

## LETTER

# Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change

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### Abstract

Mast-seeding plants often produce high seed crops the year after a warm spring or summer, but the warm-temperature model has inconsistent predictive ability. Here, we show for 26 long-term data sets from five plant families that the temperature difference between the two previous summers ( $\Delta T$ ) better predicts seed crops. This discovery explains how masting species tailor their flowering patterns to sites across altitudinal temperature gradients; predicts that masting will be unaffected by increasing mean temperatures under climate change; improves prediction of impacts on seed consumers; demonstrates that strongly masting species are hypersensitive to climate; explains the rarity of consecutive high-seed years without invoking resource constraints; and generates hypotheses about physiological mechanisms in plants and insect seed predators. For plants,  $\Delta T$  has many attributes of an ideal cue. This temperature-difference model clarifies our understanding of mast seeding under environmental change, and could also be applied to other cues, such as rainfall.

### Keywords

Climate cue, global warming, mast flowering, predator satiation, predictive model, wind pollination.

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## INTRODUCTION

Mast seeding (synchronous, highly variable seed production among years in a population of perennial plants) is often selectively favoured when synchrony increases the fitness of in-step plants, for example by satiating seed predators (Janzen 1971; Silvertown 1980; Kelly 1994). The resulting occasional large seed crops have many consequences for seed consumers and their predators, and other ecosystem processes including nutrient cycling and disease outbreaks (Ostfeld & Keesing 2000). It is important, therefore, to understand the cues that synchronise plant populations, both for elucidating the underlying selective processes, and to allow prediction of large seed crops for management of consumers.

The synchronising cue is almost always weather-related (Janzen 1971), although fire is a less common alternative (Kelly 1994). In principle, plants could use almost any weather cue, e.g. high or low temperatures, increased or decreased rainfall. Temperature has theoretical advantages because it is uniform on a large geographical scale, thus aiding synchronisation (Norton & Kelly 1988), and warm temperatures during the growing season are frequently associated with large seed crops in the following season. For example, warm summers were the primary cue in 17 of 18 species tested in New Zealand (Schauber *et al.* 2002), and in *Fagus orenata* in Japan (Masaki *et al.* 2008) and *Picea abies* in Norway (Selas *et al.* 2002).

Although the warm-temperature predictive model is often reported, some difficulties have arisen in attempting to apply it. First, predictions that are initially promising may falter when data

runs are extended. For example, a significant warm-temperature cue in *Phormium* spp based on 10 years of data (Brockie 1986) became non-significant when extended to 18 years of data (Schauber *et al.* 2002), showing limited predictive ability in some cases. Second, the warm-temperature model requires plants to adjust their flowering thresholds to local site mean temperature. The mechanism by which plant populations could determine long-term local mean temperature and tailor their seeding responses across a wide range of altitudes remains enigmatic (Sullivan & Kelly 2000; Kelly *et al.* 2008a). Third, a warm-temperature model alone cannot explain why two consecutive warm years rarely generate repeated high-seed years. It has therefore been necessary to include secondary resource-limitation vetoes on large seed crops (e.g. Rees *et al.* 2002).

Here, we present a new hypothesis: that mast-seeding species respond to the difference in temperature from one growing season to the next, i.e. change in temperature  $\Delta T = T_{n-1} - T_{n-2}$ , where  $T_{n-1}$  and  $T_{n-2}$  are the mean temperatures in the growing seasons 1 and 2 years prior to seed production. If seed or flower production responds to  $\Delta T$ , we would expect previous studies using both variables separately (hereafter the '2T' model) to show a positive correlation with the temperature lagged 1 year ( $T_{n-1}$ ) and a negative correlation with temperature lagged 2 years ( $T_{n-2}$ ). Only a small number of studies have reported both  $T_{n-1}$  and  $T_{n-2}$  to be significant (Schauber *et al.* 2002; Smaill *et al.* 2011; Krebs *et al.* 2012); others tested  $T_{n-1}$  and  $T_{n-2}$ , but did not find both to be significant (e.g. Sork *et al.* 1993; Clotfelter *et al.* 2007). Most studies examining masting and environmental climate variables have only included tem-

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perature from the previous growing season ( $T_{n-1}$ ), i.e. the T1 model. Correlations with one of  $T_{n-1}$  or  $T_{n-2}$  alone will generally be weaker than the proposed  $\Delta T$  model and may be easily obscured in models that screen a large number of climate variables. Such data exploration is likely to initially test each variable separately, which would fail to show that the difference between  $T_{n-1}$  and  $T_{n-2}$  gives a good fit (as is explicit in the  $\Delta T$  model). One or both variables thus might be dropped from candidate models (e.g. Selas *et al.* 2002), consistent with their being rarely reported in the literature.

In this article, we show that the  $\Delta T$  model provides a much better fit to seedfall data across a range of different plant families than the common T1 absolute temperature model, and is superior to the 2T multiple regression approach by being simpler and giving more robust predictions of seed crops. This  $\Delta T$  model also has several important novel implications for plant responses to climate change. For the species investigated here, the most appropriate weather cue is average summer temperature, although our hypothesis is equally applicable to species responding to temperatures at other times of year or to other weather cues.

## MATERIALS AND METHODS

### Study sites and data sources

We used 26 mast-seeding data sets from New Zealand spanning 15 species in five plant families, covering a range of different habitats, plant life forms and known selective benefits of mast seeding (Table 1). We included 20 data sets updated from Schaubert *et al.* (2002), i.e. all continuing data sets that we had permission to include, plus an additional species, *Celmisia hyallii*, as a representative of a fifth plant family (Asteraceae), and five additional sites for the two *Phormium* species. These very long data sets (mean 29 years, range 15–43 years) come from 12 different sites (Figure S1) and have high seedfall variability [average coefficient of variation (CV) 1.64, range 0.76–2.67; Table 2]. Some of these species had best-fit climate predictors published previously on shorter subsets of the data (Table S1), usually using previous summer temperatures ( $T_{n-1}$ ). For collection methods, see Supplementary Information.

Although it is not possible to objectively dichotomise masting datasets into high-seed and low-seed years (Kelly 1994), we tested the frequency of consecutive high-seed years by arbitrarily classifying the top 20% of seed crops within each data set as high-seed years (Supplementary Information) and recording the fraction of all possible pairs of years that had consecutive high-seed years. To see whether New Zealand was unusual in this regard, this same

approach was also applied to the longest 20 Northern Hemisphere data sets from the 570 data sets compiled by Kelly & Sork (2002). These Northern Hemisphere data sets covered 17 species in nine genera including *Quercus*, *Pinus*, *Picea*, *Abies*, *Pseudotsuga* and *Larix* (Supplementary Information).

### Climate data

All analyses used mean monthly air temperatures as predictors, within the austral summer period December–March inclusive. Most analyses used a constant *a priori* time window (January–March), although different time windows were also investigated (Supplementary Information). Temperature data were measured on site for Mt Hutt (at 1070 m from 1995 onwards: Kelly *et al.* 2008a) and Takaha Valley (1972 onwards). For other sites, the nearest weather station was taken from the New Zealand National Climate Database of the National Institute of Water and Atmospheric Research; see <http://cliflo.niwa.co.nz>. Any missing data in data sets, including at Mt Hutt pre-1995 and Takaha Valley pre-1972, were filled using data from nearby weather stations to estimate the missing daily temperatures using a linear fit, before calculating monthly means. Missing data were normally infrequent (typically < 5 days per month) and, in all cases, linear correlations between temperature data sets were tight (correlations ranged 0.85–0.99). Gaps in the Mt Hutt data until 2004 were filled by estimation from Christchurch Botanic Gardens, but thereafter were filled from additional on-site weather stations at 450 m and 1560 m elevation on Mt Hutt (Kelly *et al.* 2008a).

To test for the frequency of consecutive warm summers, the warmest 20% of years for each time series were classified as warm years and the fraction of all possible pairs of years that had consecutive warm years was recorded. To examine the relative temperature patterns associated with the observed consecutive high-seed years, we took the absolute temperatures for the 3-year period ( $T_{n-2}$ ,  $T_{n-1}$ ,  $T_n$  where  $n$  is the first high-seed year), and standardised by subtracting the mean of the three. We then compared the standardised  $T_{n-2}$ ,  $T_{n-1}$  and  $T_n$  using a single-factor ANOVA.

### Statistical analysis

All statistics were run using R version 2.13 (R Development Core Team 2011). The analysis used linear fits with log(annual seedfall) as the dependent variable. The assumptions of linear regression were all verified (Supplementary Information). If any zeros were present (i.e. no seed produced in a given year), these were replaced with values equal to half of the smallest non-zero value prior to log transforma-

**Table 1** Features of the mast-seeding species analysed, including any known selective benefits of mast seeding in each genus

Genus	species	Family	Life form	Habitat	N datasets	Selective benefits of masting*
<i>Celmisia</i>	<i>hyallii</i>	Asteraceae	dicot herb	alpine grassland	1	satiating invertebrate seed predators (1, 2)
<i>Chionochloa</i>	<i>australis</i> , <i>crassiscula</i> , <i>macra</i> , <i>pellens</i> , <i>rubra</i> , <i>rigida</i> , <i>teretifolia</i>	Poaceae	tussock grass	alpine grassland	9	satiating invertebrate seed predators (3)
<i>Elaeocarpus</i>	<i>dentatus</i>	Elaeocarpaceae	tree to 20 m tall	lowland forest	1	
<i>Nothofagus</i>	<i>fusca</i> , <i>menziesii</i> , <i>solandri</i> , <i>truncata</i>	Nothofagaceae	tree to 30 m tall	lowland to montane forest	7	enhanced wind pollination (4)
<i>Phormium</i>	<i>cookianum</i> , <i>tenax</i>	Hemerocallidaceae	monocot herb	lowland to montane	8	

Plant names follow the New Zealand Plant Names database, <http://nzflora.landcareresearch.co.nz/>.

\*References: 1 (Molloy 1975), 2 (Spence 1990), 3 (Kelly *et al.* 2008a), 4 (Kelly *et al.* 2001).

**Table 2** Seedfall data sets used in the analysis including duration, seedfall coefficient of variation (CV), comparison of T1,  $\Delta T$  and 2T regressions of temperature against log seedfall ( $r^2$  and  $P$  values), and which of the  $\Delta T$  and 2T models fit the data best, judged by lowest  $AIC_c$ , smallest RMSE when fitted to data excluding the last 5 years then used to predict the final 5 years, and narrowest 95% confidence interval for coefficients

Species	Site	Nyrs	CV	$r^2$ T1	$r^2$ $\Delta T$	$r^2$ 2T	$p$ T1	$p$ $\Delta T$	$p$ 2T	Best $AIC_c$	Best RMSE	Best C.I.
<i>Celmisia lyallii</i> *	MH	18	1.965	0.248	0.418	0.424	<b>0.035</b>	<b>0.004</b>	<b>0.016</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>Chionochloa australis</i>	MM	31	1.775	0.450	0.554	0.623	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	2T	$\Delta T$	$\Delta T$
<i>Chionochloa crassiuscula</i>	TV	38	2.665	0.333	0.411	0.444	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>Chionochloa macra</i>	MH	22	1.885	0.120	0.262	0.262	0.115	<b>0.015</b>	0.056	$\Delta T$	$\Delta T$	$\Delta T$
<i>Chionochloa pallens</i> *	MH	26	1.912	0.145	0.484	0.491	0.055	< <b>0.001</b>	< <b>0.001</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>C. pallens</i>	MM	31	1.488	0.328	0.647	0.655	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>C. pallens</i>	TV	38	1.807	0.272	0.487	0.489	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>Chionochloa rigida</i>	TV	38	2.405	0.420	0.606	0.627	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>Chionochloa rubra</i>	TV	38	1.839	0.322	0.467	0.483	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>Chionochloa teretifolia</i>	TV	38	2.500	0.381	0.525	0.549	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>Elaeocarpus dentatus</i> *	OR	43	0.834	0.226	0.362	0.365	<b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	$\Delta T$	2T	$\Delta T$
<i>Nothofagus fusca</i>	EG	21	1.607	0.224	0.556	0.556	<b>0.030</b>	< <b>0.001</b>	<b>0.001</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>N. fusca</i> *	MM	35	2.150	0.319	0.476	0.508	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	$\Delta T$	2T	$\Delta T$
<i>Nothofagus menziesii</i>	MM	35	1.451	0.284	0.354	0.399	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	2T	2T	$\Delta T$
<i>N. menziesii</i>	TK	39	1.820	0.353	0.379	0.430	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	2T	$\Delta T$	$\Delta T$
<i>Nothofagus solandri</i>	MM	35	2.073	0.321	0.331	0.405	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	2T	2T	$\Delta T$
<i>N. solandri</i>	TV	30	1.265	0.131	0.426	0.451	<b>0.049</b>	< <b>0.001</b>	< <b>0.001</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>Nothofagus truncata</i>	OR	43	2.280	0.345	0.535	0.540	< <b>0.001</b>	< <b>0.001</b>	< <b>0.001</b>	$\Delta T$	2T	$\Delta T$
<i>Phormium cookianum</i> *	MH	15	1.267	0.165	0.588	0.617	0.133	< <b>0.001</b>	<b>0.003</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>P. cookianum</i>	TH	20	0.762	0.002	0.307	0.490	0.839	<b>0.011</b>	<b>0.003</b>	2T	2T	$\Delta T$
<i>Phormium tenax</i>	AL	15	0.984	0.162	0.554	0.607	0.137	<b>0.001</b>	<b>0.004</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>P. tenax</i>	GP	15	1.415	0.125	0.518	0.596	0.197	<b>0.002</b>	<b>0.004</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>P. tenax</i>	RG	15	1.019	0.027	0.429	0.587	0.556	<b>0.008</b>	<b>0.005</b>	2T	$\Delta T$	$\Delta T$
<i>P. tenax</i>	RW	15	1.261	0.108	0.558	0.624	0.231	<b>0.001</b>	<b>0.003</b>	$\Delta T$	$\Delta T$	$\Delta T$
<i>P. tenax</i>	NG	33	1.032	0.092	0.500	0.576	0.086	< <b>0.001</b>	< <b>0.001</b>	2T	2T	$\Delta T$
<i>P. tenax</i>	TH	29	1.243	0.065	0.365	0.415	0.182	< <b>0.001</b>	<b>0.001</b>	$\Delta T$	$\Delta T$	$\Delta T$
Means			1.64	0.230	0.465	0.508						

$AIC_c$ , Akaike information criterion; RMSE, root mean square error.

Significant  $r^2$  results ( $P < 0.05$ ) are in bold.

\*Data set illustrated in Fig. 1. Full site names are given in Table S1.

tion, which is similar to the approach used by Schaubert *et al.* (2002). Comparisons were made following the methodology of Burnham & Anderson (2002). In total, four candidate models were tested:

- (1) T1 model: the mean summer temperature in the previous year ( $T_{n-1}$ ).
- (2) T2 model: the mean summer temperature 2 years previously ( $T_{n-2}$ ).
- (3)  $\Delta T$  model: the change in mean summer temperature over the two preceding years ( $T_{n-1} - T_{n-2}$ ).
- (4) 2T model: both mean summer temperature in the previous year ( $T_{n-1}$ ) and mean summer temperature 2 years previously ( $T_{n-2}$ ).

The candidate models were selected *a priori* to the comparison tests to include all additive combinations of temperature lagged by up to 2 years and the proposed  $\Delta T$  model. All models were of the standard multivariate linear regression form  $Y_j = a + b_1 T_{n-1,j} + b_2 T_{n-2,j}$  where  $T_{n-1}$  and  $T_{n-2}$  are the predictor variables (mean summer temperature in the two preceding years), and  $Y$  is the response variable (log(seedfall)). The T1, T2 and  $\Delta T$  models therefore had two fitted parameters (as they are constrained by  $b_2 = 0$ ,  $b_1 = 0$  and  $b_2 = -b_1$  respectively), whereas the 2T model had three parameters. The four candidate models were compared using  $r^2$  and the small-sample Akaike information criterion ( $AIC_c$ ).  $AIC_c$  measures the goodness of fit of a model, taking into account the number of model parameters. The smaller a model's  $AIC_c$ , the more parsimoniously it describes the data (Burnham & Anderson 2002). The likeli-

hood ratio test was then used to compare the best two candidate models for each dataset.

The 2T model can also be reformulated as  $Y_j = a + b_\Delta (T_{n-1,j} - T_{n-2,j}) + b_W (T_{n-1,j} + T_{n-2,j})$ , where  $b_\Delta = (b_1 - b_2)/2$  describes the effect of temperature change (as in the  $\Delta T$  model) and  $b_W = (b_1 + b_2)/2$  separately describes the effect of the average absolute temperature over the two preceding years. We calculated regression coefficients and their significance for each candidate model, and the reformulated version of the 2T model. We also calculated 95% confidence intervals for the regression coefficients of the  $\Delta T$  and 2T models, and checked whether the  $\Delta T$  coefficients were consistent with the values fitted in the 2T model.

A key property of a useful model is that it continues to predict new data well. We tested the predictive power of the best two models by fitting each model to each data set, omitting the final 5 years of seed data. The model was then used to predict seedfall for the final 5 years using the appropriate temperature data, and the root mean square error (RMSE) of the predictions compared to the observed seedfall was calculated.

The T1 and  $\Delta T$  models were also compared for their robustness to fine-tuning of the summer time window, and a linear mixed-effects model was used to test for random effects on model fits (Supplementary Information). Finally, the slope coefficients produced by the  $\Delta T$  model for all 26 data sets were regressed against the CV of each data set.

## RESULTS

For predicting seed crops, the widely used previous-summer temperature model (T1) often gave a reasonable fit: mean  $r^2 = 0.230$ , and 16 of 26 datasets were significant (Figs 1 and 2, Table 2). However, the  $\Delta T$  model gave a much improved fit: mean  $r^2 = 0.465$  with higher  $r^2$  values for all 26 datasets, and all 26 datasets were significant (Table 2). Furthermore, the  $\Delta T$  model still fitted better than the T1 model after allowing independent fine-tuning of the time windows used to define summer temperature (Table S2).

When comparing all four candidate models, the  $r^2$  values for the T1 and T2 single-temperature model were similar and both were notably lower than  $r^2$  values for the  $\Delta T$  and 2T models across all data sets (Table S3). The single-temperature models did not have the best AIC<sub>c</sub> value for any of the 26 data sets. Hence, the T1 and T2 models were excluded from further model comparisons.

The 2T model will always fit the data as well or better (i.e. have an equal or higher likelihood) than the  $\Delta T$  model, as it includes the  $\Delta T$  model as a special case (when  $b_1 = -b_2$ ). However, the increase in  $r^2$  gained from the 2T model over the  $\Delta T$  model was very small (0.042 on average; ranging from < 0.001 to 0.182) relative to the increase gained by the  $\Delta T$  model over the T1 model (0.236 on average; ranging from 0.01 to 0.449). When the number of model parameters is taken into account (using AIC<sub>c</sub>), the  $\Delta T$  model outperformed the 2T model in 19 of the 26 datasets (Table 2). With the exception of two data sets, the AIC<sub>c</sub> for the  $\Delta T$  model never exceeded that for the 2T model by more than 3 (Table S3). The likelihood ratio test suggested that the 2T and  $\Delta T$  models were equivalent ( $P > 0.05$  for 23 of the 26 datasets, and  $P > 0.01$  for all 26 datasets; Table S3). These results indicate that, overall, the 2T model did not provide a more parsimonious description of the data than the  $\Delta T$  model.

The confidence interval for the regression coefficient in the  $\Delta T$  model was narrower than those for the 2T model in all 26 datasets (Table S4). The RMSE of predictions for the final 5 years of seedfall data was lower for the  $\Delta T$  model than the 2T model for 19 of the 26 data sets (Table 2). This shows that the  $\Delta T$  model has less uncertainty and is more robust to new data than the 2T model. In the 2T model, the coefficient of  $T_{n-1}$  was positive and the coefficient of  $T_{n-2}$  was negative in all 26 datasets (Table S5). Moreover, when the 2T model was reformulated so that the variables are temperature change and average absolute temperature (see Methods), the coefficient for temperature change was always significant ( $P < 0.05$ ), but the coefficient for absolute temperature was only significant in four of the 26 datasets (Table S5). The single regression coefficient for the  $\Delta T$  model was within the 95% confidence intervals of the coefficients for the 2T model for all 26 datasets (Table S4). In other words, the results from the 2T model indicate that plants are responding to the temperature difference  $\Delta T = T_{n-1} - T_{n-2}$ , rather than using  $T_{n-1}$  and  $T_{n-2}$  as independent temperature cues.

The  $\Delta T$  model is considered to be the preferred model for two reasons. First, the principle of parsimony: it outperforms both other two-parameter models tested (T1 and T2) by a wide margin, is comparable to the three-parameter model (2T) based on AIC<sub>c</sub> scores, but outperforms the 2T model at prediction (lower RMSE and narrower confidence intervals). Second, the  $\Delta T$  model makes a testable hypothesis with a simple biological interpretation: seedfall for temperature-driven masting plants is proportional to the change in

mean summer temperature over the preceding 2 years. In contrast, the magnitudes of the coefficients for the 2T model vary without apparent pattern, meaning that no cross-species or cross-genus prediction can be made about the response of masting plants to climate variables.

These results suggest that  $\Delta T$  is likely the climate cue used by these plants. As previous temperature  $T_{n-1}$  is correlated with  $\Delta T$ , warm summers (T1 model) should show some correlation with seedfall data as a proxy for  $\Delta T$ . Such proxies should fit well to highly variable species (i.e. those with a large seedfall CV) that show a strong response to climate, but fit poorly to species with a lower seedfall CV and a consequently lower signal-to-noise ratio. In contrast, the actual cue should fit low-CV and high-CV data sets equally well, because species of both types are responding to the same cue, merely with different amplitudes. We found exactly that pattern. The regressions predicting seedfall from  $\Delta T$  showed no effect of CV on model fit ( $r^2 = 0.01$ ,  $P = 0.57$ , Figure S2), whereas the T1 model was consistent with being a proxy for the  $\Delta T$  model, having worse fits than  $\Delta T$  (Fig. 2), and a strong relationship between CV and scatter ( $r^2 = 0.539$ ,  $P < 0.001$ ; Figure S2, Table S6). Furthermore, the sensitivity of a plant's response to change in temperature is positively related to CV (Fig. 3 and Supplementary Figure S2).

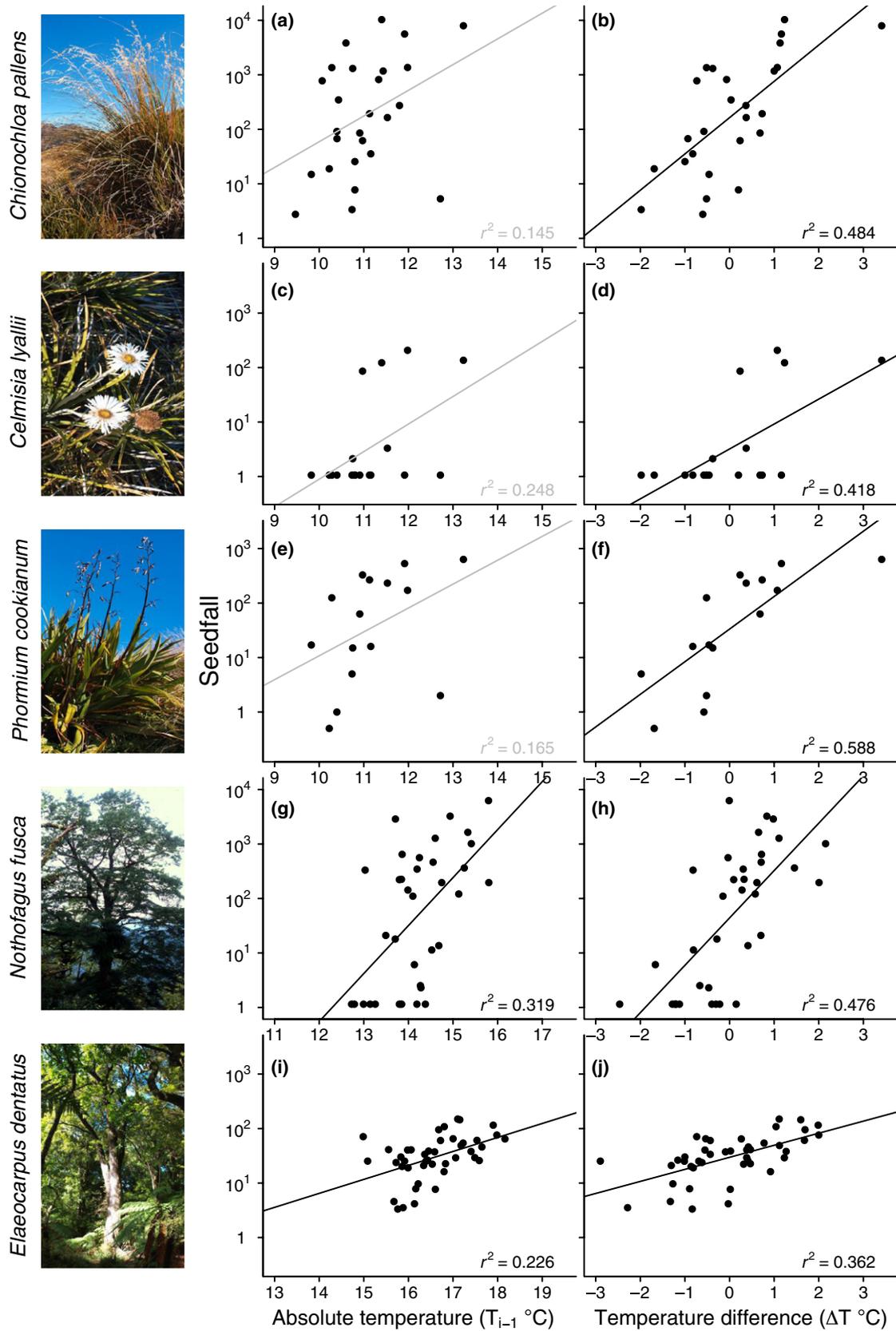
The good fit of the  $\Delta T$  model for five plant families from New Zealand is supported by data from two other families in the Northern Hemisphere. For *Picea glauca* (Pinaceae) in northern Canada (Krebs *et al.* 2012), we calculated that  $\Delta T$  fitted better (T1 model  $r^2 = 0.150$ ,  $\Delta T$  model  $r^2 = 0.344$ , see Supplementary Information). Also, seeding of *Fagus sylvatica* (Fagaceae) in Sweden (Drobyshev *et al.* 2010) was positively correlated with  $T_{n-1}$  and negatively with  $T_{n-2}$ , also consistent with the  $\Delta T$  model.

Consecutive warm summers occurred in 3.8% of pairs in the New Zealand data sets. This is approximately what would be expected if mean summer temperature in a given year is independent of that in the previous year. Consecutive high-seed years were much less common (1.3% of pairs in the New Zealand datasets; 1.4% in the Northern Hemisphere datasets; see Supplementary Information). The  $\Delta T$  model predicts that consecutive high-seed years will occur, but only following two positive  $\Delta T$  values, which requires a specific sequence of absolute temperatures (cold, moderate, hot). Analysis of the standardised temperatures leading up to the nine observed double high-seed events showed significant differences in means among the 3 years ( $F = 34.5$ ,  $df = 2, 24$ ,  $P < 0.001$ ), which matched the predicted sequence (Fig. 4).

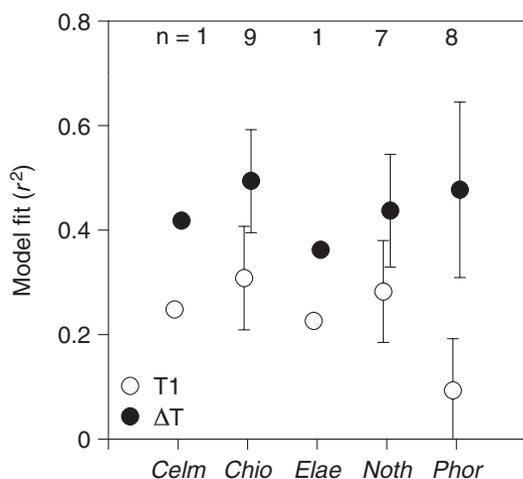
## DISCUSSION

### Benefits of the $\Delta T$ model

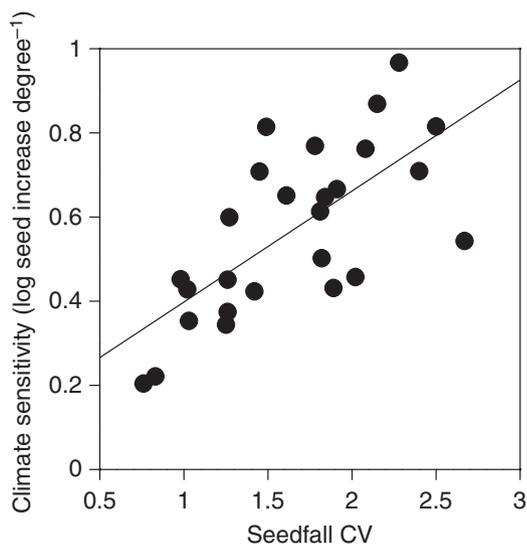
The  $\Delta T$  model overcomes problems raised by the absolute temperature (T1) model. First, it provides better predictions and is more robust to the introduction of additional data. Second, the  $\Delta T$  model solves the enigma of adjustment to local microclimates across altitudes, by providing a mechanism which responds only to temperature differential, not local mean temperature. Third, it explains the rarity of consecutive high-seed events relative to consecutive warm years, because the second of two warm summers will usually have a low  $\Delta T$  value and thus a small seed crop. For example, in data for *Chionochloa pallens* flower crops, the second (1999) of two



**Figure 1** In five diverse plant families, seed crops were better predicted using temperature differential  $\Delta T$  (summer temperature in the previous year minus summer temperature 2 years before, right column) than previous summer absolute temperature  $T_{i-1}$  (centre). The horizontal axes have different minima, but identical ranges. Light grey  $r^2$  values and regression lines were not significant. Summer is January–March in all cases. For information on all 26 datasets see Table 2.

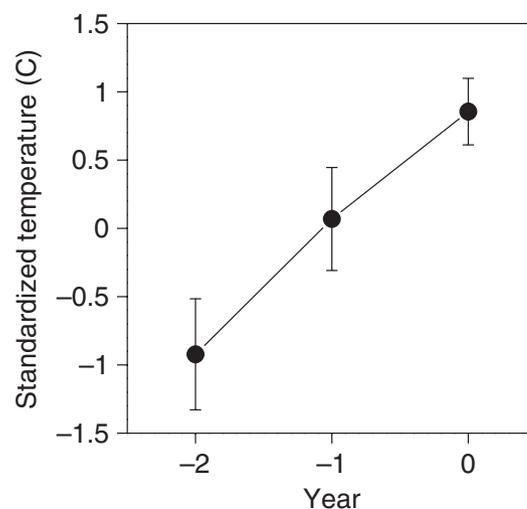


**Figure 2** Model fit (mean  $r^2 \pm 95\%$  CI) by genus for predictions of seed crops using the previous summer (January–March inclusive) absolute temperature model T1 and the temperature differential model  $\Delta T$  (previous summer minus the one before) for 15 species from five genera (*Celmisia*, *Chionochloa*, *Elaeocarpus*, *Nothofagus*, *Phormium*). Number of data sets for each genus ( $n$ ) is indicated at the top.



**Figure 3** The relationship between seedfall variability (coefficient of variation, CV) and climate sensitivity (the change in log flowering per  $1^\circ\text{C}$  increase in  $\Delta T$ ). There was a very strong relationship ( $r^2 = 0.49$ ,  $F_{1,24} = 22.8$ ,  $P < 0.001$ ), showing that all species are using the same climate cue, but strongly masting species are hypersensitive to the cue.

consecutive warm years at Mt Hutt did not produce a large flowering effort in 2000 (the outlier at bottom right in Fig. 1a). Kelly *et al.* (2008a) ascribed this anomaly to exhaustion of plant resources after the previous year's heavy flowering, and so excluded that point from their regression of  $T_{n-1}$  against flowering. In essence, the T1 model requires a secondary stored-resources constraint to explain the rarity of consecutive high-seed years (Rees *et al.* 2002). However, the  $\Delta T$  model avoids the need to invoke resource constraints: note lack of outlier in Fig. 1b. The  $\Delta T$  model does not mean that plant internal resources are irrelevant to masting (Satake & Iwasa 2000; Kelly & Sork 2002), but certainly reduces their importance



**Figure 4** Mean standardised absolute temperatures (i.e. each 3-year temperature sequence offset so that the mean of the sequence is zero) leading up to the nine observed double high-seed years (occurring in years 0 and 1). The differences among years were highly significant (single-factor ANOVA  $F = 34.5$ ,  $df = 2, 24$ ,  $P < 0.001$ ). Error bars are 95% C.I.s.

for explaining the rarity of consecutive high-seed years, thereby simplifying predictions.

The  $\Delta T$  model predicts that consecutive high-seed events can occur, but only after a specific sequence of absolute summer temperatures (Fig. 4). Consecutive high-seed years are occasionally observed (1.3% of pairs in our datasets). One example was 1999 and 2000 in *Nothofagus fusca* in the Eglinton Valley, a seedfall sequence that had serious consequences for invasive mammal outbreaks and subsequent mortality of threatened endemic birds (Dilks *et al.* 2003). The ability of the  $\Delta T$  model to predict the weather patterns causing these rare events is an additional benefit to conservation managers.

#### Consistency with previous literature

Very few studies have reported significant links between seedfall and temperature in both of the two preceding years. Three studies found that  $T_{n-1}$  was positively correlated and  $T_{n-2}$  was negatively correlated with seed production: Schaubert *et al.* (2002) for many of the species included in our article; Smaill *et al.* (2011) for *Nothofagus solandri*; and Krebs *et al.* (2012) for *Picea glauca* in north-western Canada. A fourth study pointed out that in *Fagus sylvatica* (European beech) 'a cold growing season followed by a warm growing season, which, in turn, was followed by a mast year, was a pattern replicated in respect to ... total growing season temperature' (Drobyshev *et al.* 2010, p. 2163). Although this hypothesis for the occurrence of high-seed years is clearly supported by the  $\Delta T$  model, it does not predict what temperatures lead to moderate-seed years, or the conditions which would lead to two consecutive high-seed years, both of which are explicit in the  $\Delta T$  model.

Thus, to our knowledge, only three past studies have presented multiple regression models, which include both  $T_{n-1}$  and  $T_{n-2}$  as significant predictors. Although such multiple regressions can have fits that are similar to the  $\Delta T$  model, they are slightly worse at predicting new data and lack a clear hypothesis for the expected relationship between the two predictors. This lack of an expected

relationship could explain why, even when a negative correlation has been found between seed production and  $T_{n-2}$ , the implications of this fact (and therefore the  $\Delta T$  model) have not previously been recognised (Schauber *et al.* 2002; Krebs *et al.* 2012).

For some species, seed crop predictions may be improved by testing temperature in different seasons, such as spring (Sork *et al.* 1993), or by constructing more complex models that incorporate  $\Delta T$  with other climate variables (for example, variables that correlate with resource availability, e.g. nitrogen; Smaill *et al.* 2011). At a minimum, however, we advocate including  $\Delta T$  as a predictor variable (rather than  $T_{n-1}$  and  $T_{n-2}$  independently) if the effect of multiple climate variables on mast seeding is to be best inferred from a set of candidate models. More generally, difference models could be applied to other weather variables such as rainfall (Piovesan & Adams 2001).

### Implications of the $\Delta T$ model

That masting of species from a wide range of different plant families respond to  $\Delta T$  has at least four important implications.

#### *Climate change*

There has been widespread interest in how increases in local mean temperature might affect masting (McKone *et al.* 1998; Rees *et al.* 2002; Schauber *et al.* 2002; Richardson *et al.* 2005; Overgaard *et al.* 2007), but postulated plant responses were uncertain, ranging from constant heavy flowering to desynchronisation. In contrast, the  $\Delta T$  model makes a firm prediction: mast seeding will be unaffected by gradual increases in mean temperature, because these have almost no effect on  $\Delta T$  values. If local site mean temperatures increase, plants will not show a higher frequency of high-seed years.

Under the  $\Delta T$  model, the only way global climate change might affect masting would be through changes in year-to-year weather variability. If variability increases,  $\Delta T$  values will become larger in absolute value, resulting in exaggerated differences between high- and low-seed years and increasing the CV. Predictions of trends in temperature variability are less certain than predictions of temperature means. There are indications that variability will increase globally (Schar *et al.* 2004; Kharin *et al.* 2007), including in New Zealand (Mullan *et al.* 2001). Importantly, this prediction (seed production might become more extreme with occasional very large seed crops, increasing the CV) is the opposite of current assumptions under the T1 model (that large seed crops would be more frequent because most years are warm, reducing the CV) (McKone *et al.* 1998). Conversely, a decrease in temperature variability (Michaels *et al.* 1998) would result in smaller seed crops at shorter intervals; but with updated global projections, this is deemed less likely [IPCC 2007 (see pp 778 and 786)]. We suggest that the overall effect of increased variability will be small compared with the dominant conclusion from the  $\Delta T$  model that masting will be insensitive to increases in global mean temperature.

#### *Hypersensitivity*

Under the economies-of-scale hypothesis, masting is selectively favoured in plant species where occasional large reproductive efforts are more efficient than regular small ones (Kelly 1994). Forty years ago, Janzen (1971) predicted that this is achieved by species with large economies of scale being selected to show hypersensitivity to a climate cue. Our data add weight to Janzen's prediction (Fig. 3):

all species that we studied responded to the same climate cue, but the high-CV species were hypersensitive (steeper slopes). This supports theoretical predictions (Janzen 1971; Norton & Kelly 1988) that low- and high-CV plants should often use the same temperature cue, but with different sensitivities.

#### *Masting predictions and trophic interactions*

Mast seeding has a major influence on ecological interactions because its ephemeral pulse of bottom-up resource input can influence dynamics and interactions among species at multiple trophic levels (Jones *et al.* 1998; Ostfeld & Keesing 2000; Kelly *et al.* 2008b) and it is a major driver of the abundance and dynamics of small mammals and birds (Fryxell *et al.* 1998; Clotfelter *et al.* 2007). It can also have indirect effects by increasing the abundance of predators, which may in turn reduce the abundance and productivity of bird populations (McShea 2000), a particular problem in invaded ecosystems (Dilks *et al.* 2003). The pulsed input of resources also influences omnivores (Eiler *et al.* 1989), herbivores (Jones *et al.* 1998), invertebrates (Elkinton *et al.* 1996; Poncet *et al.* 2009) and disease and parasite outbreaks (Ostfeld 1997; Pedersen & Greives 2008). The  $\Delta T$  method gives improved predictions using readily available temperature data, without the need to measure and model plant resource dynamics. Better prediction of consumer responses to masting has important implications for ecosystem function, human health and management of threatened and invasive species (Mills & Childs 1998; Ostfeld 2008). In particular, the improved prediction of consecutive high-seed years by the  $\Delta T$  model is valuable for conservation managers (Dilks *et al.* 2003).

#### *Nature of an ideal cue*

The  $\Delta T$  model has many attributes of an ideal cue: it is based on temperature, which changes synchronously across large spatial scales (Norton & Kelly 1988); it rarely requires the plant to seed heavily in consecutive years; and it triggers big seed crops following a warm summer, which may have facilitated greater resource acquisition. The economies-of-scale hypothesis predicts that the fundamental requirement of the climate cue is simply that it provides good synchronisation, so given the contingency of evolution, the cue need not always correlate with resources (Norton & Kelly 1988), and a number of plant species mast in response to cues which have a negative effect on resources (e.g. drought, fire, cold summers: Kelly & Sork 2002, p. 431). However, cues that provide synchrony and also correlate with resources (such as  $\Delta T$ ) may be selectively advantageous compared with cues that are uncorrelated with resources. The  $\Delta T$  cue may also be harder for seed predators to track (see below). These desirable features of the  $\Delta T$  model may explain why it is a common climate cue across widely divergent plant families.

#### *Mechanisms and future testing*

The T1 model implicitly requires plants to adapt temperature thresholds to local conditions. In principle, this would require plants to assimilate temperature data over an extended number of years and tune their responses accordingly (Kelly *et al.* 2008a). No plausible mechanism that would allow plants to implement this has been proposed. The  $\Delta T$  model requires a simpler mechanism that only uses temperature data from the previous 2 years.

The  $\Delta T$  model also generates two testable hypotheses for future investigation. First, it implies that masting requires a two-part physiological trigger in the plant. Plant flowering is controlled by an array

of hormones, including various gibberellins (GAs), whose synthesis and subsequent degradation are temperature sensitive (Pharis & King 1985). In the masting species *Chionochloa macra*, low doses of exogenous gibberellins during long days triggered floral induction (Martin *et al.* 1993). The gibberellin GA<sub>3</sub> is associated with induction of floral apices in *Chionochloa* spp, while GA<sub>4</sub> promotes subsequent development of induced floral buds that might otherwise remain dormant (Turnbull *et al.* 2012). Previous work is consistent with warm T<sub>n-1</sub> temperatures increasing flowering by elevating levels of florigenic GAs. However, the ΔT model shows that cool temperatures 2 years before (T<sub>n-2</sub>) also promote flowering, perhaps by priming plants in a cool year to be more responsive to a subsequent flowering signal. Flowering would thus be proportional to ΔT, due to the interaction between a cold-enhanced process 2 years before and a warmth-enhanced process 1 year before flowering. The specific time periods during which these events occur can help guide a search for the physiological mechanism.

Second, some specialist invertebrate seed predators, including a seed predator of *Chionochloa* (Kelly *et al.* 2000; Kolesik *et al.* 2007), have predictive extended diapause whereby the insects can wait several years to preferentially emerge in years of higher seed crops (Brockerhoff & Kenis 1997). Because the fitness of diapausing insects depends on accurately predicting high-seed crops, such insects should be selected to also use the ΔT climate signal to trigger emergence from diapause. However, there are limitations: insects cannot use ΔT in their first year, as they were not alive the previous year to experience T<sub>n-2</sub>, which may provide a selective advantage to the plant.

The ΔT model solves several puzzles about masting cues, generates additional testable hypotheses, and provides a simple predictive tool, based on readily available weather data, which will greatly increase our understanding of mast seeding and its manifold ecological consequences.

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## AUTHORSHIP

AG discovered the ΔT model and collated temperature data. DK, AG, AJ, EPH, MJP and AEB designed the analyses and wrote the paper. DK, AJ, EPH and AG ran the analyses. DK, REB, PEC, GAH, WGL, MJM, AFM, JAM and PRW provided long-term data sets. All authors discussed the results and commented on the manuscript.

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