Climate effects and temperature thresholds for Eucalypt flowering: a GAMLSS ZIP approach

I.L. Hudson[a], S.W. Kim[b], and M.R. Keatley [c]

[a] *School of Mathematical and Physical Sciences, University of Newcastle, NSW, Australia*
[b] *Flinders Centre for Epidemiology and Biostatistics, Flinders University, Adelaide, South Australia*
[c] *Dept of Forest and Ecosystem Science, The University of Melbourne, Creswick, Victoria, Australia*
Email: *Irene.Hudson@newcastle.edu.au*

Abstract: Long-term phenological studies are limited in Australia, and meta-analytic studies of these almost nonexistent (Chambers and Keatley, 2010a,b, Hudson, 2010a, Hudson and Keatley, 2010a). 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 extends the Generalised Additive Model for Location, Scale and Shape (GAMLSS) approach to incorporate the zero-inflated (ZIP) Poisson family and to study the flowering records of 8 eucalypt species, *Eucalyptus camaldulensis, E. goniocalyx, E. leucoxylon, E. macrorhyncha, E. melliodora, E. microcarpa, E. polyanthemos* and *E. tricarpa*a - with the aim, in part, of detecting non-linear responses to climate. Regardless of the cyclicity of flowering, each species flowering is shown to be significantly influenced by temperature and this effect is non-linear. The main driver for flowering in *E. leucoxylon*, *E. macrorhyncha*, *E. camaldulensis* and *E. melliodora* is minimum temperature with flowering intensity less for *E. leucoxylon* for warmer minimum temperatures, while flowering intensities increase for the other 3 species in a similar climatic environment; with minimum temperatures in the region under study having decreased significantly by 0.1°C between 1998 and 2007. Maximum daily temperature has increased by 0.6°C and mean daily temperature by 0.3°C. More intense flowering is evident in *E. goniocalyx* and *E. microcarpa* as well as *E. polyanthemos,* which are positively influenced by mean temperature (for *E. goniocalyx* and *E. microcarpa*) and maximum temperature (for *E. polyanthemos*). Flowering in *E. tricarpa* is expected to be less intense over this period, as it is negatively influenced by maximum temperature and positively influenced by minimum temperatures (after accounting for maximum temperature). Base threshold temperatures were similar for *E. camaldulensis*, *E. melliodora*, and *E. macrorhyncha*, between 8.3°C and 9.3°C; and 9.8°C for *E. tricarpa*. By contrast *E. microcarpa* has a higher threshold temperature of 16.5°C, similar *E. polyanthemos* (17.1°C) and *E. goniocalyx* (13.6°C) - indicating their flowering is in a heat-demanding developmental period (Wielgolaski, 1999). *E. polyanthemos* has the highest base temperature but the shortest interval, 1 month, between the pre-determined start date and peak flowering. *E. leucoxylon* commences flowering the latest, with the lowest temperature requirement for development – as supported by its lowest threshold temperature (3.3°C). Of the eight species upper threshold temperatures (when a phase ceases) only one has previously been determined for *E. leucoxylon* (Hudson et al., 2003). Flowering of all species was positively and significantly correlated with last month's flowering (except for *E. macrorhyncha*); and with flowering 11-12 months earlier for 4 of the species. There is a clear cycling of the direction of effects of the short term (< 6 months) flowering state lags for 3 of the 8 species - *E. camaldulensis, E. melliodora* and *E. polyanthemos*. These 3 species had 2-3 month short term lag effects of past flowering (apart from the positive lag 1 effect) that negatively impact on current flowering. For *E. polyanthemos* there is also a highly significant but opposite, positive 4 month lag effect. These eight species are shown to be significantly influenced by temperature and as a consequence their flowering phenology will possibly change in response to climate change, with changes in temperature likely to translate to changes in both the timing of flowering commencement and intensity. GAMLSS analysis demonstrates the same contemporaneous effect of climate on flowering for *E. tricarpa* and *E. leucoxylon*, which constitutes one species pairing; for *E. goniocalyx*, *E. microcarpa* and *E. macrorhyncha;* and for *E. camaldulensis*, *E.melliodora* and *E. polyanthemos*, both species triples whose members were shown recently to flower synchronously (Hudson et al., 2011a,b). GAMLSS are thus able to assist in delineating the unique climatic signatures for species which synchronise flowering.

Keywords: Multiple Time series, Climate change, Generalised Additive Model for Location, Scale and Shape, Thresholds, Non-linear impacts

1. INTRODUCTION

Phenology (Hudson, 2010a, b): involves the recording of recurring natural events such as the commencement of flowering (Leith 1974, Keatley et al., 1999a, Koch, 2000, Hudson et al., 2005) or the arrival of migratory birds and the influence on such events climatic and edaphic factors; timing of biological events (life stages such as flowering, fruiting, bird arrival) influences many different ecological processes (Forrest and Miller-Rushing 2010). These processes also have a significant role in shaping society's values (e.g. human health, biodiversity, forestry, agriculture and tourism (Beggs 2004; Fitter and Fitter 2002; van Vliet 2010). Since the 1990s primarily due to climate change (Keatley and Hudson 2010) phenological time series have been used to determine and report the impacts of global warming in both natural and managed systems (Menzel et al.*,* 2006; Rosenzweig et al., 2008; Sparks et al,. 2005). Long-term phenological studies are limited in Australia, and meta-analytic studies of these almost nonexistent (Chambers and Keatley, 2010a,b, Hudson, 2010a,b, Hudson and Keatley, 2010a, Hudson, 2011). Eucalypts form the focus of known Australian phyto-phenological studies, as they are the dominant species both in a botanical and economic sense (Keatley and Hudson, 2007). 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). This study extends the Generalised Additive Model for Location, Scale and Shape (GAMLSS) approach of Hudson et al. (2009) to incorporate the zero-inflated (ZIP) Poisson family (Lambert 1992) and to study the flowering records of 8 eucalypt species, *Eucalyptus camaldulensis, E. goniocalyx, E. leucoxylon, E. macrorhyncha, E. melliodora, E. microcarpa, E. polyanthemos* and *E. tricarpa* - with the aim, in part of detecting non-linear responses to climate. The response of *E. leucoxylon* has previously been shown to be non-linear (Hudson et al., 2003)

GAMLSS, are part of the Generalized Linear Models (GLM) and Generalized Additive models (GAM) 'family' were developed by Rigby and Stasinopoulos (2005) (Stasinopoulos and Rigby, 2007) 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. Recent applications of GAMLSS involve modelling climate with Sudden Infant Death Syndrome (Hudson et al., 2008) and the establishment of the global standard child growth curves by the WHO (Borghi et al,. 2006) (see also http://en.wikipedia.org/wiki/Generalized_additive_model_for_location,_scale_and_shape) and the modelling 4 of the 8 species studied here via GAMLSS with Poisson link (Hudson et al., 2010c; Hudson et al., 2009). The latter represented the first attempt to utilise phenological data to determine the responses of flowering to climate using GAMLSS; and the data set under study represents a long time series by Australasian standards, with more than 30 years of monthly readings, and more than 400 flowering/climate points.

2. DATA AND METHODS

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 focus on the flowering of eight 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 January 1938- March 1972 were collated. 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. Each model tested assumed that the flowering series represent zero-inflated Poisson (ZIP) process 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 lags. Zero-inflated Poisson (ZIP) models provide a way to model data with excess zeroes. ZIP regression models have been utilised in diverse applications, e.g., modeling fish counts (Mayer et al., 2005).

3. RESULTS

Table 1 shows the results of a GAMLSS ZIP 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 1 we see that the temperature variants had singly (or jointly in the case of *E. tricarpa*) 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 effects of temperature and previous flowering lags were accounted for (thus it was omitted from the model by the stepwise procedure). 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 (Table 1).

For each species, except *E. macrorhyncha,* flowering one month prior significantly increased the likelihood of current flowering (a positive lag1 effect (P <0.0001, Table 1). A significant positive lag effect was found in *E. microcarpa* and *E. polyanthemos*, with current flowering positively correlated with flowering one year (lag 12) earlier. Similarly a significant lag 11 effect was found in *E. camaldulensis* and *E. melliodora* with current flowering positively correlated with flowering 11 months earlier. There is also a clear cycling of the direction of effects of the short term (< 6 months) flowering state lags for 3 of the 8 species, namely, *E. camaldulensis, E. melliodora* and *E. polyanthemos*. These 3 species had short term lag effects (apart from the positive lag 1 effect of past flowering) that negatively impact on current flowering: at 3 months for both *E. camaldulensis* ($\beta = -1.50$, P <0.0001) and *E. melliodora* ($\beta = -0.24$, P <0.0001); and at 2 months for *E. polyanthemos* ($\beta = -0.17$ P = 0.10). For *E. polyanthemos* there is also a highly significant but positive lag 4 effect ($\beta = 1.24$, P <0.0001) - a swap in the sign of the effect of past flowering state between 2 and 4 months (Table 1).

The main climatic driver for flowering, after adjusting for flowering status at earlier lags, in *E. leucoxylon*, *E. macrorhyncha*, *E. camaldulensis* and *E. melliodora* is minimum temperature - with flowering intensity being less for *E. leucoxylon* when there are warmer minimum temperatures ($\beta = -0.1024$, P <0.0001); whilst flowering increases for the other 3 species in a similar climatic environment; for *E. macrorhyncha* ($\beta = 0.12$, P <0.0001); *E. camaldulensis* ($\beta = 0.10$, P <0.0001); and *E. melliodora* ($\beta = 0.12$, P <0.0001, Table 1). *Eucalyptus tricarpa* flowers less intensely in response to predicted increases in maximum temperature ($\beta = -0.10$, P = 0.02), but more intensely with increased minimum temperature (after accounting for maximum temperature) ($\beta = 0.23$, P <0.0001, Table 1). *Eucalyptus tricarpa* thus has two main but opposing temperature drivers, in that *E. tricarpa* prefers cooler maximum temperature but warmer minimum temperature. It is noteworthy that *E. leucoxylon* flowers less intensely in response to predicted increases in minimum temperature, which have decreased significantly by 0.1°C between 1998 and 2007 in the region under study and this species, along with *E. tricarpa,* are the only species whose *main* temperature driver has a negative impact on flowering. More intense flowering is evident in *E. goniocalyx* and *E. microcarpa* as well as *E. polyanthemos,* as they are positively influenced by mean temperature (for *E. goniocalyx* ($\beta = 0.19$, P <0.0001) and *E. microcarpa* ($\beta = 0.17$, P <0.0001) and maximum temperature (for *E. polyanthemos* ($\beta = 0.08$, P <0.0001). All GAMLSS models fitted well (not shown here). *E. goniocalyx* gave the best fit as evidenced by its low value of scaled deviance statistic (GD = 366.3) (Table 1).

Table 1. Parameter estimates and goodness of fit statistics of the GAMLSS (ZIP2) model for eight species.

Species	Predictors	β estimate	SE	t value	P	GD$^\phi$	AIC	SBC
E. goniocalyx	Intercept	-55.16	1.38	-40.08	0.00	366.3	394.4	448.4
	meanT	0.19	0.03	6.87	0.00			
	lag1	1.44	0.07	20.64	0.00			
E. microcarpa	Intercept	-6.56	0.41	-16.07	0.00	513.8	541.8	596.5
	meanT	0.17	0.02	8.27	0.00			
	lag1	1.17	0.05	22.50	0.00			
	lag12	0.31	0.06	5.18	0.00			
E. macrorhyncha	Intercept	-1.62	0.24	-6.89	0.00	663.7	675.7	698.8
	minT	0.12	0.02	4.98	0.00			
E. camaldulensis	Intercept	-4.31	0.59	-7.35	0.00	400.5	436.5	506.1
	minT	0.10	0.05	2.12	0.03			

						GD	AIC	SBC
	lag1	1.45	0.07	20.84	0.00			
	lag3	-1.50	0.03	-46.22	0.00			
	lag11	2.40	0.10	23.08	0.00			
E. melliodora	Intercept	-3.24	0.37	-8.87	0.00	589.0	625.0	695.3
	minT	0.12	0.03	3.69	0.00			
	lag1	0.61	0.05	12.41	0.00			
	lag3	-0.24	0.06	-3.95	0.00			
	lag11	0.26	0.05	5.13	0.00			
E. polyanthemos	Intercept	-5.02	0.68	-7.38	0.00	501.6	545.6	631.5
	maxT	0.08	0.03	3.28	0.00			
	lag1	0.83	0.10	8.15	0.00			
	lag2	-0.17	0.11	-1.63	0.10			
	lag4	1.24	0.09	13.55	0.00			
	lag12	0.32	0.09	3.58	0.00			
E. leucoxylon	Intercept	0.40	0.17	2.33	0.02	942.0	962.0	1001.1
	minT	-0.10	0.02	-5.01	0.00			
	lag1	0.36	0.04	8.11	0.00			
E. tricarpa	Intercept	-0.43	0.42	-1.01	0.31	638.9	674.9	745.2
	maxT	-0.10	0.04	-2.33	0.02			
	minT	0.23	0.07	3.24	0.00			
	lag1	0.36	0.07	5.43	0.00			
	lag5	-0.01	0.08	-0.08	0.94			

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

Thresholds for start and finish of flowering: The β estimates in Table 1 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 1) 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 (e.g. 17.1°C maximum temperature for *E. polyanthemos,* previously 14°C by Keatley and Hudson (2000)). 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 (e.g 26.5°C maximum temperature for *E. polyanthemos*). The resultant temperature thresholds for all eight species show that the base threshold temperatures were similar for *E. camaldulensis*, *E. melliodora*, and *E. macrorhyncha*, between 8.3°C and 9.3°C; and 9.8°C for *E. tricarpa* (previously 11.7°C (Keatley and Hudson, 2000)). By contrast *E. microcarpa* has a higher threshold temperature of 16.5°C, similar to that of *E. polyanthemos* (17.1°C) and *E. goniocalyx* (13.6°C) - indicating that their flowering is in a heat-demanding developmental period (Wielgolaski, 1999). *Eucalyptus leucoxylon* has the lowest threshold (3.3°C).

4. DISCUSSION AND CONCLUSIONS

This study shows that each specie's flowering is significantly influenced by temperature and that this effect is non-linear. The non-linear effect of temperature is well recognised for crops (Loomis and Connor, 1992) but less so for native species (Sparks et al., 2000). The main driver for flowering in *E. leucoxylon*, *E. macrorhyncha*, *E. camaldulensis* and *E. melliodora* is minimum temperature. This is in agreement with other studies for *E. leucoxylon* (Hudson and Keatley, 2010a,b; Hudson et al., 2010; Keatley et al., 2002; Keatley and Hudson, 2000) and *E. macrorhyncha* (Hudson et al., 2011a,b). The authors found *E. macrorhyncha* is influenced positively by both minimum and maximum temperatures, with minimum temperatures at the 4 month scale being the most significant. However, the main driver for the other two species has previously been determined to be maximum temperature; and likewise recently by wavelet correlation (but only just significant) (Hudson et al., 2011a,b). Flowering is less for *E. leucoxylon* for warmer minimum temperatures,

while flowering increases for the other 3 species in a similar climatic environment. More intense flowering occurs in *E. goniocalyx* and *E. microcarpa* as well as *E. polyanthemos,* as they are positively influenced by mean temperature (for *E. goniocalyx* and *E. microcarpa*) and maximum temperature (for *E. polyanthemos).* *E. tricarpa's* flowering is expected to be to less over this period, as it is negatively influenced by maximum temperature and positively by minimum temperatures (after accounting for maximum temperature).

Base threshold temperatures (when a plant becomes physiologically active) have not been previously determined for five of these eight species: *E. camaldulensis E. goniocalyx, E. macrorhyncha, E. melliodora,* and *E. microcarpa*. GAMLSS ZIP modelling showed that base threshold temperatures were similar for *E. camaldulensis*, *E. melliodora*, and *E. macrorhyncha*, between 8.3°C and 9.3°C; and 9.8°C for *E. tricarpa*. By contrast *E. microcarpa* has a higher threshold temperature of 16.5°C, similar to that of *E. polyanthemos* (17.1°C) and *E. goniocalyx* (13.6°C). A base temperature of 11.7°C for *E. tricarpa* and 14.1°C for *E. polyanthemos* (via methods developed by Yang et al. (1995)) - regression coefficient and coefficient of variation (CV) has previously been calculated by Keatley and Hudson (2000). Ranges of a similar magnitude in base temperatures have previously been reported for other eucalypts (e.g. for *E. regnans* between 5 °C and 7.5 °C (Ashton, 1975; Nitschke and Hickey, 2007)). Some of these differences can be attributed to the statistical methods used to determine the threshold temperatures. Indeed a method for evaluating the most appropriate threshold temperatures is yet to receive widespread acceptance (Snyder, 1999). The higher thresholds for *E. microcarpa, E. polyanthemos* and *E. goniocalyx* indicate that their flowering 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 and peak flowering (Keatley and Hudson, 2007). *Eucalyptus leucoxylon* commences flowering the latest, in May, indicating that it has the lowest temperature requirement for development, as supported by its lowest threshold temperature (3.3°C). Of the eight species upper threshold temperatures (when a phase ceases – in this case flowering) only one temperature threshold has previously been determined for *E. leucoxylon* – this using mean temperature an upper threshold of 18°C was determined (Hudson et al., 2003).

There is a clear cycling of the direction of effects of the short term (< 6 months) flowering state lags for *E. camaldulensis, E. melliodora* and *E. polyanthemos*. For *E camaldulensis* and *E. melliodora* their dependency cycled, from positive to negative, from lag 1 to lag 3 months, and oppositely from negative to positive from lag 3 to 11 months prior. These 3 species had significant short term lag effects (apart from the positive lag 1 effect of past flowering state) that *negatively* impact on current flowering: at 2 months for *E. polyanthemos* and at 3 months for both *E. camaldulensis* and *E. melliodora* – this species triple was recently identified as synchronous (Hudson et al., 2011a,b). The change in direction of the effect of past flowering may well reflect the dynamic cycling impacts of climate and flowering as evidenced by both wavelets (Hudson et al (2010a,b) and singular spectrum analysis (Hudson and Keatley, 2010b) of the same eight species. Also confirmed recently by multivariate mixture approaches (Kim et al., 2011). Lags of 11 and 12 months are intuitively expected given that an annual flowering is expected, but evidenced only in 4 of the 8 species. What differentiates these with later lags versus those without? For each species one can consider a combination of five flowering characteristics: the highest value of the likelihood of flowering commencing in a given month in a flowering year; the number of months that flowering generally starts in; the number of months that flowering generally commences in, the probability of flowering success for a given month each year and how often flowering fails. Two of the species, *E. microcarpa* and *E. melliodora*, with late lags have been shown by Keatley and Hudson (2007) to have high values for the likelihood for the month they commence flowering in (> 0.60). For the others it is a combination of lower number of months that flowering occurs in or where flowering is spread over, and a low flowering failure rate/high annual flowering success rate. *Eucalyptus camaldulensis* commences flowering in four months and these four months are adjacent to each other. Flowering in this species also has a commencement likelihood of 0.39 for two months: November and December. Those that do not have this can commence flowering in a large number of months (> 7months) (*E. tricarpa*, *E. leucoxylon* and *E. macrorhyncha*) and hence have a low value of likelihood of commencement. *Eucalyptusgoniocalyx* can commence in five months the same as *E. polyanthemos* but has the lowest value for flowering success (0.58) and as a consequence fails to flower every 2.4 years. Note that *E. leucoxylon* has the highest flowering success rate (1.00) but still doesn't have a 11 or 12 month lag. GAMLSS ZIP analysis demonstrates the same contemporaneous effect of climate on flowering for *E. tricarpa* and *E. leucoxylon*, which constitutes one species pairing; for *E. goniocalyx*, *E. microcarpa* and *E. macrorhyncha;* and for *E. camaldulensis*, *E.melliodora* and *E. polyanthemos*, both species triples whose members were shown recently via wavelets to flower synchronously (Hudson et al. 2011a,b). GAMLSS are thus able to assist in delineating the unique climatic signatures for species which synchronise flowering.

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