Climatic influences on the flowering phenology of four Eucalypts: a GAMLSS approach

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Abstract: Phenology involves the recording of recurring natural events such as the commencement of flowering or the arrival of migratory birds, and the influence on such events by edaphic and climatic factors. Analyses of phenological data have been used to examine the impacts of climate change. These studies, however, have thus far used data concentrated in the Northern Hemisphere. Indications are that long-term phenological studies, within any discipline, are limited in Australia. Datasets spanning a century or more such as are found in Europe are unlikely in Australia, given the short period of European settlement (e.g. since 1788 for Sydney, 1835 for Melbourne). Eucalypts form the focus of known Australian phyto-phenological studies, as they are the dominant species both in a botanical and economic sense. This study represents the first attempt to apply the Generalised Additive Model for Location, Scale and Shape (GAMLSS) technique to study a phenological data set, with the aim, in part of detecting non-linear responses to climate change (contrasting earlier stepwise regression approaches). The flowering records of four species (*Eucalyptus leucoxylon*, *E. microcarpa, E. polyanthemos* and *E. tricarpa*) is used here as a case study. This data set represents a long time series, by Australasian standards, using more than 30 years of monthly readings, in excess of 400 flowering and climate time points. Regardless of the cyclicity of flowering over time, this study shows that each species flowering is significantly influenced by temperature and that this effect is non-linear. Stepwise GAMLSS showed that the main temperature driver of *E. leucoxylon* flowering is minimum temperature ($P<0.0001$), maximum temperature for *E. polyanthemos* ($P<0.0001$), both minimum and maximum temperature ($P<0.0001$) for *E. tricarpa*, and mean temperature for *E. microcarpa* ($P<0.0001$). Rainfall is not a significant predictor of flowering via the stepwise GAMLSS procedure. Importantly GAMLSS also allows for the identification of lower /upper thresholds of temperature for flowering commencement /cessation; for the estimation of long and short-term non-linear effects of climate, and for the identification of lagged cyclic effects of previous flowering. Flowering intensity of all species was positively and significantly correlated with last month's flowering ($P<0.0001$); and with flowering 12 months earlier for *E. polyanthemos* and *E. microcarpa*. Flowering of *E. polyanthemos* was negatively and significantly correlated with flowering intensity 2 and 4 months prior; in the case of *E. microcarpa* with flowering 6 and 8 months earlier. Overall *E. microcarpa* and *E. polyanthemos* flower more intensely in response to predicted increases in mean and maximum temperature, respectively. *E. leucoxylon* flowers less intensely with predicted increases in minimum temperature; *E. tricarpa* flowers less intensely with increased maximum temperature, but more intensely with increased minimum temperature (after accounting for maximum temperature). These four species are significantly influenced by temperature and as a consequence their flowering phenology will possibly change in response to climate change. GAMLSS add credibility to the use of phenological records to detect phenological phases, local climatic impacts on flowering and possibly global climate change *per se.*

Keywords: *Multiple Time series, Climate change, Generalised Additive Model for Location, Scale and Shape, Thresholds, Cubic smoothing splines*

1. INTRODUCTION

Phenology involves the recording of recurring natural events such as the commencement of flowering (Keatley et al., 1999a, Koch, 2000, Hudson et al., 2005) or the arrival of migratory birds and the influence on such events by edaphic and climatic factors. Analyses of phenological data have been used to examine the impacts of climate change (IPCC, 2007, Rosenzweig et al., 2007, Sagarin and Micheli, 2001, Whitfield, 2001). These studies, however, have thus far used data concentrated in the Northern Hemisphere. Indications are that long-term phenological studies, within any discipline, are limited in Australia (Manning and Nobre, 2001). Datasets spanning a century or more such as are found in Europe are unlikely in Australia, given the short period of European settlement (e.g. since 1788 for Sydney, 1835 for Melbourne). Eucalypts form the focus of known Australian phytophenological studies, as they are the dominant species both in a botanical and economic sense (Ashton, 1975, Cremer, 1975, Law et al., 2000, Keatley et al., 2002, Bassett et al., 2006, Keatley & Hudson, 2007). In this paper we illustrate the benefit of GAMLSS in modelling and interpretation of climatic impacts on Euclaypt flowering.

GAMLSS, are part of the Generalized Linear Models (GLM) and Generalized Additive models (GAM) 'family' were developed by Rigby and Stasinopoulos (2005) to deal with non normally distributed data (e.g. highly skewed, or kurtotic continuous and discrete distributions). Current updates of GAMLSS can deal with up to 50 different types of distributions (Stasinopoulos and Rigby, 2007). Recent applications of GAMLSS have involved modelling climate with Sudden Infant Death Syndrome (Hudson et al., 2008) and the establishment of the world standard child growth curves by the WHO (WHO Multicentre Growth Reference Study Group, 2006) (see also examples in Rigby and Stasinopoulos 2005 and in Stasinopoulos and Rigby, 2007). Hudson et al. (2003) also used GAMs, the precursor to GAMLSS, to model *E. leucoxylon* flowering and found significant non-linear effects of mean temperature on flowering intensity.

The benefits of GAMLSS for phenological data (which is a time series) are that they: [1] can identify the main drivers of the event interest from a multiplicity of predictors such as climate and food sources etc.; [2] allow for non linear impacts of the explanatory variables or predictors; [3] can statistically detect thresholds, for example, the lowest temperature for the commencement of flowering; [4] can model or account for the auto-correlated nature of the phenological series, for example by incorporating lag effects.

This paper represents the first attempt to utilize phenological data to determine the responses of flowering to climate using GAMLSS. We use the flowering of four species (*Eucalyptus leucoxylon, E. microcarpa, E. polyanthemos and E. tricarpa*) as a case study. The primary aim of this paper is to investigate the relationship between flowering intensity and three temperature variants, minimum, maximum and mean temperature, since temperature is a major climatic influence on phenological events such as flowering (Schwartz, 2000, Snyder et al., 2001) and with rainfall (Hudson et al., 2003, 2005, 2008).

2. DATA AND METHODS

2.1. Phenological and climate data

Flowering observations were undertaken on a monthly basis at the population level by Forests Commission observers. They categorised their observations of flowering according to the quantity and distribution of flowering across the population. Flowering quantity was ranked from 'No flowering' to 'Heavy flowering', whilst distribution ranges from 'Isolated' to 'General'. Flowering was thus quantified by assigning a rank value to these descriptions according to the formulation in Keatley and Hudson (2007). Flowering intensity (ranging from 0 to 5) was calculated, based on the sum of the quantity and distribution of the rank values, where a score of 0 indicates that no flowering occurred whilst a score of 5 indicated that flowering was heavy and distributed throughout the observation area. These flowering records are the basis of this study, which focuses on the flowering of four species: *Eucalyptus leucoxylon, E. tricarpa, E. microcarpa* and *E. polyanthemos*. This is part of a larger study examining eight Eucalypt species (Keatley at al., 1999, Keatley et al., 2002). Monthly flower counts for flowering intensity and mean monthly readings of climate (Minimum and Maximum Temperature (°C), Mean Diurnal Temperature (°C) and Rainfall (mm)) for the historical time period Jan 1938- Mar 1972 were collated. For example *E. leucoxylon* flower counts (which ranged from 0.0 to 5.0) for the study period (1940-1971) constituted 409 monthly time points. Table 1 provides the mean, median duration of flowering for the 4 species in addition to the most probable month of flowering per year as calculated by Keatley and Hudson (2007).

2.2. GAMLSS Methodology

The GAMLSS framework of statistical modelling is implemented in a series of packages in R, (R Development Core Team, 2007), a free software (see URL http://www.R-project.org). The packages can be downloaded from the R library, CRAN, or from http://www.gamlss.com. For this study the GAMLSS procedure was used with a cubic spline smoothing function and a forwards stepwise stepGAIC function in GAMLSS (Stasinopoulos and Rigby, 2007). Each model tested assumed that the flowering series represents Poisson counts and the RS algorithm (Stasinopoulos and Rigby, 2007) was used to obtain the estimates of the climatic predictors. Lagged dependencies of current with past flowering (up to 12 months prior) were added as auto-regressive (AR) lags.

Table 1. Mean (months $\pm$ 1 SD) and median flowering duration and the most probable flowering month .

Species	Mean duration (months)	Median duration (months)	Month of peak intensity
E. leucoxylon	9.7 $\pm$ 4.2	9.0	Sept
E. microcarpa	4.0 $\pm$ 1.0	4.0	March
E. polyanthemos	3.6 $\pm$ 1.5	3.5	Nov/Dec
E. tricarpa	6.2 $\pm$ 2.1	6.0	July

3. RESULTS

Table 2 shows the results of a GAMLSS modelling using a forwards stepwise selection procedure via the stepGAIC function in GAMLSS (Stasinopoulos and Rigby, 2007). All effects shown are non-linear effects (cubic splines (cs())). From Table 2 we see that the temperature variants had singly or jointly highly significant ($P <0.0001$) non-linear effects on flowering for each species. Rainfall was not a significant factor in predicting flowering intensity after the effect(s) of temperature and previous lags were accounted for (thus it was omitted from the model by the stepwise procedure). For each species flowering one month prior significantly increased ($P <0.0001$) the likelihood for current flowering (a positive though non-linear lag1 effect (Table 2)). Indeed for all species flowering one month prior significantly increased ($P<0.0001$) the likelihood for current flowering (a positive lag1 effect). A significant lag 12 effect was found in *E. microcarpa* and *E. polyanthemos* only.

For *E. polyanthemos* there is a highly significant and non-linear (positive) effect of maximum temperature on flowering (Table 2) and particularly significant and non-linear (negative) lag effects of previous flowering at 2 and 4 months prior in relationship to current flowering (Table 2). This means that flowering 2 and 4 months earlier were highly correlated with a decreased likelihood of current flowering in *E. polyanthemos* (i.e. *E. polyanthemos* usually does not flower 2 and 4 months prior to current flowering). The 6 and 8 month lags for *E. microcarpa* had a similar negative effect on current flowering (Table 2). These negative lags agree with the autocorrelation (ACF) plot (not shown) for *Eucalyptus microcarpa* which shows negative lags for 6 and 8 months and positive lagged dependencies at 1 and 12 months: the ACF lags correlations are (0.67, -0.26, -0.21, 0.32) for lags (1, 6, 8, 12 months prior) in that order. For *E. microcarpa* and *E. polyanthemos* there is a significant and non-linear effect of temperature in that they flower more intensely in response to predicted increases in mean and maximum temperature, respectively (see the positive and highly significant β estimates ($P <0.0001$) in Table 2. *Eucalyptus leucoxylon* flowers less intensely in response to predicted increases in minimum temperature whereas *E. tricarpa* flowers less intensely in response to predicted increases in maximum temperature, but more intensely with increased minimum temperature (after accounting for maximum temperature); indicating for *E. tricarpa* there are two main but opposing temperature drivers. *E. tricarpa* prefers cooler maximum temperature but warmer minimum temperature. All the GAMLSS models fitted the original data very well (see the observed and fitted time series plots in Figure 1). The best fit was obtained for *E. microcarpa* as evidenced by *E. microcarpa* GAMLSS model's low value of scaled deviance statistic (GD) in Table 2. GAMLSS analysis found the same contemporaneous effects of climate on flowering for *Eucalyptus tricarpa* and *E. leucoxylon*, which constitutes one species pairing; and for *E. microcarpa* and *E. polyanthemos* (the other species pairing).

Thresholds for start and finish of flowering: The β estimates in Table 2 and the GAMLSS term plot for each model (not shown here) demonstrate the cubic spline effect of each predictor (whether climatic or lag

in Table 2) after the other effects in the model have been accommodated for. Reading off the exact temperature at which the spline line and its 95% confidence limits go above zero for the partial residuals gives the lower temperature threshold for flowering commencement for a given species (17.5°C maximum temperature for *E. polyanthemos*). Similarly reading off the exact temperature at which the spline curve and its 95% confidence limits go below zero for the partial residuals gives the higher temperature threshold for finish of flowering for a given species (25.9°C maximum temperature for *E. polyanthemos*), when they exist from the resultant cubic spline. The resultant temperature thresholds for all four species are listed in Table 3.

Table 2. Parameter estimates and goodness of fit statistics for the GAMLSS models.

Species	Predictors cs( )	β estimate	Std error	t value	P	GD$^\phi$	AIC$^\phi$	SBC$^\phi$
E. leucoxylon	intercept	0.42	0.14	3.07	<0.0001	942.7	960.7	995.9
	minT	-0.10	0.01	-7.14	<0.0001			
	lag1	0.39	0.03	11.71	<0.0001			
E. tricarpa	intercept	0.72	0.36	1.97	0.05	641.6	675.6	742.1
	maxT	-0.17	0.04	-4.65	<0.0001			
	minT	0.21	0.06	3.71	<0.0001			
	lag1	0.60	0.05	12.49	<0.0001			
	lag5	-0.14	0.06	-2.35	0.02			
E. microcarpa	intercept	-3.37	0.33	10.09	<0.0001	484.4	526.4	608.5
	meanT	0.15	0.02	7.97	<0.0001			
	lag1	0.60	0.04	13.39	<0.0001			
	lag6	-1.29	0.60	-2.15	0.03			
	lag8	-0.45	0.16	-2.85	<0.0001			
	lag12	0.14	0.06	2.53	0.01			
E. polyanthemos	intercept	-2.47	0.40	-6.21	<0.0001	507.1	549.1	631.1
	maxT	0.06	0.02	3.47	<0.0001			
	lag1	0.56	0.06	9.67	<0.0001			
	lag2	-0.28	0.07	-4.2	<0.0001			
	lag4	-0.38	0.11	-3.52	<0.0001			
	lag12	0.22	0.06	4.01	<0.0001			

$^\phi$ GD denotes the scaled deviance statistic; AIC denotes the Akaike information criterion and SBC denotes the Schwarz Bayesian Criterion goodness of fit statistics.

Table 3 Temperature thresholds for the start and finishing of flowering.

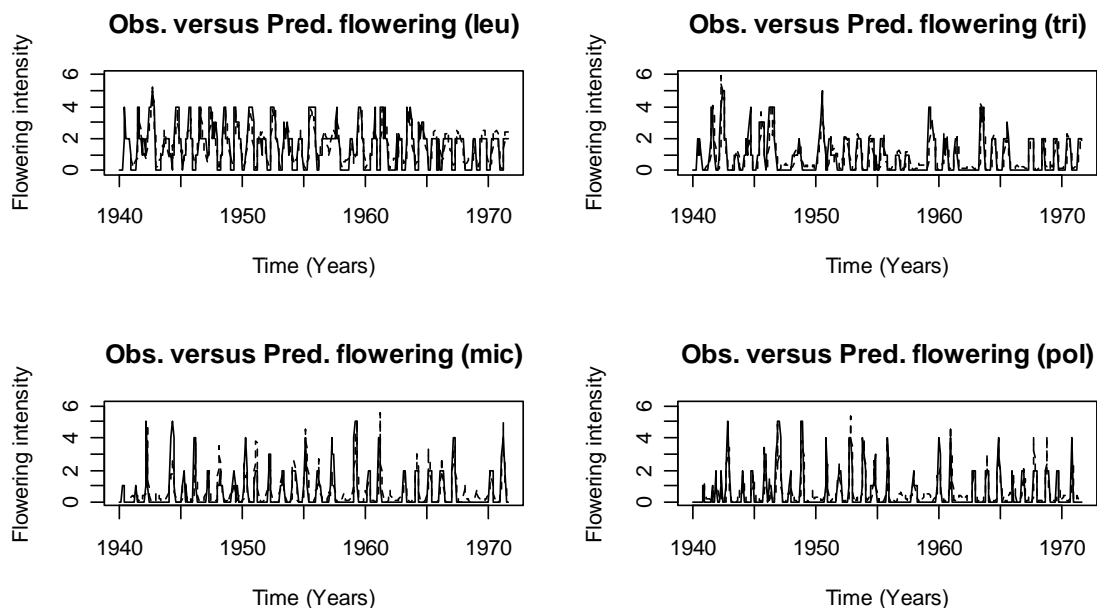| Species	MinT (°C)		MeanT (°C)		MaxT (°C)	
	Start	Finish	Start	Finish	Start	Finish
E. leucoxylon	8.0	-	-	-	-	-
E. tricarpa	10.2	-	-	-	-	21.3
E. microcarpa	-	-	16.1	-	-	-
E. polyanthemos	-	-	-	-	17.5	25.9

Fig. 1. Predicted fit (dashed line) of the GAMLSS model for *E. leucoxylon* (leu), *E. tricarpa* (tri), *E.microcarpa* (mic) and *E. polyanthemos* (poly) overlaid with the observed data (solid line).

Discussion and Conclusion

The GAMLSS analysis shows that flowering in each of these Eucalypt species is influenced by temperature. This is in agreement with previous studies on these eucalypts (Porter 1978; Keatley and Hudson 2000; Keatley et al. 2002). However, this study confirms that this effect is non-linear for *E. leucoxylon* (Hudson et al. 2003) and is also non-linear for the remaining species. The non-linear effect of temperature is well recognized for crops (Loomis and Connor 1992) but less so for native species (Sparks et al. 2000).

The main driver for flowering in *E. leucoxylon* is minimum temperature with flowering intensity being less when there are warmer minimum temperatures; minimum temperatures in the region where these observations were recorded have decreased significantly by 0.1°C between 1998 and 2007. Hence over this period it is expected that flowering intensity has been slightly more intense. More intense flowering should have been evident in *E. microcarpa* and *E. polyanthemos* as they are positively influenced by maximum and mean temperatures, respectively: maximum daily temperature has increased by 0.6°C and mean daily temperature by 0.3°C. Flowering in *E. tricarpa* would be expected to be to less intense over this period, as it is negatively influenced by maximum temperature and positively influenced by minimum temperatures. This study identified a lower threshold temperature of 8°C to induce flowering in *E. leucoxylon* which is lower than the base temperatures of 9.9°C previously determined by Keatley and Hudson (2000) (using of the methods developed by Yang *et al.* (1995)). Keatley and Hudson (2000) assumed a linear relationship between temperature and flowering which could account for some of the difference. Whilst no upper threshold temperature was identified in this current study, Hudson et al. (2003) had previously estimated 18°C. Both *E. tricarpa* and *E. polyanthemos* were also included in the study of Keatley and Hudson 2000, therefore their base temperatures were identified, 11.7°C and 14.05°C, respectively compared to 10.2°C and 17.5°C in this current study. Keatley and Hudson (2000) concluded that further work was required in determining the base temperature of *E. polyanthemos* (14.05°C) because of the large co-efficient of variation in the calculated growing degree days; hence the 17.5°C is probably correct. This current work is the first time that upper threshold temperatures have been determined for either of these species. *Eucalyptus microcarpa* has not previously had a lower threshold temperature identified. Its temperature of 16.1°C, along with that of *Eucalyptus polyanthemos* are quite high indicating that flowering for these species is in a heat-demanding developmental period (Wielgolaski 1999). *Eucalyptus polyanthemos* has the highest base temperature but the shortest interval, 1 month, between the pre-determined starting date (1st of September) and flowering (Keatley and Hudson 2007). *Eucalyptus leucoxylon* commences flowering the latest, in May, indicating that it has the lowest temperature requirement for development and this assumption is supported

by it having the lowest threshold temperature. Knowing what the main driver for a species is, say a particular temperature variant, may assist us in interpreting the possible changes in flowering due to climate change. Specifically *E. leucoxylon's* flowering intensity at the study site has probably increased slightly because of the decrease in minimum temperature. However, in other parts of its range, minimum temperature has increased significantly by 0.3°C, hence flowering intensity in this region should have decreased. Additionally, these new lower threshold temperatures can be used in both the re-calculation and calculation of growing degree days (GDD) (Wielgolaski, 1999) for these species. GDD assumes that there is a relationship between the development rate and temperature for the phenological stage being examined and that this development only occurs above a base or (lower) threshold temperature

Flowering intensity and flowering commencement in these species will be affected by climate change (Keatley et al. 2002). These changes can be regarded as the short-term implications of climate change (Rehfeldt et al. 2004). The longer-term consequences are changes in their individual reproductive success and distribution. For example, the flowering period of *E. leucoxylon* and *E. tricarpa* are synchronous but their peak flowering is well separated (Keatley et al. 2004). Flower production in *E. tricarpa* at this site is positively skewed, in that flowers are produced quickly with a comparatively slow decrease in the intensity of production. In *E. leucoxylon* flower production is negatively skewed, the opposite mode of production. Rapid production of flowers, or positive skewness, is believed to quickly accustom potential pollinators to a 'new' food source (Thomson 1980). *Eucalyptus leucoxylon* and *E. tricarpa* are placed in the same series (Pryor and Johnson 1971) and are therefore taxonomically close, with morphologically similar flowers. *Eucalyptus leucoxylon* flowers would thus be already familiar to potential pollinators as *E. tricarpa* had already flowered. Consequently, the production of *E. leucoxylon* flowers possibly does not have to be rapid to attract pollinators or enable them to adjust to a new food source. However, this facilitation of pollination may occur later in the flowering period of *E. leucoxylon* if there a decrease in its flowering intensity resulting in less seed production; or if there is an increase in flowering intensity this switch could occur earlier, increasing not only the competition for pollinators between the species but also the possibility of hybridization. Any change in reproductive behaviour also has implications for the pollinators and the species which depend on eucalypts as a food source: 20 percent of resident vertebrate Box-Ironbark species are nectarivorous (Tzaros 2005). Eucalypt flowers also attract invertebrates which contribute to the diet of nectarivorous birds (Tzaros 2005). Changes in phenology have led to mismatches in food abundance and breeding which has resulted in decreased reproductive success (Visser and Both 2005). These species contribute significantly to the honey industry in Victoria and therefore changes in flowering would have significant economic consequences. In summary changes in temperature are likely to translate to changes in both the timing of flowering commencement and in terms of flowering intensity as shown here. Ultimately these changes may result in a change to species composition, as the relative reproductive success of the species changes over time. We show here that GAMLSS modelling allows for the identification of upper and lower thresholds of flowering temperature and the estimation of long and short-term non-linear effects on flowering of climate, and the lagged cyclic effects of previous flowering. GAMLSS add credibility to the use of phenological records to detect phenological phases, local climatic impacts on flowering and possibly global climate change *per se.*

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