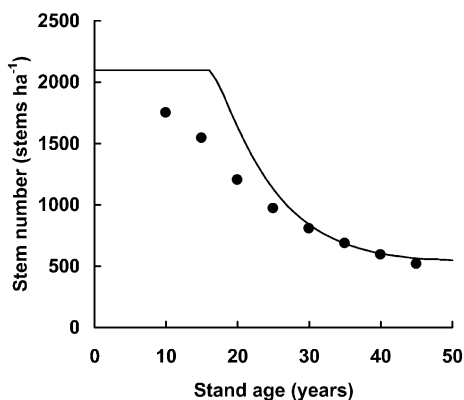


Fig. 12. Comparison of the observed (—) and predicted (●) stand stem number over an extended period at a site in northern Tasmania, showing how 3-PG predictions fail to reproduce observed early on-set of mortality.

more usually single-tree data (as here), and because the exponents in this relationship are high (typically 2.5–3), there can be significant effects of non-linearity. This area needs further attention, and may entail inclusion of a predictive model of stem diameter distribution.

Only a limited number of parameters were assigned values or directly estimated specifically for *E. globulus* in this study (see Table 1). This was because of the data available and the structure of the model. As no data were available for rigorous testing or parameter estimation of the water balance sub-model, nor were any data available on root biomass dynamics, default values from other studies were assumed for the various parameters in these relationships.

The manner in which factors that potentially affect water use are incorporated in the model make a rigorous examination and estimation of these relationships difficult even when time-series data on soil water content are available. For example, to properly separate out the effects of VPD and available soil water or canopy conductance will require some means of independently identifying the relevant modifiers ( $f_{VPD}$  and  $f_{SW}$ ) with physiological factors, e.g. dawn water potentials. Sap-flow data might also provide a means of validating or estimating the water balance side of the model through its connection to transpiration.

Without data on root dynamics it is not possible to parameterise the relationship for root biomass partitioning, or to separate effects of site fertility on

root partitioning and canopy quantum efficiency, or to distinguish between variations in the ratio  $Y$  of net to gross primary production, and quantum efficiency. This is because the growth rate of both stem and foliage biomass is proportional to the product  $(1 - \eta_R)\alpha_C Y$ . Now,  $\alpha_C = f_T f_E f_N \varphi \alpha_{Cx}$ . Granted that independent data has fixed  $f_T, f_E$  and  $\varphi$ , it follows that estimation based on stem and foliage biomass can only determine the product  $(1 - \eta_R)f_N \alpha_{Cx} Y$ . Hence, without data on root biomass and root turnover rate to enable parameters in  $\eta_R$  to be independently estimated, it is impossible to separate effects of fertility rating FR on root biomass partitioning from its effects on canopy quantum efficiency. This study therefore assumed  $f_N = 1$  and  $m = FR$ . It is also impossible to determine separately  $\alpha_{Cx}$ ,  $Y$  and the parameters  $\eta_{Rn}$  and  $\eta_{Rx}$ .

During this study, 3-PG was subject to a thorough examination of its basic assumptions. Structural changes from Landsberg and Waring (1997) were required. First, a temperature-dependent growth modifier affecting canopy quantum efficiency, but not canopy conductance, was introduced to reduce production on cool sites relative to warm sites. Second, simulation of canopy development prior to canopy closure required that specific leaf area be age-dependent. An empirical relationship parameterised with observed data on specific leaf area was used. Finally, the conversion of predicted stem biomass into outputs of practical relevance to forest managers, such as stem volume or MAI, required that the fraction of stem biomass as branch and bark be age-dependent. An empirical relationship parameterised from observed data was used. Basic density is entered as a parameter, although it too will vary with growth conditions and (possibly) stand age.

Our testing of 3-PG emphasised tests of its individual components. Unless the individual components of a model function properly, confidence in the model is low, especially when applied close to or beyond the boundary of conditions employed during its development. This is consistent with the approach advocated by Passioura (1973) for establishing testable and useable models. Accordingly, 3-PG's failure to properly predict early canopy development, litter-fall and mortality, are areas that need addressing even though their consequences for predicted productivity were minor.



A simple, flexible implementation (3PGpjs) of 3-PG as Visual Basic macros using Excel spread-sheets for the user interface and data input and output (Sands, 2000) was built as a result of this examination of 3-PG. Errors and inconsistencies in earlier implementations were corrected, and modifications introduced in this study were included. The use of 3PGpjs, together with changes in the way key functional relationships in the model were parameterised (i.e. so that parameters had direct or intuitively obvious biological meanings) facilitated the parameterisation process.

All fitting was by hand, and all runs were made using 3PGpjs. There are significant advantages to be gained through use of automated non-linear parameter estimation techniques, e.g. generalised least squares and Levenburg–Marquardt algorithms (Marquardt, 1963; Press et al., 1986). For instance, more than the very small number of parameters considered above can be readily estimated simultaneously, a much better optimal fit can be obtained, and standard errors on the estimated parameters can be obtained. Although suitable software was not available for this study, Visual PEST (Waterloo Hydrogeologic, 2000) is now being used to parameterise 3-PG for *E. grandis* (Williams, personal communications). However, our experience has shown that manual estimation is possible, especially when coupled with an intimate knowledge of the system or model.

## 7. Concluding remarks

A set of parameters for 3-PG which characterise growth of *E. globulus* in even-aged, intensively-managed, and fertilised stands was determined by fitting 3-PG output to observed stand leaf area index and stem biomass data. Specific leaf area and branch-plus-bark fraction were made age-dependent, and a temperature-dependent modifier of canopy quantum efficiency was introduced. Parameters in the allometric relationship between stem biomass and diameter, the age dependences of specific leaf area and the branch-plus-bark fraction, and leaf litterfall rate, were assigned on the basis of independent data from *E. globulus* stands. Other species-specific parameters were determined by fitting 3-PG output to observed data. These were maximum canopy quantum efficiency, the cardinal temperatures for canopy

production, and the ratio of foliage-to-stem biomass partitioning ratio. Only multiplicative combinations of some sets of parameters could be estimated because available data did not allow their effects in 3-PG to be separated. These and other parameters were given default values, e.g. from Landsberg and Gower (1997).

It was found that possible effects of environmental factors on litterfall should be included, especially the effects of extensive frosts, that the early phase of canopy development needs more detailed attention, and that early mortality was not accounted for by the mortality submodel.

It is concluded that 3-PG, as modified here together with the parameter values in Table 1, provides a useful tool for modelling the time-course of stand development of intensively managed, even-aged *E. globulus*, given observed initial biomass data and stem number. Further, it can be used as a predictive tool for modelling long-term stand development when initialised with typical seedling stock at age 0, even though early stand development is quite sensitive to assumed initial biomass data.

## Appendix A. Changes incorporated into 3-PG

This Appendix A details changes made to 3-PG as part of this study, including changes in how key relationships were parameterised. It presumes familiarity with Landsberg and Waring (1997).

### A.1. How environmental modifiers are taken into account

A modifier  $f_T(T_a)$  that depends on the monthly mean temperature  $T_a$  has been introduced. The definition of  $f_T$  is

$$f_T(T_a) = \left( \frac{T_a - T_{\min}}{T_{\text{opt}} - T_{\min}} \right) \times \left( \frac{T_{\max} - T_a}{T_{\max} - T_{\text{opt}}} \right)^{(T_{\max} - T_{\text{opt}})/(T_{\text{opt}} - T_{\min})} \quad (\text{A.1})$$

where  $f_T = 0$  if  $T_a \leq T_{\min}$  or  $T_{\max} \leq T_a$ , and  $T_{\min}$ ,  $T_{\text{opt}}$  and  $T_{\max}$  are the minimum, optimum and maximum temperatures for net photosynthetic production, and known as cardinal temperatures. A modifier  $f_N(\text{FR})$

which depends linearly on the site fertility rating FR has also been introduced:

$$f_N(\text{FR}) = f_{N0} + (1 - f_{N0})\text{FR} \quad (\text{A.2})$$

where  $f_{N0}$  is the value of  $f_N$  when  $\text{FR} = 0$ .

The modifiers  $f_{\text{VPD}}$  and  $f_{\text{SW}}$  (see Landsberg and Waring, 1997) reduce both canopy conductance ( $g_c$ ) and canopy quantum efficiency ( $\alpha_c$ ) through a multiplier  $\varphi$  defined by

$$\varphi = f_{\text{age}} \min\{f_{\text{VPD}}, f_{\text{SW}}\}. \quad (\text{A.3})$$

Here,  $f_{\text{age}}$  is the age-dependent modifier simulating possible decline in hydraulic properties with age (Eq. (3) in Landsberg and Waring, 1997). The temperature, frost and nutrition modifiers affect  $\alpha_c$  multiplicatively because these are assumed to have independent effects on photosynthesis. Thus,

$$\alpha_c = f_T f_F f_N \varphi \alpha_{c_x} \quad (\text{A.4})$$

where  $\alpha_{c_x}$  is the theoretical maximum canopy quantum efficiency. The relationship between gross primary production  $P_G$  and PAR absorbed by the canopy ( $\phi_{\text{pa}}$ ) is then given by

$$P_G = \alpha_c \phi_{\text{pa}} = f_T f_F f_N \varphi \alpha_{c_x} \phi_{\text{pa}} \quad (\text{A.5})$$

## A.2. Biomass partitioning

The relationship for the root biomass partitioning ratio  $\eta_R$  is now parameterised by the maximum and minimum partitioning ratios  $\eta_{R_x}$  and  $\eta_{R_n}$  so

$$\eta_R = \frac{\eta_{R_x} \eta_{R_n}}{\eta_{R_n} + (\eta_{R_x} - \eta_{R_n})m\varphi}, \quad (\text{A.6})$$

where  $m$  is given by Eq. (A.7) below. With parameters from Eq. (15) of Landsberg and Waring (1997),  $\eta_{R_x} = 0.8$  and  $\eta_{R_n} = 0.25$ . The variable  $m$  in Eq. (A.6) depends linearly on site fertility rating:

$$m = m_0 + (1 - m_0)\text{FR} \quad (\text{A.7})$$

where  $m_0$  is the value of  $m$  for sites of poor fertility, i.e.  $\text{FR} = 0$ .

Landsberg and Waring (1997) based above-ground partitioning on observed allometric relationships between foliage and stem biomass, and stem diameter  $B$  (cm). Their key result was that the ratio  $p_{\text{FS}} = \eta_F / \eta_S$  of foliage biomass partitioning to stem biomass partitioning is also an allometric function of stem

diameter  $B$ , i.e.

$$p_{\text{FS}} = a_p B^{n_p} \quad (\text{A.8})$$

where in terms of the original allometric parameters  $a_F$  and  $n_F$ , and  $a_S$  and  $n_S$ ,

$$a_p = \frac{a_F n_F}{a_S n_S}, \quad n_p = n_F - n_S \quad (\text{A.9})$$

However, after canopy closure  $W_F$  is in quasi steady-state whereas  $B$  continues to grow, so the allometric relationship between  $W_F$  and  $B$  breaks down. Therefore, in the modified 3-PG biomass partitioning is based directly on Eq. (A.8). Further, it is easier to understand the behaviour of the partitioning relationships if  $p_{\text{FS}}$  is parameterised in terms of its values  $p_2$  and  $p_{20}$  at  $B = 2$  and 20 cm, respectively, rather than in terms of  $a_p$  and  $n_p$ . Given  $p_2$  and  $p_{20}$

$$n_p = \frac{\ln(p_{20}/p_2)}{\ln 10}, \quad a_p = \frac{p_2}{2^{n_p}}. \quad (\text{A.10})$$

For example, if  $p_2 = 1$  and  $p_{20} = 0.15$ , then  $n_p = -0.824$  and  $a_p = 1.77$ .

## A.3. Litterfall

The relationship for the monthly litterfall rate  $\gamma_F$  is now parameterised by the rate of litterfall at age 0 ( $\gamma_{F0}$  (per month)), the maximum rate of litter fall ( $\gamma_{F_x}$  (per month)), and the age ( $t_{\gamma F}$  (months)) at which the litterfall rate is  $\frac{1}{2}(\gamma_{F0} + \gamma_{F_x})$ . Then

$$\gamma_F(t) = \frac{\gamma_{F_x} \gamma_{F0}}{\gamma_{F0} + (\gamma_{F_x} - \gamma_{F0}) e^{-k_\gamma t}} \quad (\text{A.11})$$

$$k_\gamma = \frac{1}{t_{\gamma F}} \ln \left( 1 + \frac{\gamma_{F_x}}{\gamma_{F0}} \right) \quad (\text{A.12})$$

where  $t$  is stand age in months. The relationships between the new and old parameters are:

$$\gamma_{F0} = \frac{\gamma_{F_x}}{(1 + c_\gamma)}, \quad t_{\gamma F} = \frac{1}{k_\gamma} \ln(2 + c_\gamma). \quad (\text{A.13})$$

With parameters from Eq. (7) of Landsberg and Waring (1997),  $\gamma_{F_x} = 0.02$  per month,  $\gamma_{F0} = 0.00125$  per month and  $t_{\gamma F} \approx 24$  months.

## A.4. Stem mortality

Stem mortality is determined by using the self-thinning rule (Eq. (8), Landsberg and Waring, 1997) to

determine the maximum permissible single-tree stem biomass  $w_{Sx}$  (kg per tree) as a function of the current stem number  $N$  (trees  $\text{ha}^{-1}$ ). This has been rewritten as

$$w_{Sx} = w_{Sx1000} \left( \frac{1000}{N} \right)^{3/2} \quad (\text{A.14})$$

where  $w_{Sx1000}$  (kg per tree) is the value of  $w_{Sx}$  when the stem number is 1000 trees per hectare (Note that if the stem number is 1000 trees per hectare, then this equation implies that the total stem biomass on the stand at which self-thinning commences is about  $w_{Sx1000}$  t  $\text{ha}^{-1}$ ). Iterative application of the self-thinning law is required to ensure it is satisfied for the new state. When stems are removed it is assumed that each stem removed has approximately 20% of the biomass of the average stem, and that no foliage biomass is lost.

#### A.5. Specific leaf area depends on stand age

Specific leaf area as a function of stand age  $t$  (years) is given by the empirical relationship

$$\sigma = \sigma_1 + (\sigma_0 - \sigma_1) e^{-(\ln 2)(t/t_\sigma)^2} \quad (\text{A.15})$$

where  $\sigma_0$  and  $\sigma_1$  ( $\text{m}^2 \text{kg}^{-1}$ ) are specific leaf areas at age 0 and for mature stands, respectively, and  $t_\sigma$  (years) is the stand age at which  $\sigma = \frac{1}{2}(\sigma_0 + \sigma_1)$ .

#### A.6. Calculation of stand volume

Stand volume  $V$  ( $\text{m}^3 \text{ha}^{-1}$ ) is determined from stem biomass  $W_S$  ( $\text{t ha}^{-1}$ ) and basic density  $\rho$  ( $\text{t m}^{-3}$ ), and is discounted for the fraction  $p_B$  of above-ground woody biomass as branch and bark:

$$V = \frac{(1 - p_B)W_S}{\rho} \quad (\text{A.16})$$

Observations from a range of eucalypt stands show  $p_B$  declines with stand age:

$$p_B = p_{B1} + (p_{B0} - p_{B1}) e^{-(\ln 2)t/t_{pB}} \quad (\text{A.17})$$

where  $p_{B0}$  and  $p_{B1}$  are branch and bark fractions at age 0 and for mature stands, respectively, and  $t_{pB}$  (years) is the stand age at which  $p_B = \frac{1}{2}(p_{B0} + p_{B1})$ .

#### A.7. Other modifications to early 3-PG implementations

Other modifications to the early implementation of 3-PG were as follows. The daylength associated with

each month is computed from site latitude, and is the daylength on the 15th day of each month. An attempt has been made to ensure that the model is properly state-determined, so all intermediate variables and all explicitly age-dependent variables are determined from the state of the system at the beginning of a time step, and all output variables are determined from the state at the end of a time step. The annual output from 3-PG included canopy LAI at the end of the year. Because LAI can vary seasonally, this was changed to an annual average of LAI. If output is monthly, LAI is the monthly value. The start of a growth season is arbitrary, but by default is January for northern latitudes, and July in the southern hemisphere.

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