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Using seasonal measurements to inform ecophysiology: extracting cardinal growth temperatures for process-based growth models of five *Eucalyptus* species/crosses from simple field trials

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Abstract

Background: Development of a relatively simple growth modelling approach for plantation species that allows derivation of cardinal (base, optimum and ceiling) air temperatures for growth, whilst accounting for changes in organism size, would represent a considerable advance over existing models. Such an approach would provide insight into species phenology and, in an agronomic setting, allow growers to closely match species to sites. Here, a model is described that can be used to predict seasonal variation in growth and cardinal air temperatures from simple seasonal measurements at a single site.

Methods: The model was applied to data from an irrigated trial comprising two *Eucalyptus* species and three *Eucalyptus* crosses. Using measurements of mean daily air temperature data and stem volume, taken over a two year period, the model was fitted to the data and used to estimate cardinal air temperatures for the five species/crosses.

Results: The model predictions corresponded well to the actual data for all five species/crosses, with R^2 ranging from 0.993 to 0.999. The optimum air temperature, T_o, for *E. camaldulensis* x *E. globulus* of 26.9°C significantly exceeded T_o for the other four species/crosses, where T_o ranged from 15.4 to 18.7°C. As T_o for *E. camaldulensis* x *E. globulus* was close to the highest mean daily air temperature recorded at the study site, the air temperature modifier for this species was almost always sub-optimal and consequently this cross was not well matched to the site. In contrast, T_o for the other four species/crosses were considerably closer to the mean air temperature of the site with T_o for *E. nitens* most closely approximating the mean air temperature (15.4 vs. 13.0°C).

Conclusion: The described approach can be used to account for complex variation in seasonal growth patterns and provides insight into how well a species may be matched to a particular site. As climatic information is available at a range of scales (from local to global), this type of model is likely to be useful for producing maps that describe species growth and areas of optimal suitability.

Keywords: Air temperature; Eucalyptus; Hybrid model

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Background

Process-based ecological models are applied in a wide variety of fields from agriculture to zoogeography. They are used in simulations at a range of scales from an individual organ to populations. The main attraction of these models is that they can be used to capture the general behaviour of the entity being simulated in relation to environmental covariates. This allows them to be applied to novel situations with greater confidence than simpler, purely empirical statistical models (Wang et al. 2013; Perez-Cruzado et al. 2011). This generality is useful for applications involving novel environments that might occur under biological invasions and climate change. The generality of process-based models, however, comes at a cost of greater complexity, and potentially reduced precision (Levins 1966; Sharpe 1990). This added complexity poses significant methodological challenges. The researcher has to find ways to characterise the response of the organism to significant environmental variables (most notably temperature and moisture) at a temporal scale that is relevant to the system being simulated and the questions being addressed.

Many entomologists, agronomists and pathologists have chosen to study short-lived organisms whose growth responses to air temperature are easy to characterise through simple temperature series experiments. The duration of the developmental period required to transition between two selected lifestages (e.g. seed to germinant, egg to pupa) across a range of temperatures can indicate the growth rate as a function of temperature. A simple examination of the response rate as a function of time can result in the extraction of the minimum, maximum and optimum temperatures for development (Dumar et al. 1990; Togashi 1931; Pradhan 1946; Wang et al. 2013).

Process-based models of individual and population growth for tree species are typically more complex to develop. Process-based plant growth models are often used to simulate and integrate complex processes such as carbon assimilation and partitioning, respiration and phenology (Battaglia et al. 2004; Kirschbaum 1999) so considerable complexity and a large number of parameters are often incorporated into them. Frequently, models contain parameters that are difficult to estimate or fit. As a consequence, these models often require extensive calibration to empirical growth measurements to ensure that results lie within realistic bounds (Kirschbaum and Watt 2011). Despite this complexity, process-based based models have been successfully fitted to several tree species using calibrated parameter values (Wang et al. 2013; Campoe et al. 2013; Perez-Cruzado et al. 2011; Rodriguez et al. 2009; Almeida et al. 2004a).

Plant growth models have recently been developed that combine elements of both process-based and empirical models. Such hybrid models incorporate increased biological realism over traditional empirical growth models, yet they reduce the number of parameters to be fitted. In developing a hybrid model, it is important to incorporate the key process-based elements that have most influence on growth. Air temperature and soil moisture are widely recognised as being two key factors that regulate plant growth at both seasonal and annual timescales (Sampson et al. 2006; Bollmann et al. 1986; Jones et al. 1991; Battaglia et al. 1996; Duchesne and Houle 2011; Wang et al. 2013).

Most hybrid modelling has been undertaken using annual timesteps. Typically these hybrid models modify the trajectory of empirical growth curves through incorporation of modifiers for environmental factors that have been averaged at an annual level. Substantial gains in predictive precision over purely empirical models have been reported through use of these models for a diverse range of plant species (Tian et al. 2012; Sampson et al. 2006; Waterworth et al. 2007; Mason et al. 2011; Miehle et al. 2009; Battaglia et al. 1999; Reed et al. 2003; Perez-Cruzado et al. 2011; Wang et al. 2013).

Development of a sub-annual timestep hybrid model that can be fitted to readily obtainable seasonal plant measurements and that is sensitive to both plant size and key environmental factors would represent a considerable advance over existing models. This type of model can be applied to novel climate situations, and could be used to estimate growth at time scales as fine as the available meteorological data. Such models could also be used for exploring the impacts of pests and diseases more usefully than current models by accurately simulating seasonal growth patterns. Using such a model to infer responses to air temperature and soil water balance would allow cardinal values to be determined, which would provide a useful approach for matching species or genotypes to sites (Almeida et al. 2004b; Esprey et al. 2004; Battaglia and Sands 1997) and for scheduling management operations (e.g. fertilisation, weed control) for crop species (Mason and Dzierzon 2006; Pinkard and Battaglia 2001). This type of information is also useful for parameterising more detailed process-based models that can be used to simulate changes in productivity under climate change scenarios (Medlyn et al. 2011; Kirschbaum et al. 2012).

This paper describes an inverse or inferential modelling method for deriving cardinal air temperatures from seasonal growth measurements obtained from a simple field trial. Specific objectives were to (i) develop a hybrid model that can be fitted to periodic growth measurements and (ii) use this model to estimate cardinal air temperatures. Data were obtained from an irrigated trial of five different *Eucalyptus* species/crosses to illustrate the utility of the model.

Methods

Description of the model

The model uses an empirically derived form to describe growth under optimal environmental conditions. Growth is reduced from this optimal rate by a modifier that includes the discounting impacts of various sub-optimal environmental conditions. Required inputs for the model include the growth measurement of interest (e.g. height, diameter, volume) and data describing the growth-constraining environmental variables. The model may be run at any timestep over which unique sequential environmental data are available. A daily timestep is likely to be most appropriate for determination of cardinal values for key environmental variables such as air temperature. The model is fitted to the growth measurements and this data can be of a far coarser temporal resolution than the environmental data.

Growth under optimal environmental conditions (e.g. air temperature, root-zone water storage) is described by either a power or sigmoidal function (see Kimberley and Richardson, 2004 for a range of functional forms). The model fitted to the trial data described here is based on the following power function,

$$y_t = at^b \tag{1}$$

where y_t is the response, t is time after commencement of measurement, and a and b are empirically derived parameters.

Assuming that the effect of environmental conditions is constant over the interval t to $t + \Delta t$, growth can be expressed as a difference equation (Kimberley and Richardson 2004),

$$y_{t+\Delta t} = y_t + \left[f\left(f^{-1}(y_t) + \Delta t \right) - y_t \right] m \tag{2}$$

where m is a modifier describing the impacts of environmental conditions on growth and $f^{-1}(y_t)$ is the inverse of Equation 1, i.e.,

$$f^{-1}(y_t) = \left(\frac{y_t}{a} \right)^{1/b} \tag{3}$$

Combining Equations 2 and 3 the full difference equation is,

$$y_{t+\Delta t} = y_t + \left[a \left(\left(\frac{y_t}{a} \right)^{\frac{1}{b}} + \Delta t \right)^b - y_t \right] m \tag{4}$$

This method can be extended to empirical functional forms other than the 2-parameter power function, including 3-parameter sigmoidal growth functions (Kimberley and Richardson 2004).

The modifier m, which scales between 0 and 1, reduces growth when environmental conditions such as air temperature and root-zone water balance are sub-

optimal. The data used here were from a well-watered trial so this modifier was only required to account for air temperature. However, under conditions where soil root-zone water storage is sub-optimal, a water-balance modifier could also be incorporated into the model.

The following modifier (m) developed by Yin et al., (1995) based on the beta distribution, was used to describe the response of plant growth to air temperature, T,

$$m = \left[\left(\frac{T - T_b}{T_o - T_b} \right) \left(\frac{T_c - T}{T_c - T_o} \right)^{\frac{T_c - T_o}{T_o - T_b}} \right]^c \tag{5}$$

The modifier is defined for $T_b \leq T \leq T_c$, where T_b is the base or minimum, T_c the ceiling or maximum air temperature, and T_o the optimum air temperature. Outside this temperature range, $m=0$. The response has a maximum value of 1 at T_o, and declines to 0 at both T_b and T_c. The parameter c controls the shape of the response to temperature with the weight in the tails declining with increasing values of c. For a symmetric response (where T_o is midway between T_b and T_c), the response approaches the shape of a normal distribution for values of c greater than 10. The modifier described in Equation 5 is quite flexible in that it can be used to describe either asymmetric or symmetric temperature responses.

Data used for the model

Study area

Data used to fit the model was obtained from a trial established approximately 45 km south of Los Angeles in the Bio-Bio region of Chile (latitude 37°45´S longitude 72°18´W, elevation 204 m a.s.l., Figure 1). Soil at the site is classified as part of the Collipulli soil series Typic Rhodoxeralfs (Besoain 1985). Such soil is developed from old volcanic ashes that have formed deep highly weathered red clay soils on slightly undulated terrain in the central valley of Chile (Besoain 1985).

The area was previously occupied by an *Eucalyptus* spp. seed orchard and measurements at the site, prior to the trial installation, showed high levels of soil fertility and water holding capacity (Table 1). The climate of the area is warm and temperate. Mean annual rainfall is 1,200 mm with most of the precipitation occurring during winter. Mean annual temperature is 13.1°C with a maximum summer mean of 18°C and a minimum winter mean of 6°C.

Trial design and treatments

An irrigated and completely randomised block design was established in mid-spring (28 October) 2008 with three replicates of two *Eucalyptus* species (*Eucalyptus globulus* Labill. and *E. nitens* H. Deane & Maiden) and three *Eucalyptus* crosses (*E. camalulensis* Dehnh x *E. globulus*, *E. nitens* x *E. camaldulensis* and *E. nitens* x *E.*

Figure 1 Map showing the location of the trial.
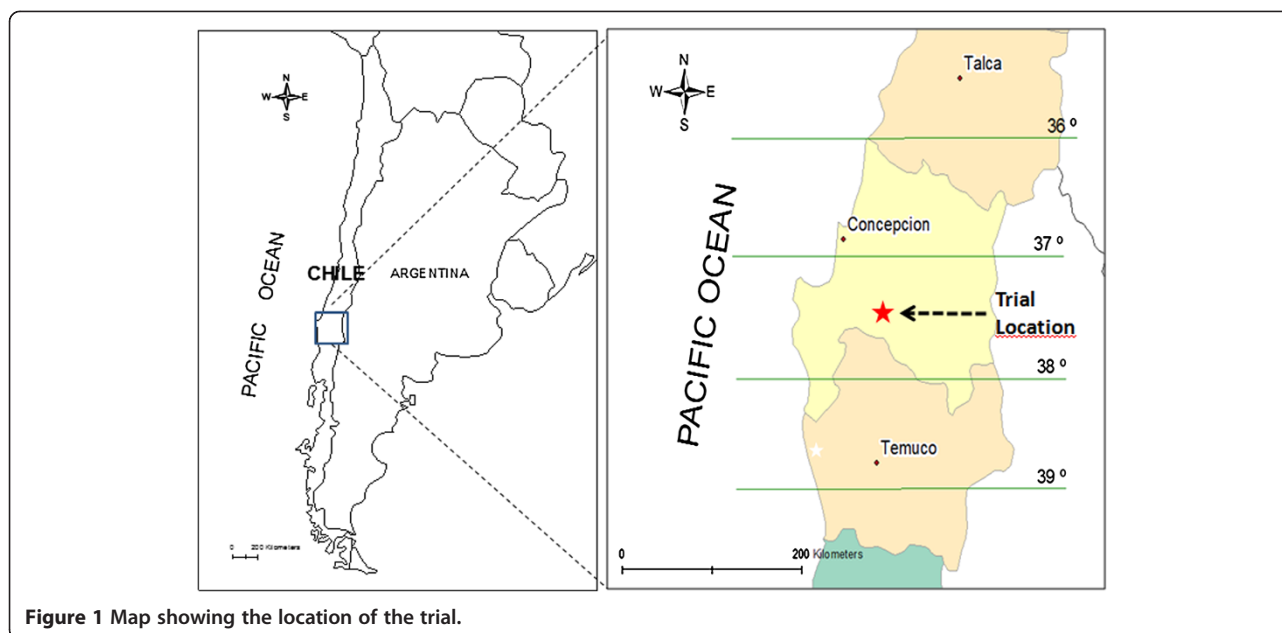
globulus). Trial units consisted of four contiguous plants established in a planting line. Different species/crosses were assigned randomly to trial units within each block (1 – 3). Genetic material consisted of selections from the Forestal Mininco *Eucalyptus* tree-improvement programme.

Plants of homogeneous size (2-3 mm root collar diameter and 30 cm height) for each species/cross were selected from seven-month-old nursery material. Plants were established at a stand density of 1,666 trees ha^{-1} which equates to a spacing of 2 × 3 m. Broadcast chemical weed control was applied before and three times after establishment (Glyphosate 3 L ha^{-1}, Monsanto) to maintain weed-free conditions over the two-year period of the trial.

Irrigation was applied regularly to achieve field capacity based on evapotranspiration records from a Class-A evaporation pan (McMahon et al. 2013). The irrigation treatment was applied from September to March during both years using 1.6 L h^{-1} drippers inserted every 33 cm on a plastic pipe line that ran parallel to the planting line at a

distance of 15 cm. The total irrigation applied during the spring and summer months was 508.3 mm during the first year (from October 2008 to March 2009) and 329.7 mm during the second year (from September 2009 to March 2010).

To avoid any potential nutrient limitations, plants were fertilised with 30 g of a controlled release fertiliser containing 16% N + 8% P_2O_5 + 12% K_2O + 2% MgO + 5% SO_2 + 0.4% Fe + 0.05% Cu + 0.06% Mn + 0.02% Zn + 0.02% B + 0.02% Mo. During the first season, an additional 3 L ha^{-1} input of 3 mg L^{-1} N + 3 mg L^{-1} P_2O_5 + 3 mg L^{-1} K_2O + 3 mg L^{-1} MgO + 3 mg L^{-1} S + 3 mg L^{-1} FeEDTA + 3 mg L^{-1} Cu + 3 mg L^{-1} Mn + 3 mg L^{-1} Zn + 3 mg L^{-1} B + 3 mg L^{-1} Mo was applied as liquid fertiliser.

Measurements

Measurements of two trees from each trial unit were obtained approximately every three weeks over two growing seasons from late spring (4 November) 2008 to

Table 1 Average physical and chemical soil properties sampled from two soil pits (1 m × 1 m × 1 m dimension) located in the area before establishment of the trial

Soil horizon	Depth	Coarse fragments	Bulk density	PWP	FC	pH	OM	N	P	K	B
	(cm)	(%)	(g cm^{-3})	---- % ----		1:2.5	%	----- (mg Kg^{-1}) -----			
A	5	0	0.7	24.3	44.7	5.5	7.6	41	5.3	250	1.3
BA	15	0	1.1	22.0	42.1	5.3	5.9	38	0.75	75	1.0
B1	33	5	1.1	20.3	42.1	5.7	2.3	22	0.28	25	0.3
B2	33-100	10	1.2	23.9	43.5	5.3	4.2	24	1.05	33	0.8

PWP: Permanent wilting point; FC: Field capacity; pH: acidity determined on a 1:2.5 soil:water ratio; OM: organic matter determined by LOI at 450°C; N: Available N extracted with 2 M KCl and determined by titration; P: soil available phosphorus Olsen extraction and determined colorimetrically; K. available soil potassium via ammonium acetate extraction and determined via atomic absorption spectrometry; B: available boron extracted with hot water and determined colorimetrically.

mid-winter (31 July) 2010. Tree height (H) and diameter (D) at 10 cm height above the ground line were measured. A volume index, V, was determined from these measurements as,

$$V = 0.33\pi\left(D^2/4\right)H \qquad (6)$$

Daily minimum, mean and maximum air temperatures were collected from a weather station (Davies Instruments Co.) located 140 m from the trial.

Data analyses

All analyses were undertaken using SAS software (SAS Institute Inc. 2008). Growth in V over two years was modelled using block-level measurements. To achieve this, Equation 4 was applied using a daily step length with the modifier described in Equation 5 calculated using measurements of daily mean air temperature. This calculation provided daily predictions of V that could be compared against measured V at each assessment date. The model parameters for Equations 4 and 5 were estimated so as to minimise the sum of squares of differences between predicted and measured values, with separate parameters being obtained for each block × species/cross combination. This analysis was carried out using the SAS NLIN procedure. Model fit was assessed by the root mean square error (RMSE) and coefficient of determination (R^2).

This procedure provided estimates of the model parameters a, b, T_b, T_o, and T_c for each block × species/cross. Attempts were also made to obtain estimates for parameter c (Equation 5). However, model convergence was generally not achieved when fitting c. It was found that the RMSE was lowest at $c = 2$ when c was kept fixed to a global value across all species/crosses, although there was little change in the RMSE for all values of c between 1 and 10. However, the RMSE increased when c was less than 1, both across all species/crosses and for each individual species/cross. A fixed value of $c = 2$ was, therefore, used in all models.

Plots of modifier against temperature were not symmetrical for the range studied. The values at which $m = 0.05$ in the lower and upper part of the distribution were determined to avoid the effects of long tails in the plots of the modifier (m) against temperature. These two values are referred to, as T_b' and T_c' respectively. These values appeared to give a better indication of the base and ceiling temperatures than T_b and T_c, as they showed greater consistency between blocks for each species/cross, and lower error sums of squares in analyses of variance comparing species/crosses. The parameters T_b' and T_c' were estimated using an iterative procedure detailed in Appendix 1.

One-way analyses of variance fitted using the SAS procedure MIXED were used to test for significant species/cross differences in the model parameters a, b, T_b, T_o, T_c, mean values for the air temperature modifier, m, the adjusted base and ceiling temperatures T_b' and T_c', and plant size (H, D and V) at the end of the trial. Multiple comparisons between the different species/crosses were undertaken using Tukey's method as implemented in the SAS mixed model procedure.

Results

Site range in air temperature

There was wide annual variation in mean air temperature at the site with air temperature peaking in late summer and reaching minimum values during mid-winter (Figure 2a). The overall minimum and maximum daily air temperatures recorded over the period of the study were –3.7 and 37.7°C, respectively. A total of 39 frosts were recorded. The mean daily temperature over the period of the study averaged 13.0°C and ranged from 0.27°C to 26.12°C (Figure 2a).
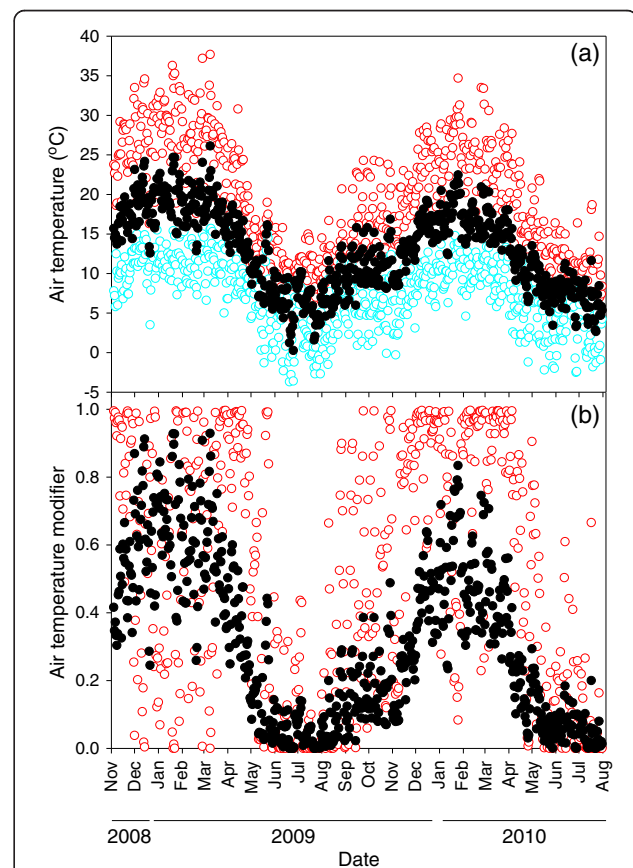

Figure 2 Variation in (a) minimum (open blue circles), mean (closed black circles) and maximum (open red circles) air temperature and (b) air temperature modifier over the course of the trial for *E. camaldulensis* x *E. globulus* (closed black circles) and *E. nitens* (open red circles).

Variation in tree dimensions

Tree height, diameter and volume index varied widely among the five species/crosses (Figure 3a, b and c, respectively). Changes in dimensions over the two years exhibited marked seasonal variation and an exponential increase between the first and second year occurred for both H and V (Figure 3a and c). Significant species/cross differences were observed by the end of the trial for H ($P = 0.0141$), D ($P = 0.0002$) and V ($P < 0.0001$). Species/cross variation at the end of the trial was most marked for V, which ranged three-fold between the poorest performing cross, *E. camaldulensis* x *E. globulus* and the best performing species, *E. nitens* (Figure 3c; Table 2).
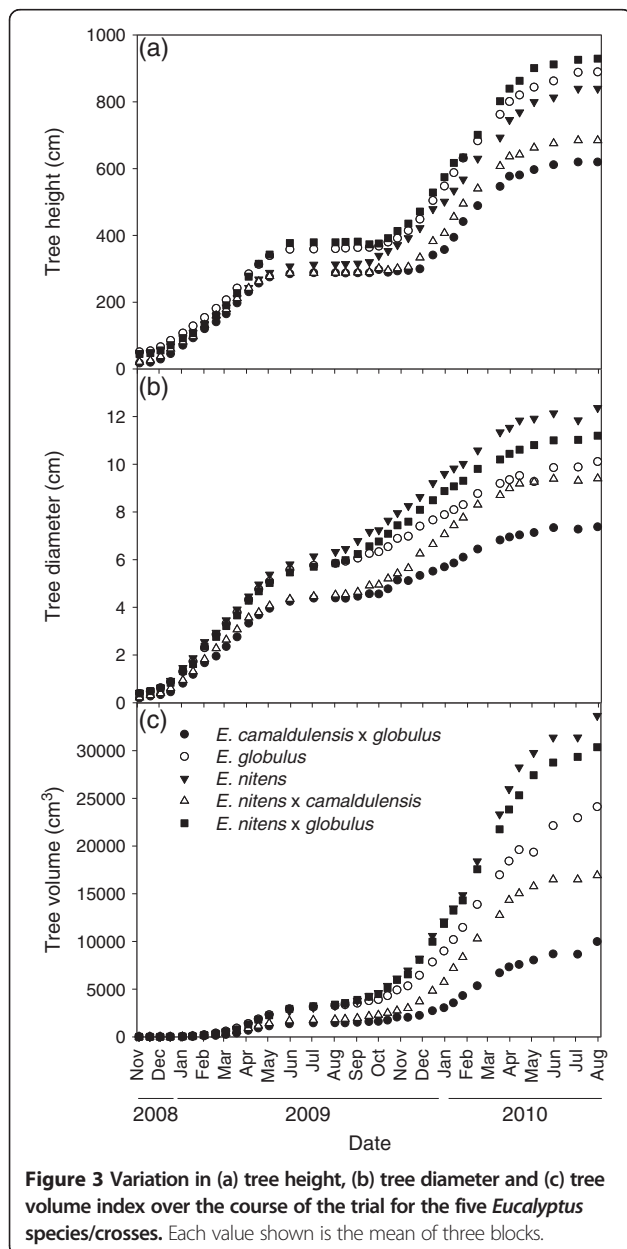
Figure 3 Variation in (a) tree height, (b) tree diameter and (c) tree volume index over the course of the trial for the five *Eucalyptus* species/crosses. Each value shown is the mean of three blocks.

Model fit

The model predictions corresponded well to the actual data for all species/cross x block combinations (see Additional file 1 for fit statistics). Across the 15 combinations examined, the coefficient of determination ranged from 0.993 to 0.999, averaging 0.998. The RMSE was very low, ranging from 111 cm^3 to 657 cm^3 and averaged 370 cm^3 (Additional file 1). Little apparent bias in model fit was evident against month as shown for block-level means of the two species/crosses representing the extremes in growth, *E. camaldulensis* x *E. globulus* (Figure 4a-c) and *E. nitens* (Figure 4d-f).

Model parameters

Highly significant species/cross differences were found for the fitted values of T_o (Table 2). The T_o for *E. camaldulensis* x *E. globulus* of 26.9°C significantly exceeded that of all other species/crosses, where T_o ranged from 15.4 to 18.7°C (Table 2; Figure 5). The parameter T_b varied from 3.2°C to 6.2°C but this difference was not statistically significant. Although variation in parameter T_c was relatively wide, standard errors were high, and only the two extreme species/crosses (*E. nitens* x *E. globulus* at 21.6°C and *E. camaldulensis* x *E. globulus* at 29.8°C) differed significantly.

The derived metric T_b' did not differ significantly among species/crosses, ranging from 6.4 to 7.4°C (Table 2; Figure 5). The derived metric T_c' for *E. camaldulensis* x *E. globulus* with a value of 29.8°C was significantly higher than that of the other species/crosses which ranged between 21.1 to 22.7°C. The temperature difference between the derived metrics T_b' and T_c' was greatest for *E. camaldulensis* x *E. globulus* (22.4°C) followed by *E. globulus* (16.3°C), *E. nitens* x *camaldulensis* (16.1°C), *E. nitens* (14.8°C) and *E. nitens* x *E. globulus* (13.9°C) (Figure 5).

Air temperature modifier and response function

The air temperature response function varied markedly between *E. camaldulensis* x *E. globulus* and the other four eucalypt species/crosses (Figure 6). The parameter T_o for *E. camaldulensis* x *E. globulus* was close to the highest mean daily air temperature recorded during the study (dotted line, Figure 6). As a result, the air temperature modifier was almost always sub-optimal for this cross (Figure 2b), with peaks corresponding to higher air temperatures (Figure 2b) in late summer. In contrast, T_o for other functions were considerably closer to the mean air temperature of the site (Table 2), with T_o for *E. nitens* most closely approximating the mean site air temperature (15.4 vs. 13.0°C). As a result, the air temperature modifier for *E. nitens* exhibited dual peaks during late spring/early summer and then again in early autumn when air temperatures were closest to T_o (Figure 2b).

Table 2 Species/cross variation in final stem volume index growth, model parameters and values derived from the fitted model

	Species/cross[1]					Analyses of variance
	E. c. x *E. g.*	*E. n.* x *E. c.*	*E. g.*	*E. n.* x *E. g.*	*E. n.*	
Parameters						
a	63,539	34,336	27,962	49,973	44,745	1.73[ns]
b	3.11 a	2.84 ab	2.52 b	2.43 ab	2.61 ab	3.78*
T_b (°C)	3.2	4.4	4.7	5.9	6.2	1.59[ns]
T_o (°C)	26.9 a	18.7 b	16.7 b	15.7 b	15.4 b	17.84***
T_c (°C)	29.8 a	22.8 ab	23.0 ab	21.6 b	23.1 ab	3.69*
Derived metrics						
T_b' (°C)	7.4	6.6	6.4	7.2	7.4	0.56[ns]
T_c' (°C)	29.8 a	22.7 b	22.7 b	21.1 b	22.2 b	5.25*
Mean m	0.292 a	0.461 b	0.535 b	0.465 b	0.491 b	8.12**
Final V (cm^3)	9,256 a	21,188 b	26,780 bc	30,360 cd	33,649 d	61.28***

Derived values include the air temperature modifier (m) averaged over the trial duration and the temperatures at which $m = 0.05$ in the lower (T_b') and upper (T_c') parts of the distribution. Each value shown is the mean of three blocks. For the analysis the F values are given followed by the P-category. Asterisks ***, ** and * denote significance at $P = 0.001$, 0.01 and 0.05 respectively; ns represents not significant at $P = 0.05$. Values in a row followed by the same letter do not significantly differ.
[1]*E. g.* = *Eucalyptus globulus*; *E. c.* = *Eucalyptus camaldulensis*; *E. n.* = *Eucalyptus nitens*.
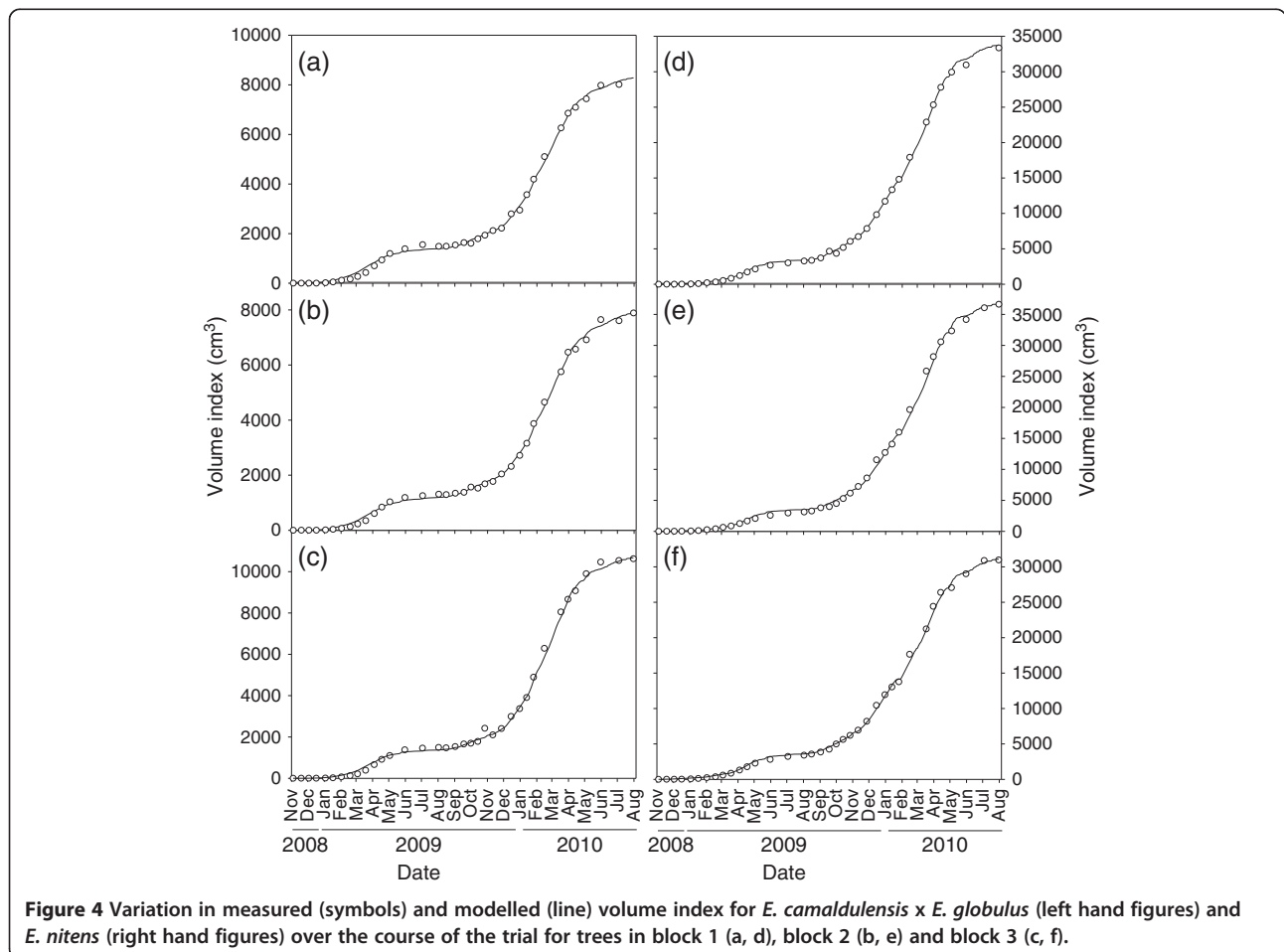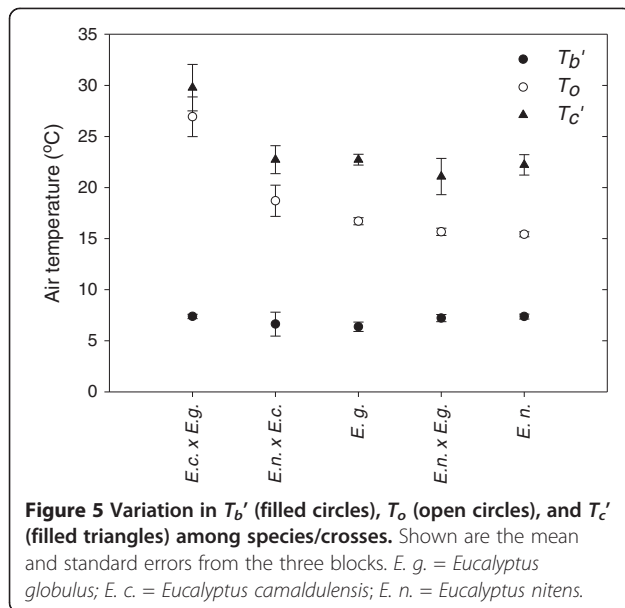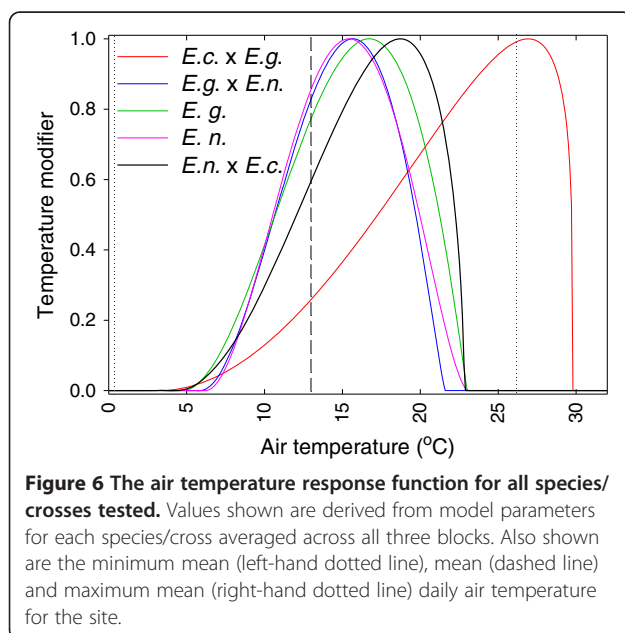

Figure 4 Variation in measured (symbols) and modelled (line) volume index for *E. camaldulensis* x *E. globulus* (left hand figures) and *E. nitens* (right hand figures) over the course of the trial for trees in block 1 (a, d), block 2 (b, e) and block 3 (c, f).

Figure 5 Variation in T_b' (filled circles), T_o (open circles), and T_c' (filled triangles) among species/crosses. Shown are the mean and standard errors from the three blocks. *E. g.* = *Eucalyptus globulus*; *E. c.* = *Eucalyptus camaldulensis*; *E. n.* = *Eucalyptus nitens*.

The mean value of the air temperature modifier was significantly lower for the *E. camaldulensis* x *E. globulus* (0.292) cross than all other species/crosses and highest for the species *E. globulus* (0.535) and *E. nitens* (0.491) (Table 2).

Discussion

The model described in this paper provides a simple method for estimating cardinal air temperatures of tree species used in plantation forestry. A major advance is that this method can be used to normalise the effect of changing plant size on expected growth so that the growth response

Figure 6 The air temperature response function for all species/ crosses tested. Values shown are derived from model parameters for each species/cross averaged across all three blocks. Also shown are the minimum mean (left-hand dotted line), mean (dashed line) and maximum mean (right-hand dotted line) daily air temperature for the site.

to air temperature can be more clearly defined. The utility of this modelling method was demonstrated by the close correspondence between empirical measurements and estimated values of growth for the five *Eucalyptus* species/ crosses to which the model was fitted.

This model can be used to estimate how well a species will be suited to a particular site. In this study, the site was abundantly irrigated and fertilised, and hence air temperature was the dominant environmental factor affecting site suitability for each species. Both the proximity of T_o to the mean site air temperature and the range between T_c' and T_b' are important factors affecting suitability of each species to the site. *Eucalyptus nitens*, *E. globulus* and the cross between these two species were most closely adapted to this particular site as T_o for these species were relatively close to the mean site air temperature. Compared to *E. nitens* and the *E. nitens* x *E. globulus* cross, there was a greater range between T_c' and T_b' for *E. globulus* that allowed greater growth at sub- and supra-optimal air temperatures resulting in a higher value of the temperature modifier for this latter species. Clearly, *E. camaldulensis* x *E. globulus* was not well adapted to the site. Although this cross had the widest range between T_c' and T_b' of the trial species/ crosses tested, T_o was substantially higher than the mean air temperature of the site and relatively close to the highest mean daily air temperature recorded on the site. Consequently, growth was almost always sub-optimal for this cross.

The optimal air temperatures described here are consistent with previous research describing climatic requirements of different *Eucalyptus* species. *Eucalyptus camaldulensis* has been found to be most suited to climates with mean annual air temperatures ranging from 18 – 28°C for the northern province and 13 – 22°C for the southern provenance. In contrast, *E. nitens* and *E. globulus* are more suited to cooler climates with optimal mean annual air temperatures ranging from 9 – 18°C (Booth and Pryor 1991).

The model described here can be used to account for complex variation in seasonal growth patterns between species. For *E. nitens,* the temperature modifier had high values over a broad time period with dual peaks occurring either side of mid and late summer (data not shown), when air temperatures were close to the optimum. The characterisation of these dual peaks by the model represents a refinement over previous, more empirical methods (e.g. use of a sine curve linked to Julian day) that can only be used to simulate a single growth peak throughout the growing season. In contrast, as T_o was very close to the highest mean daily air temperature for *E. camaldulensis* x *E. globulus*, the phenology of this cross closely tracked the daily air temperature of the site peaking in mid to late summer.

Although the model described here only included air temperature, other important growth limiting variables, such as soil moisture, could be readily added to this framework. These variables could be introduced into the model as response functions that affect values of the modifier (m) in a similar manner to that of air temperature, arranged in accordance with the ecological Law of the Minimum (reviewed by van der Ploeg et al. 1999). A suitable response function should accord with the Law of Tolerance (reviewed in Shelford 1963). Fitting the response function to data should allow extraction of cardinal values for variables such as fractional available volumetric water content, θ, (i.e. minimum, optimum and maximum θ for plant growth) to be estimated.

The type of model described here is likely to be useful for producing robust maps that describe species growth and areas of optimal suitability (e.g., the annual Growth Index, GI_A in CLIMEX, Sutherst et al. 2007). Such models have often had to rely upon informed guesses for parameters describing the soil moisture and air temperature growth response functions. Some CLIMEX and DYMEX (Maywald et al. 2007) models have employed growth responses that have been parameterised based on trial observations (Kriticos et al. 2009), few have used phenological observations to infer cardinal temperatures (De Villiers et al. 2012), and none that we know of have involved perennial species.

A key issue facing any grower of commercial agricultural or forestry crops is to understand how best to match species or genotypes to a particular site. Often there is insufficient information on which to base these decisions particularly for different genotypes of the same species. The methodology described here could greatly simplify this process as cardinal air temperatures can be defined for all species and genotypes of interest from a single trial. Using these cardinal temperatures in simple growth index models such as CLIMEX, maps describing growth could then be developed from underlying climatological datasets. The optimal species for each grid cell in a given area could be extracted by overlaying a number of these maps and selecting the most economically attractive species based on growth rates and relevant market information. As spatial information describing climate is available at a range of resolution and spatial extent such maps could be generated at scales ranging from local to global.

There were limitations within the dataset that should be taken into account when interpreting the results. The sample size was relatively small and measurements were taken from a single trial over a relatively short time period on juvenile trees. Use of a dataset covering a greater environmental range and trees that are older is likely to produce more robust estimates of cardinal air temperatures. Results show that T_b' and T_o were precisely estimated for all species. However, values of T_c' were less precisely estimated, particularly for the *E. camaldulensis* x *E. globulus* cross as the highest mean daily air temperature was lower than T_c'. The reported values for T_c' were also markedly lower than values reported previously for *E. globulus* and *E. nitens* (Sands and Landsberg 2002; Fontes et al. 2006; Perez-Cruzado et al. 2011). This highlights the need for careful placement of trials in climates where the natural range in air temperature covers the expected range of $T_b' - T_c'$ for the species/crosses being evaluated. Covering this range may require installation of more than one trial in locations with contrasting climates. Despite these dataset limitations we consider the methodology to provide a robust means of determining cardinal air temperatures of different species.

Conclusions

The methodology outlined in this paper describes how data from simple trials can be effectively used within a model to gain considerable insight into plantation crop species climatic preferences. Adoption of such an approach could augment or replace extensive and costly trial networks that need to be monitored over long time periods. Further research should extend the described modelling approach to situations where other environmental factors such as root-zone water storage limit growth. Inclusion of a frost modifier within the modelling framework may also improve the predictive precision and provide insight into how different species respond to frost.

Appendix 1 Iterative procedure for estimating T_b' and T_c'

Because plots of the modifier (Equation 5) against c can have long tails, especially for large values of c, T_b and T_c can sometimes provide exaggerated base and ceiling temperatures. Better representations of these temperatures may be indicated by the temperatures at which the modifier m equals some small value h, say $h = 0.05$. These modified base and ceiling temperatures are represented by T_b' and T_c' respectively. The following iterative procedure can be used to calculate them.

Let, $k = (T_c - T_o)/(T_o - T_b)$,
and, $l = h^{1/c}(T_o - T_b)(T_c - T_o)^k$

Starting with $L_0 = 0$ and $U_0 = 0$, perform the following iterations for $i = 1, 2,...$ until convergence is achieved for U and L:

$$L_{i+1} = l \Big/ \left((T_c - T_b)^{k+1}(1 - L_i)^k \right)$$

and, $$U_{i+1} = \left(l \Big/ \left((T_c - T_b)^{k+1}(1 - U_i) \right) \right)^{1/k}$$

Finally, calculate T_b' and T_c' as follows: $T_b' = T_b + L(T_c - T_b)$ and, $T_c' = T_c - U(T_c - T_b)$

Additional file

Additional file 1: Model fit statistics, parameter values, derived values and final measured volume index growth for all block – species/cross combinations.

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