Application of sensitivity analysis to a model of *Eucalyptus globulus* plantation productivity.

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Abstract

A simple forest growth model, PROMOD, has been developed to assess potential productivity by plantation grown *Eucalyptus globulus*. Although PROMOD was intended for use primarily as a simple screening test for potential plantation sites, it has wider application as it is based on a sound understanding of the basic physiology of tree growth and explicitly incorporates simple but realistic models for key physiological processes. Output from PROMOD is affected by the processes included as part of the model structure, the physiological parameters characterising these processes, and the variables characterising the climate and soil of a site. A sensitivity analysis based on predicted net total annual production (G_a) and annual water use efficiency (ω_a) was applied to the structure of PROMOD and to its parameter values. Sensitivity to climatic and site variables was not considered. The sensitivity analysis with respect to model structure showed that, with the possible exception of the temperature dependence of respiration, simplification of any of the processes included in PROMOD resulted in a loss of generality. The sensitivity analysis of the physiological parameters show that G_a and ω_a are highly sensitive to a small subset of parameters: the light saturated photosynthetic rate, the shape of the light response curve and its dependence on temperature, the low temperature response of LAI, and parameters in the relationship between water use efficiency and VPD. Importantly, there is little or no sensitivity to some difficult to measure parameters. In many cases sensitivity varied significantly from site to site. This information is important when PROMOD is to be parameterised for different species, and has an impact on traits to be selected for in a tree-breeding program.

1.1 Introduction

Many complex, highly-parameterised models of forest or tree growth describe the underlying physiological processes in great detail and with presumed realism. At the other end of the spectrum are a large number of simple models developed for specific management or research applications. Such models claim to capture the essential components of the system and remain phenomenologically "true", but are nevertheless simple enough to allow quantification of system fluxes at many locations. The link between these two scales of application is not always clear: that is, it is not readily apparent what criteria have been used to determine the structure of the simple models, and in particular to select which processes are included. Furthermore, most parameters in growth models are estimated from a restricted experimental base. The consequences of inaccuracy in these estimates, and the extent to which the model's predictions can be improved by better parameter estimates, often remain undefined. Although a comparison of a model's outputs with observed data can give some confidence in its structure and parameter values, model validation often faces the problem of insufficient or inaccurate data, or data that covers only a limited range of environmental conditions. This is especially the case with tree-growth models because the spatial and temporal scales inherent in production forestry generally exceed the scale of basic research projects.

This paper reports a sensitivity analysis of a simple forest growth model, PROMOD (Battaglia and Sands, 1997a), intended for use primarily to screen potential plantation sites. In the present paper, simpler formulations of process-based sub-models are substituted into PROMOD to test the extent to which their inclusion changes the model's predictive power. This paper also reports results from a sensitivity analysis of PROMOD's physiological parameters. This analysis serves two functions. Firstly, it indicates which parameters must be accurately determined if PROMOD is to be applied to species other than that for which it was initially parameterised (*Eucalyptus globulus*), and those for which approximate values will suffice. Secondly, in so far as the model realistically represents plant function, the sensitivity of its output to physiological parameters provides an indication of traits that may have value in a tree-breeding program. In this context, the interaction between physiological traits and the environment is of particular interest because changes in some physiological parameters may affect model output on all sites, whereas changes in others may be most marked under particular environmental conditions. This will suggest which traits could be targeted in a breeding-program designed to provide an improvement in general performance, and which could be targeted to improve performance under particular environments or site conditions.

The results obtained from any sensitivity analysis of either the structure or parameters of a model depend heavily on the actual values of the parameters of the model being studied (Waide and Webster, 1976). This is

because the behaviour of the system can undergo important changes as a result of non-linear physiological responses to driving variables, and because output can be a strongly non-linear function of physiological parameters. Our sensitivity analysis investigates these effects by considering PROMOD's predictions at each of nine sites with contrasting environments, and by considering joint variation of pairs of parameters.

1.2 The productivity model ProMod

PROMOD predicts the leaf area index, annual biomass production and water use, and peak MAI of a plantation following canopy closure. It is intended primarily for screening prospective plantation sites. PROMOD requires only simple input data of a quality and quantity that forest managers can readily and cheaply obtain. This data comprises site latitude, simple soil factors and climatic data. The soil factors are maximum soil water storage, the degree to which the soil is prone to water-logging and a rating of soil fertility. Climatic factors are daily values of maximum and minimum air temperatures, incoming solar radiation, precipitation and irrigation, vapour pressure deficit and open-pan evaporation. If daily values are not available, monthly means estimated using a bioclimatic package such as ESOCLIM (McMahon *et al.*, 1996) can be used.

PROMOD comprises empirical relationships for the closed-canopy leaf area index, a canopy photosynthetic production model, relationships for water use efficiency, evapotranspiration and respiration, a soil water balance model, and an empirical relationship for biomass partitioning into stem-wood. Net canopy production is calculated daily and then summed to give annual production. Biomass partitioning is applied annually. A detailed description of PROMOD is given in Battaglia and Sands (1997a). The present study is based on PROMOD parameterised for *E. globulus*. Table 1 lists the meaning and value of key parameters in PROMOD. Full details of parameterisation and validation are given in Battaglia and Sands (1997a).

1.3 Methods

1.3.1 Data used for sensitivity analysis

The data used in the sensitivity analysis are from 28 sites at which *Eucalyptus globulus* Labill. plantations had been established in three geographic regions of Australia, namely southern Tasmania, northern Tasmania and south-western Western Australia (Table 2). These regions represent quite different combinations of environmental conditions. The Northcliffe (WA) and Forcett (SE Tasmania) sites are among the most productive in temperate Australia. At others, production is severely limited by water, temperature or the interaction of these factors.

Table 1. Definition of those PROMOD physiological parameters subjected to sensitivity analysis

Name	Value	Units	Meaning
a_w	2.5		Slope of linear portion of crop-factor soil-water curve
A^*_{xpt}	17	μmol m^{-2}leaf s^{-1}	Optimum value of A_x
e_{c0}	0.325		Lower limit of $\bar{e}_{ca}$ for canopy development
k	0.5	m^{2}ground m^{-2}leaf	Canopy extinction coefficient
k_{d0}	0.09	°C^{-1}	Value of k_d at temperature $T=T_0$
k_{d1}	0.015	°C^{-1}	Temperature sensitivity of $k_d(T_{av})$
k_{dav}	0.03	°C^{-1}	Temperature rate constant for r_{dav}
k_M	0.026	°C^{-1}	Temperature rate constant for r_M
L_x	6.5	m^{2}leaf m^{-2}ground	Maximum value of L
r_{d0}	1	μmol m^{-2}leaf s^{-1}	Value of r_{dav} at temperature $T=T_0$
r_{M0}	0.3		Value of r_M at temperature $T=T_0$
$t_{1/2}$	11	°C	Determines sensitivity of A_x to low diurnal temperatures
$t^*_{1/2-}$	15	°C	Determines acclimation of A_{opt} to low seasonal temperatures
$t^*_{1/2+}$	25	°C	Determines acclimation of A_{opt} to high seasonal temperatures
T_{L0}	7.8	°C	Low-temperature threshold for leaf area index
T_{L1}	22	°C	High-temperature threshold for leaf area index
T_{Lopt}	13.5	°C	Optimum temperature for leaf area index
T_{pref}	23	°C	Parameter determining seasonal acclimation of T_{opt}
T^*_{opt}	15	°C	Optimum temperature for photosynthesis
w_0	0.3		Value of w for which $e_c=0.5$
α_0	0.05	mol mol^{-1}	Value of α at temperature $T=T_0$
α_1	0.016	°C^{-1}	Temperature sensitivity of α
θ	0.95		Shape of single-leaf light response curve
τ	0.2		Determines extent of seasonal acclimation of T_{opt}
ω_x	12.5×10^{-3}	kgDM kg^{-1}H$_2$O	Maximum water-use-efficiency
ω_0	7×10^{-3}	kgDM kPa kg^{-1}H$_2$O	Parameter in water-use-efficiency VPD function

Sources of all parameter values are given in Battaglia and Sands (1997a).

Table 2. Details of sites used in the sensitivity analysis. Peak MAI is in m³ha⁻¹yr⁻¹.

Table 2. Details of sites used in the sensitivity analysis. Peak MAI is in m³ha⁻¹yr⁻¹. The regions NT, ST and WA are Northern Tasmania, Southern Tasmania and Western Australia, respectively. Further details of sites, original sources of information, and details of predictions are in Battaglia and Sands (1997a).

Site name and region		Soil water store (mm)	Total annual radiation (GJ m⁻²)	Mean annual temp. (°C)	Mean annual rainfall (mm)	Mean annual evap. (mm)	Obs. peak MAI
Esperance 1	ST	187	4.81	10.6	1052	871	18
Esperance 2	ST	187	4.70	9.2	1295	794	27
Esperance 3	ST	187	4.56	9.2	1847	682	14
Esperance 4	ST	187	4.63	8.6	1628	650	0.1
Forcett	ST	170	5.00	12	1800	1444	38
Darkan	WA	221	6.50	16.4	590	1627	11
Manjimup	WA	510	6.12	15.6	950	1247	29
Mumbalup	WA	221	6.30	16.1	1050	1652	19.2
Northcliffe	WA	1000	5.94	16.4	1450	1262	48.6
V-1	NT	168	5.18	11.1	1145	1004	29.8
V-2	NT	168	5.06	10.5	1187	1035	24.3
V-3	NT	168	5.20	11.1	1087	1023	25.6
V-4	NT	168	5.21	12.2	1034	1031	24.2
V-5	NT	168	5.38	12.6	858	1096	19.1
V-6	NT	68	5.38	12.6	858	1096	13.1
V-7	NT	168	5.22	11.8	1084	1024	13.9
V-8	NT	149	5.33	12.1	903	1091	20.2
V-9	NT	55	5.25	11.4	954	1108	11
V-10	NT	122	5.16	10.9	1034	1076	17
V-11	NT	56	5.16	10.9	1034	1076	11.8
V-14	NT	168	5.14	10.7	1331	972	30.2
V-16	NT	168	5.17	10.7	1024	1052	15.6
V-18	NT	168	5.14	10.4	1159	1032	21.6
V-20	NT	149	5.27	12.3	990	1060	10.8
V-21	NT	168	5.29	12.4	964	1064	15.3
V-22	NT	168	5.29	12.4	964	1064	19.7
V-25	NT	50	5.22	11.4	973	1107	11.5
V-27	NT	168	5.07	10.4	1457	999	24.8

1.3.2 Structural sensitivity analysis

Six simplifications of PROMOD were independently tested for their effect on the goodness of fit of predicted to observed peak MAI: a) respiration rates is a fixed proportion of annual production; b) photosynthesis does not acclimate to seasonal temperatures but has a fixed temperature optimum; c) a simplified water-use model in which VPD does not affect water stress and in which stand evapotranspiration is determined only by soil water content; d) diurnal temperature variation is ignored and mean daily temperature is used to determine light utilisation efficiency and respiration rates; e) photosynthetic parameters are considered to be independent of temperature; f) leaf area index is assumed to be constant across all site conditions.

1.3.3 Parameter sensitivity analysis

Twenty-six physiological parameters from PROMOD were examined in the parameter sensitivity analysis. Table 1 gives the definition and normal operating value for *E. globulus* of each of these parameters. The relative sensitivity (defined below) of annual net biomass production and of water-use efficiency to variations of each parameter was computed and used to assess the sensitivity of PROMOD to changes in its parameter values. The *relative sensitivity* $\sigma(X; p)$ of an output variable X with respect to a parameter p is the change ΔX in X produced by a change Δp in p relative to the original values of X and p (Brylinsky, 1972), i.e. $\sigma(X;p)=(\Delta X/X)/(\Delta p/p)$.

The sensitivity of PROMOD to the parameters in Table 1 was tested at each of the 9 southern Tasmanian and Western Australian sites. For each parameter, PROMOD was run with that parameter set at its nominal value and perturbed by ±10%, ±20% and ±30% of the nominal value.
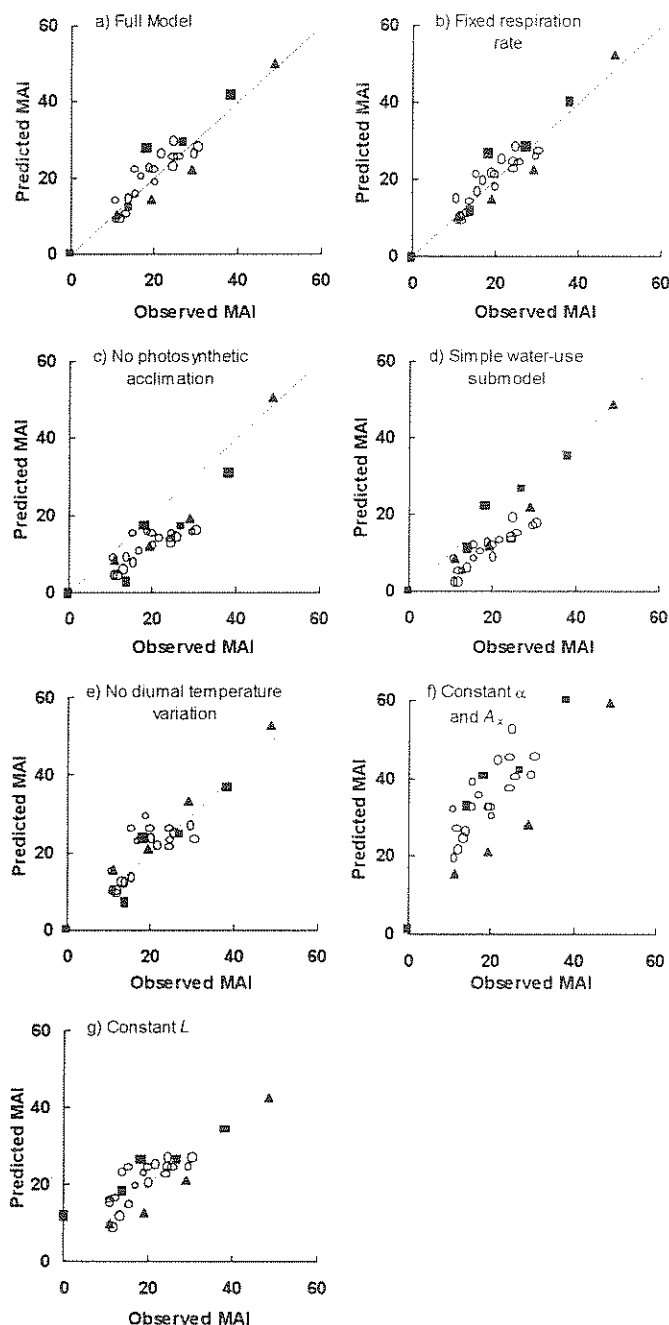

Figure 1. Comparison of predicted and observed peak MAI for the original model and the 6 simplifications described in the text. Data is shown for the NTas (O), STas (■) and WA sites (▲).

1.4. Results

1.4.1 Structural sensitivity analysis

Fig. 1 compares predicted and observed site productivity (peak MAI) resulting from the six model simplifications described above. The original model adequately predicts productivity (Fig. 1a) within each of the three geographic regions (r^2=0.88), and shows no evidence of bias. This suggests that PROMOD has sufficient generality (*sensu* Stapper, 1986) to deal with the multiple and simultaneous constraints of temperature, VPD, soil water, fertility, and waterlogging.

a) Respiration rates are independent of temperature

In this simplification respiration was treated as a constant fraction of daily carbon uptake, so assimilate use efficiency Y is constant. Output from the full model shows that Y varies little over the 28 sites, i.e. Y=0.46±0.009, so in this simplification Y was assigned the fixed value 0.46. Comparison of Figs. 1a and 1b show this hardly changed the model's predictive quality across all sites. This suggests that for the range of environments represented in the study sites (mean annual temperature 8 to 16°C) a detailed consideration of respiration adds little to predictions at the time and spatial scale applied. However, the assumption of constant respiration rates might need to be re-examined if production at much warmer sites is considered, e.g. in Portugal where mean summer night-time temperatures exceed 20°C.

b) Photosynthesis does not acclimate to seasonal temperatures

The removal of seasonal photosynthetic temperature acclimation from PROMOD resulted in reduced goodness of fit to observed MAI (r^2=0.62). Predicted MAI (Fig. 1c) at all but one site (Northcliffe) is reduced, and there is consistent bias in the predicted MAI. The degree of reduction was slight on warm sites but marked on cold sites. The net result of the removal of photosynthetic acclimation from PROMOD is to introduce a bias related to site mean annual temperature. This bias could be partially removed by increasing the light-saturated photosynthetic rate, but this would place A^*_{opt} somewhat larger than values observed in the field. However, there would still be a loss of generality of PROMOD because of the differentiation of cool and warm sites.

c) A simplified water-use model

Simplification of the water-use model clearly differentiates geographic regions (Fig. 1d), with sites in Western Australia and southern Tasmania in one group and sites in northern Tasmania in another. The simplified water-use model imposes an inherently stronger limitation due to soil-water stress than does PROMOD, but relaxes the constraint on water-use efficiency due to high VPD. As a result there is a general decrease in production at water limited sites a), but this may be mollified at sites which experience high VPD. The southern Tasmanian sites are largely free of soil water limitations, so changing the water-use model has a negligible effect at these sites. The northern Tasmanian sites are all water-limited to some extent, but generally experience only low VPD, so the simplification results in reduced production overall. The Western Australian sites experience both significant soil water stress and high VPD, and as noted above, in the simplified model these two effects counter each other so there is little net change in production relative to PROMOD. Simplification of the water-use model has thus reduced the generality of PROMOD, although within a particular region the correlation between observed and predicted production is still high.

d) Diurnal temperature variation is ignored

Removal of the effects of diurnal temperature variation on photosynthetic rate decreased production on the cooler sites (Fig. 1e) but had little effect on production on the warmer sites where temperatures are closer to the optimum for photosynthesis. The effect was most marked on sites with strong diurnal temperature variations, in particular the higher altitude Tasmanian sites, and a large number of the northern Tasmanian sites are no longer differentiated. This indicates that even if predictions are required on only an annual time step, the use of mean daily temperature alone is insufficient for reasonable estimates of production (r^2=0.82 in Fig. 1e) and maximum and minimum temperatures are both required. Using the day-time mean temperature improved the fit (r^2=0.87) but led to a significant bias in the estimates, and would still require knowledge of mean maximum and minimum temperatures (Sands, 1995). Thus, ignoring diurnal temperature variations results in loss of generality.

e) Photosynthetic parameters are independent of temperature

If the temperature sensitivity of photosynthesis is ignored, light use efficiency is independent of temperature and consequently temperature directly affects production only through closed canopy leaf area index. Fig. 1f shows that the model's predictive power relative to the full model is decreased and there is both a general and marked overestimation of production and an increase in scatter (r^2=0.69). Under this simplification the light saturated photosynthetic rate A_x was assumed to be at its optimum value. As a result the MAI predicted for the cool Tasmanian sites is almost double the observed MAI, but MAI predicted for the Western Australian sites is close to the observed MAI. To some extent the over-estimation of production can be removed by reducing A_x to typical average daily values for each region. The scatter in Fig. 1f arises in part from the fact that distinct temperature regimes are experienced at sites in Western Australia and at low and high altitude sites in Tasmania, and in part from the fact that the primary limitation to growth at some

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sites is temperature whereas at others it is water stress. As a result, the appropriate value for A_x would be region-specific. Thus, the removal of the temperature dependence of photosynthesis leads to a marked loss of generality across sites of radically differing temperature regimes.

f) Leaf area index is constant

When L is treated as a constant across all sites the response of the model to site conditions is decreased (Fig. 1g). Under this simplification predicted differences in site productivity are based on ε and annual PAR alone. L usually increases as site quality increases and so the proportion of intercepted PAR increases. The converse applies as site quality declines. Consequently, making L constant over-estimates production on poor sites and under-estimates on good sites. Although both predicted L and ε are correlated with observed site productivity ($r^2=0.63$ for L and 0.24 for ε), a good estimate of productivity requires consideration of both factors ($r^2=0.88$ for the full model). The simplification of PROMOD by ignoring site and climatic effects on L leads to poor discrimination of sites and loss of generality.

1.4.2 Parameter sensitivity analysis

a) Net annual production as a function of parameter values

The dependence of net annual production G_a as a function of selected parameters is shown in Fig. 2 at four contrasting sites. These figures are typical for parameters with respect to which G_a is strongly (e.g. $A*_{opt}$ and $t_{1/2}$) or moderately (e.g. k and r_{d0}) sensitive and for which sensitivity exhibits no (e.g. r_{d0}) or strong (e.g. ω_0 and T_{Lopt}) site-dependence. Others (e.g. α_1, k_{d0} and k_{d1}, not shown) show a completely flat response at the four sites

b) Relative sensitivity and environmental variation

Mean sensitivity and environmental variation of sensitivity in Table 3 have been ranked using a simple scheme, based on the distribution of values of μ and $\mu \times E$, and conveniently differentiates parameters to which output from PROMOD is or is not sensitive. Table 3 provides a simple summary of graphs similar to Fig. 4 for all 26 parameters studied in this sensitivity analysis. For instance, Fig. 2b shows that $A*_{opt}$ has high sensitivity across all sites, and from Table 3 it receives a ranking of 3 for μ but only 1 for $\mu \times E$. Fig. 42 shows that the sensitivity of T_{Lopt} is strongly site dependent, and from Table 3 it receives a ranking of 4 for $\mu \times E$.

Examination of Table 3 shows a group of parameters with respect to which output from PROMOD is basically insensitive. These are parameters determining the seasonal temperature acclimation of leaf respiration (k_{d0} and k_{d1}), the temperature response of quantum efficiency (α_1), the seasonal temperature variation of optimum light-saturated photosynthetic rate ($t*_{1/2-}$ and $t*_{1/2+}$), and the response of canopy leaf area development (e_{C0}) and water use (a_w and w_0) to soil water content. If PROMOD is parameterised for another species, there is no need to determine accurate values for these parameters. However, parameters determining seasonal temperature acclimation of photosynthesis (τ) and the optimum temperature for photosynthesis ($T*_{opt}$) have a sensitivity ranking of 1, and $T*_{opt}$ has an environmental variation of sensitivity ($\mu \times E$) ranking of 3, so care is required when values are assigned to these parameters for species with a radically different temperature range to that for $E.\ globulus$.

The parameters with the highest sensitivity ranking are those which determine the light saturated photosynthetic rate ($A*_{opt}$) and its diurnal temperature variation ($t_{1/2}$), the shape of the light response curve (θ), a parameter determining the seasonal temperature acclimation of photosynthesis (T_{pref}) and the cardinal temperatures for canopy development (T_{L0}, T_{Lopt} and T_{L1}). With the exception of $A*_{opt}$, these parameters also have a very high $\mu \times E$ ranking. It is important that accurate values be obtained for these 7 parameters when PROMOD is extended to novel species.
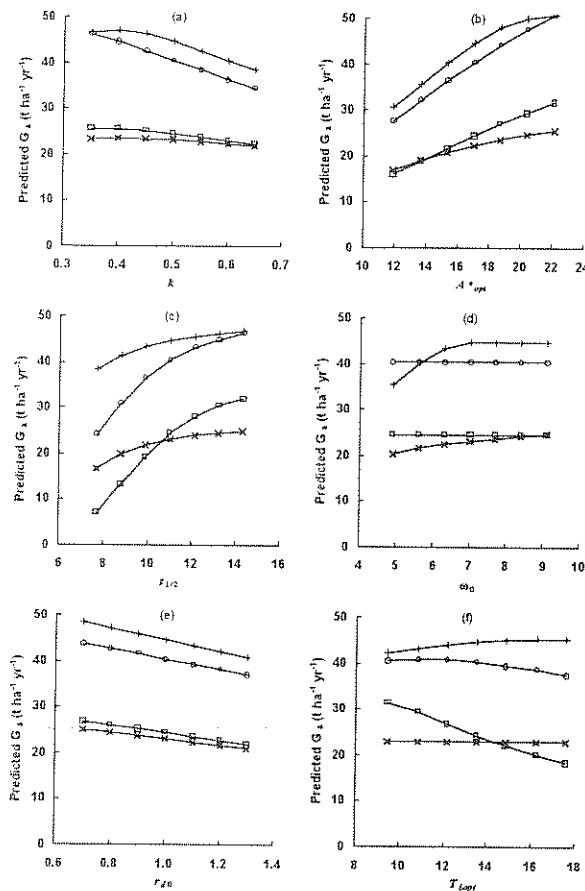

Fig. 2. Predicted annual net production G_a as a function of parameters (a) k, (b) $A*_{opt}$, (c) $t_{1/2}$, (d) ω_0, (e) r_{d0} and (f) T_{Lopt} at sites Esperence 3 (□), Darkan (×), Forcett (○) and Northcliffe (+).

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Table 3. The sensitivity of annual net canopy production (G_a) and annual canopy water-use efficiency (ω_a) to 30% variation of model parameters above and below the normal operating value. The mean sensitivity (μ) is the mean of relative sensitivity of G_a or ω_a to the given parameter across the 9 Western Australian and Southern Tasmanian sites. The environmental variation ($\mu \times E$) of sensitivity is the variability of relative sensitivity as measured by the coefficient of variation of mean relative sensitivity across the 9 sites. Ranking of sensitivity and variability is on a scale with 0 low and 4 high.

| Parameter | Mean sensitivity (μ) | | | | Environmental variation ($\mu \times E$) | | | | Ranking of sensitivity | |
| | G_a | | ω_a | | G_a | | ω_a | | | |
	−	+	−	+	−	+	−	+	μ	$\mu \times E$
k_{d1}	0.00	0.00	0.00	0.00	-36	-36	-36	-36	0	1
k_{d0}	0.00	0.00	0.00	0.00	-70	-63	-70	-63	0	1
α_1	0.02	0.02	0.01	0.01	36	36	12	11	0	1
$t^*_{1/2+}$	0.04	0.02	0.02	0.01	122	129	122	115	0	2
$t^*_{1/2-}$	0.02	0.01	0.01	0.00	157	157	150	149	0	3
w_0	-0.04	-0.04	0.01	0.01	-103	-98	147	142	0	3
e_{c0}	-0.03	-0.06	-0.01	-0.02	-175	-179	-177	-183	0	3
a_w	0.00	0.00	0.00	0.00	124	126	219	202	0	4
τ	0.17	0.16	0.06	0.05	91	100	77	76	1	2
T^*_{opt}	0.08	-0.07	0.03	-0.03	91	-162	105	-143	1	3
r_{d0}	-0.31	-0.31	-0.31	-0.31	-10	-10	-10	-10	2	0
r_{M0}	-0.44	-0.44	-0.44	-0.44	-7	-7	-7	-7	2	0
k_{dav}	0.35	0.19	0.35	0.19	49	43	49	43	2	1
α_0	0.38	0.19	0.15	0.07	17	20	30	27	2	1
k_M	0.41	0.23	0.41	0.23	33	29	33	29	2	1
ω_0	0.31	0.10	0.67	0.34	83	116	17	54	2	2
L_x	0.36	0.22	0.03	0.02	65	114	142	133	2	3
k	-0.10	-0.28	0.09	0.02	-177	-61	22	297	2	4
ω_x	0.14	0.00	0.58	0.17	100	288	42	108	2	4
T_{Lopt}	-0.62	-0.31	0.00	0.00	-262	-143	928	-206	2	4
A^*_{opt}	0.97	0.64	0.40	0.22	18	41	22	17	3	1
$t_{1/2}$	1.41	0.56	0.78	0.18	55	89	69	53	3	2
T_{pref}	-0.87	-2.29	-0.27	-1.79	-92	-36	-44	-71	3	2
θ	0.42	1.41	0.14	0.36	133	122	152	152	3	3
T_{L0}	-0.94	-1.00	0.00	0.07	-276	-142	-205	213	3	4
T_{L1}	1.48	0.00	0.21	0.00	120	305	167	-305	3	4

The remaining parameters have moderate sensitivity and determine the quantum efficiency (α_0), the basic level of respiration (r_{d0} and r_{M0}) (and hence the value of Y), the dependence of respiration on long-term temperatures (k_{dav} and k_M), the peak canopy leaf area index (L_x), the maximum water use efficiency (ω_x) and its dependence (ω_0) on VPD, and the canopy extinction coefficient k. Some of these have a high ranking for environmental variation, especially the parameters determining water use efficiency and maximum leaf area index, and would need to be determined accurately if the model is to apply across a wide range on environments.

The ranking imposed in Table 3 was based on the sensitivity of both annual net canopy production G_a and water use efficiency ω_a. Certain parameters affect primarily only one of these variables. For instance, parameters affecting L have negligible affect on canopy water use efficiency. This is because water use efficiency is tied strongly to the mechanism of photosynthesis, not the actual capture of light by the canopy. The parameters determining instantaneous water use efficiency have a far more pronounced effect on ω_a than on G_a. Surprisingly, the parameters with the highest sensitivity for ω_a are $t_{1/2}$, which determines diurnal variation of photosynthesis, and T_{pref}, which determines seasonal temperature acclimation of photosynthesis.

Comparison of the (−) and (+) sensitivities in Table 3 reveal marked nonlinearity in the sensitivity of several parameters. In the case of θ this is because photosynthesis is a highly nonlinear function of θ. In other cases the environmental range encompassed by the study sites does not impinge on the full range of the parameter in question. For instance, the nominal upper limit for canopy development is $T_{L1}=22°C$. Since the highest mean annual temperature at the study sites is only 16.5°C, increases in T_{L1} have little effect on L whereas decreases can have a marked effect. c) Joint sensitivity of pairs of parameters

Since PROMOD is nonlinear with respect to most of its parameters the calculated sensitivities depend on the values of the parameters. Further, uncertainties in parameter values are seldom confined to isolated parameters. It is therefore of interest to consider the effects of joint variation of selected parameters. Fig. 3 illustrates these effects for two contrasting pairs of parameters by displaying contour plots of peak MAI as a function of the parameters.
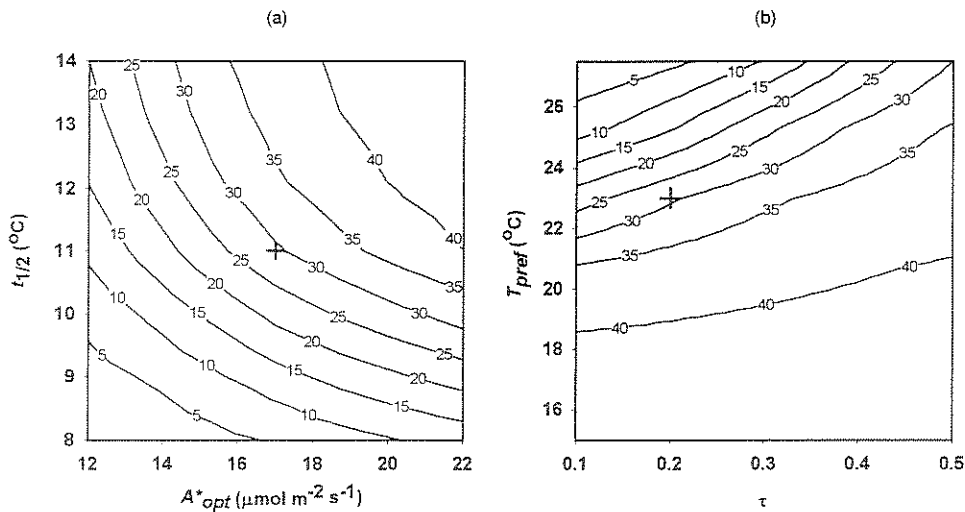
Fig. 3. Contour plots of predicted MAI (m^3 ha^{-1} yr^{-1}) at the site Esperence 2: (a) as a function of A^*_{opt} and $t_{1/2}$, and (b) as a function of τ and T_{pref}. The nominal values of these parameters for *E. globulus* are shown as +.

Close contours imply high sensitivity, and the slopes of the contours indicate the balance between the sensitivity with respect to each parameter alone. In Fig. 3, (a) illustrates a pair of highly sensitive parameters, and (b) one sensitive parameter with a high degree of nonlinearity paired with an insensitive parameter.

The effects of joint variation of parameters determining light-saturated photosynthetic rate (A^*_{opt}) and diurnal temperature variation of photosynthesis ($t_{1/2}$) around their nominal values (17 μmol m^{-2} s^{-1} and 11°C, respectively) are illustrated in Fig. 3a. If A^*_{opt} is above its nominal value, sensitivity of peak MAI decreases with increasing $t_{1/2}$. However, if A^*_{opt} is low, sensitivity of MAI increases with increasing $t_{1/2}$. Fig. 3a shows that these two parameters are located in a region of high mutual sensitivity. On the other hand, Fig. 3b illustrates the joint variation of the parameters which determine photosynthetic temperature acclimation, i.e. T_{pref} and τ (with nominal values 23°C and 0.2). Where predicted peak MAI is only weakly sensitive to one of the parameters (τ), variation in peak MAI is almost entirely due to the effect of the other (T_{pref}).

Parameter sensitivity also depends on site and environmental factors. Fig. 4 shows there is a large area of parameter space spanned by A^*_{opt} and ω_0 in which predicted productivity for each Esperence-2 and the Darkan is within 10% of the observed values (27 and 11 m^3 ha^{-1} yr^{-1}), but the area of overlap where both sites have a predicted productivity within 10% of the observed is much smaller. Thus, simultaneous prediction at multiple sites imposes constraints on parameter values. PROMOD also predicts annual canopy

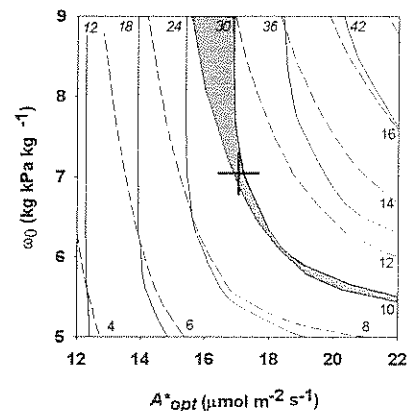water-use efficiency, and if this were also to be correctly predicted, the constraints would be even tighter.

Fig. 4. Contour plot of predicted MAI at Esperence 2 (———) and Darkan (– – –) as a function of the parameters A^*_{opt} and ω_0. The nominal parameter values are shown as +. The shaded area is the region in which the predicted MAI at both sites is within 10% of the observed MAI.

1.5 Conclusions

The results of the structural sensitivity analysis reveal a compromise inherent in modelling: where it is possible to design a simpler model, this often results in a loss of generality (*cf.* Stapper, 1986; Battaglia and

Sands, 1997b). This study indicates that the prediction of site productivity in temperate regions at the stand-scale requires explicit consideration of a number of processes (and almost certainly others not tested here). In general, each simplification resulted in a loss in accuracy of predicted productivity, or a loss in generality, or both. The single exception was that the respiration sub-model could be replaced by a constant assimilate use efficiency Y without any loss of accuracy or generality, but it is unclear whether this would be appropriate in warmer environments than those tested.

The parameters in PROMOD characterise processes underlying tree growth, so there is a correlation between parameters and physiological traits. Those parameters to which productivity is predicted to be most sensitive (i.e. high μ, Table 3) and for which substantial natural variation exists suggests traits that are most likely to be useful in breeding programs. For example, Table 3, Figs. 4b-c and Fig. 5a all indicate that significant productivity gains could be made by increasing $A*_{opt}$ and $t_{1/2}$. In terms of physiological traits these changes increase the light saturated photosynthetic rate and decrease the temperature sensitivity of photosynthesis, respectively. Similar data (not shown) show that productivity will be enhanced, but to a lesser extent, as θ approaches 1, and by increasing α_0; both these changes reduce the irradiance required to saturate photosynthesis. On the other hand, Fig. 4d shows that any reduction in ω_0 may result in loss of production at sites which are subject to significant water stress at some time during the year. The corresponding trait is the dependence of water use efficiency on VPD.

Explanation of genotype by environment interactions may be found in traits corresponding to parameters if high sensitivity and whose sensitivity differs between sites (i.e. both μ and $\mu \times E$ are high, Table 3). Although *E. globulus* is planted extensively in temperate regions, only a few physiological parameters have been widely studied. This makes it difficult to relate parameter sensitivity to natural variation in the corresponding physiological traits. Two traits that have been studied include leaf photosynthesis and its light and temperature dependence (Sheriff and Nambiar, 1991, Pereira 1995, Battaglia *et al.*, 1996), and water-use efficiency (Pereira 1995, Peter Dye *pers. comm.*). Our sensitivity analysis has shown that net annual production is highly sensitive to various parameters which characterise the former, and that annual water-use efficiency is highly sensitive to parameters which determine the latter.

1.6 References

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