# Climatic prediction of seedfall in *Nothofagus*, *Chionochloa* and *Dacrydium cupressinum*

Adrian Monks

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# Climatic prediction of seedfall in *Nothofagus*, *Chionochloa* and *Dacrydium cupressinum*

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## ABSTRACT

Mast seeding in *Nothofagus* (southern beech), *Chionochloa* (snow tussock) and *Dacrydium cupressinum* (rimu) is a significant conservation issue in New Zealand because of the irregular pulses of nutrients it brings to the animal populations within these systems. Climatic models were developed, which were intended to give timely and accurate predictions of seedfall in these plants, to forewarn conservation managers about changes in these systems. The models for *Nothofagus* and *Chionochloa* were based on multiple long-term datasets, primarily from the South Island, and climate records from nearby climate stations. The rimu models were based on a single dataset from Wanganui State Forest, Westland. The best *Nothofagus* and *Chionochloa* models correctly classified seedfall events as being either high or low 79% and 76% of the time respectively. High seedfall years were correctly classified with an accuracy of 80% for *Nothofagus* and 70% for *Chionochloa*. For rimu, it was not possible to satisfy the dual criteria of timely and accurate prediction: the model that gave the best fit to the data and provided good prediction when applied to a small dataset from Codfish Island (Whenuahou) would only enable predictions to be made 1–2 months before rimu fruits are falling from the trees. For all species, models performed better when previous seedfall was included as a predictor. Therefore, for the implementation of these models, it is essential that seedfall monitoring continues at sites where prediction is required. In recognition of the uncertainty in the model predictions, it is recommended that these models be implemented within a larger management framework that is flexible enough to allow rapid detection of failures in the model predictions followed by appropriate action.

Keywords: *Nothofagus*, *Chionochloa*, *Dacrydium cupressinum*, mast seedfall, irregular reproduction, linear mixed models, long-term monitoring, predictive models, time series

# 1. Introduction

Mast seeding can be defined as the 'synchronous, highly variable seed production among years by a population of plants' (Kelly 1994). This definition describes a population-level pattern of seed production. Colloquially, however, the term 'mast' is commonly used to describe particular years of high seedfall. While it is convenient to identify mast and non-mast years, these are not precise terms, because inter-annual variation in seed production is a continuous variable; consequently, the magnitude of seedfall that qualifies as a mast event remains arbitrary. Few plant species have a truly bimodal pattern of seedfall, where years can be clearly categorised as mast or non-mast years (Kelly 1994). However, among species that we identify as mast species, years with high seedfall are uncommon relative to years with low seedfall. For example, in *Nothofagus*, seedfall exceeds 1000 seeds/m² in only 26% of years, and is greater than 2000 seeds/m² in only 20% of years, with the median seedfall being only 74 seeds/m². Climate is the primary driver of reproductive output in mast species, playing a critical role in synchronising flowering within and between populations (Kelly 1994; Kelly & Sork 2002).

High seedfall events represent a massive pulse of nutrients into the ecosystem. Seeds are particularly high in nitrogen, digestible energy and trace elements (e.g. Murphy 1992). Animals can assimilate these nutrients relatively easily; thus, these pulses have important implications for animal population dynamics. In New Zealand, much of the conservation interest in masting is concerned with rodent population responses to high seedfall events. Mouse (*Mus musculus*) population increases are associated with high seedfall events in *Nothofagus*, both directly through feeding on the seeds (King 1983; Choquenot & Ruscoe 2000; Blackwell et al. 2003) and/or indirectly through feeding on the litter-dwelling invertebrate population, which increases following flowering (Alley et al. 2001). The evidence linking rat (*Rattus* spp.) population increases to masting in *Nothofagus* is more ambiguous (M.G. Efford, University of Otago, pers. comm.), although there is some evidence that rat populations also respond in some instances (Blackwell et al. 2003; Dilks et al. 2003). Current research is investigating whether rodents also respond to mast years in *Chionochloa* grasslands (Deb Wilson, Landcare Research, pers. comm.). Not only do high densities of rodents impact indigenous biota directly (reviewed by Innes 2001; Ruscoe 2001), but these seedfall-induced rodent eruptions will also result in increased densities of stoats (*Mustela erminea*). Conservation managers are particularly concerned about these stoat eruptions and the consequent impact they have on their indigenous secondary prey, such as birds (reviewed by King et al. 2001).

The breeding of some indigenous birds is also linked to high seedfall events. Since conservation management was initiated in the 1960s, kakapo have only bred during rimu-high-seedfall years (Elliott et al. 2001); thus, *in situ* monitoring of developing rimu fruit is currently used by the Department of Conservation (DOC) to predict breeding years for this species. Similarly,

breeding by kaka (*Nestor meridionalis*) (Wilson et al. 1998) and parakeets (*Cyanoramphus* spp.) (Elliott et al. 1996) is associated with high seedfall in *Nothofagus*.

Clearly, it is imperative that conservation managers be able to predict high seedfall events before they happen, so that the necessary actions can be taken ahead of time to facilitate intervention in these systems. The aim of this research was to produce climate-based predictive models of seedfall for *Nothofagus*, *Chionochloa* and *Dacrydium cupressinum* (rimu). In this report, these models are presented and evaluated.


# 2. Methods


## 2.1 SEED DATA

Fifty-two long-term seedfall datasets (Appendix 1) were collated: *Nothofagus* (25 datasets, ranging from 3 to 38 years), *Chionochloa* (23 datasets; 11–31 years, but 20 of these came from only two locations), and rimu (4 datasets; 7–33 years). All *Chionochloa* data and the majority of data for the other species were collected in the South Island, which may limit the models' predictive power at North Island sites.

*Nothofagus* and rimu seedfall was measured as the total number of seeds per square metre. It could be argued that viable seed is a better predictor of animal responses to a seedfall event, because this seed contains the nutritious endosperm. However, viable seed data were not always reliably collected, and the distinction between viable and non-viable seed is a minor one with respect to this analysis, because the amount of viable seed was strongly correlated with total seedfall (*Nothofagus*: $r = 0.89$, $n = 176$; rimu: $r = 0.94$, $n = 16$). All *Chionochloa* data were expressed as inflorescences per tussock (infl/t). Although the number of seeds per floret also varies between years, being highest during high-flowering years and very low during low-flowering years (Kelly & Sullivan 1997), individual seed data are not collected routinely during monitoring of flowering in *Chionochloa*. In all cases, the site mean, averaged over all the sampling units (seed traps for *Nothofagus* and rimu, and tussocks for *Chionochloa*), was used in the analyses. While this approach means that the within-year variability of the measurements from each site could not be modelled, this was balanced by the practical reality that individual sampling unit information was not always available. All seed and flowering data were log transformed prior to analysis.

## 2.2 CLIMATE DATA

Climate data were sourced primarily from the National Climate Database (National Institute of Water and Atmospheric Research, Wellington), with additional data being sourced from the Takahe Valley climate station, which is maintained by DOC, Te Anau. Each seed site was matched with the nearest climate station that had the appropriate records. In some instances, different sources were used for the rainfall and temperature data, when it was not possible to get both sets of data from the same site. In most cases there was a distance of several kilometres or more between the location of the seed measurements and the point of collection for the climate data. Under these circumstances, the actual values at the site of seed measurement are likely to have differed from the climate station values, due to differences in factors such as altitude, aspect and topography. To minimise this discrepancy, the climate data were standardised as deviations from the long-term mean, by subtracting the mean value of the variable for the climate station from each individual observation. In most cases, mean values were based on at least 40 observations.

Degree days were calculated for November through to April using a 6°C growing threshold (Thornley & Johnson 1990; Rees et al. 2002). Before calculation, the unstandardised temperature data were corrected for altitude at a rate of 0.6°C per 100 m difference in altitude between the climate station and the seedfall site. These values were also then expressed as deviations from the long-term degree-day means.

While climate stations with very incomplete records were not used in the analysis, some stations only had a few observations missing, and the data were otherwise complete enough not to justify using an alternative station. In these instances, the missing values were predicted from linear models relating these data to those from the next-nearest climate station.

## 2.3 ANALYSIS TECHNIQUES

All analyses were carried out in S, either using S-PLUS 2000 (Mathsoft Inc., Seattle, WA) or the open source code, R (http://cran.r-project.org).

### 2.3.1 *Nothofagus* and *Chionochloa*

The analysis of the *Nothofagus* and *Chionochloa* data followed the information theoretic paradigm advanced by Burnham & Anderson (2002). Briefly, this philosophy advocates a priori specification of a set of plausible models based on hypotheses about the generating model for the data. These models are then assessed relative to each other using data. The main tool to assess the models is the Akaike Information Criterion (AIC) and its variants. Inference is then made based on the relative weight of evidence for each of the models in the model set, taking into account the uncertainty associated with model selection. The method is inherently validatory by nature, because it relies on a set of models carefully specified on biological grounds. Prediction requires extrapolation, making the assumption that the model that has been fitted to

past data will still be correct in different places and at different times. This is more likely to be true if the model makes biological sense. Specifying models a priori also reduces the chance of overfitting: this occurs when the observed dataset is large enough that parameters can be fitted even though their effect is too small to be likely to extrapolate into predictions.

In all analyses, the small-sample Akaike Information Criterion ($AIC_c$) was used (Burnham & Anderson 2002). $AIC_c$ is a relative measure of Kullback-Leibler Information—the information lost when a fitted model is used to approximate the true generating model for the data (Burnham & Anderson 2002). Calculation of $AIC_c$ involves penalising the fit of the model (as measured by its log-likelihood) by a function of the number of parameters estimated for the model. Models with a smaller $AIC_c$ give a more parsimonious fit to the data. For a given set of models, the relative support for a particular model is given by its Akaike weight ($w_i$). Akaike weights assess the likelihood of model $i$ given the data, relative to the sum of these likelihoods for all the models in the model set. $w_i$ is interpreted as the weight of evidence in favour of model $i$ being the Kullback-Leibler best model, given that one of the models in the set is this model (Burnham & Anderson 2002).

### A priori model specification

The model fitting was constrained to series that were at least 10 years in length and to sites for which data were based on at least six independent seed trays. These restrictions were imposed to reduce variability due to small sample size and low sampling effort. A small subset of the data (two series for *Nothofagus*, both *N. solandri*, and three series for *Chionochloa*, all *C. pallens*) was used to fit preliminary mixed-effects models, which influenced the specification of the model set. For *Nothofagus*, the two series used to fit preliminary models were reused in the main analysis to maximise the precision of the parameter estimates because of the shortage of long data series for *Nothofagus* seedfall. The same analysis was run with these series omitted; this gave similar results and is not presented here. In *Chionochloa*, a small quantity of the data (three data series) was held out for validating the models; the remaining data were used to fit the a priori specified models.

The a priori models of *Nothofagus* seedfall were initially fitted using linear mixed-effects models with a random intercept term for each site (Pinheiro & Bates 2000). These models also allow autocorrelated residuals to be modelled, if necessary. Autocorrelation arises in time series data if the value of an observation is dependent on previous observations. This method proved unsuitable for modelling the *Chionochloa* data because of the extremely pulsed nature of the time series: *Chionochloa* often produced no, or very few, inflorescences within a population, but would occasionally produce large numbers of inflorescences during a high seedfall year. The *Chionochloa* data lent themselves to be transformed into a binary variable, with high seedfall years characterised as 'successes' and low seedfall years as 'failures'. The threshold for a high seedfall year was set at the 70th percentile for that species, assessed from all available data (Table 1). Selection of the 70th percentile was somewhat arbitrary, but conservatively approximated the point at which the plot of quantile score against quantile began to increase rapidly (Fig. 1). For *Chionochloa*, there was large interspecific variation in the
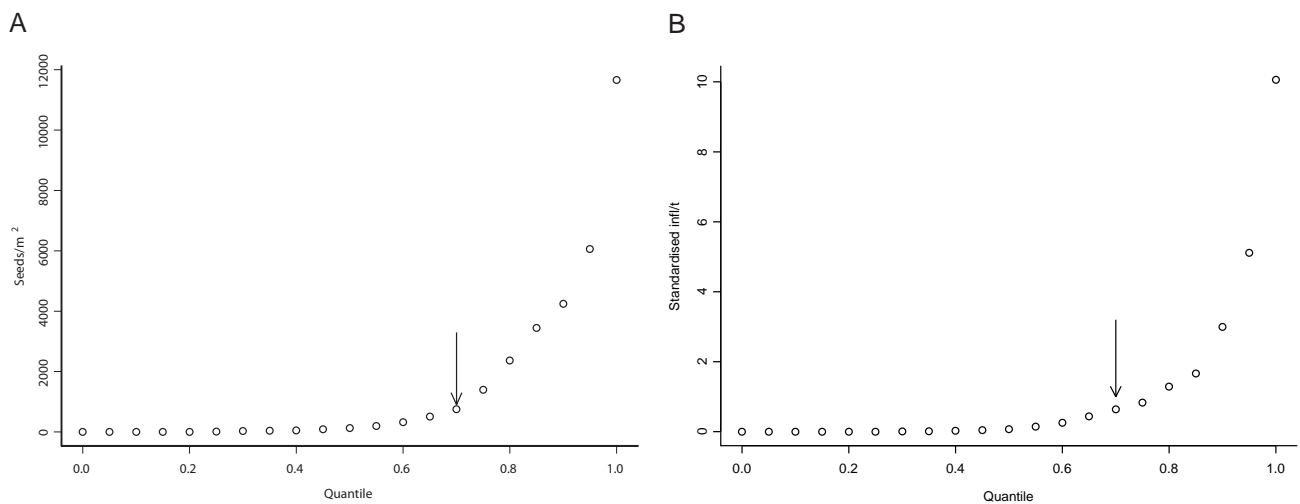
Figure 1.   Quantiles of *Nothofagus* (A) and *Chionochloa* (B) seedfall. The arrow indicates the 70th percentile.

TABLE 1.   TOTAL SEEDFALL/FLOWERING INTENSITIES CORRESPONDING TO THE 70th PERCENTILE FOR EACH *Nothofagus* AND *Chionochloa* SPECIES ANALYSED IN THIS STUDY.

These seedfall values were used as the threshold values for determining the binary high/low seedfall threshold variable used as the response in the logistic regression analyses. The number of observations that the calculation is based on is given in brackets.

| SPECIES | 70th PERCENTILE (seeds/m$^2$) | SPECIES | 70th PERCENTILE (infl/t) |
|---|---|---|---|
| *Nothofagus* | | *Chionochloa* | |
| N. fusca | 255.0 (20) | C. conspicua | 11.04 (17) |
| N. menziesii | 475.0 (65) | C. crassiuscula | 0.21 (46) |
| N. solandri | 1293.0 (146) | C. flavescens | 0.60 (20) |
| N. truncata | 149.9 (33) | C. macra | 5.55 (9) |
| | | C. oreophila | 0.92 (17) |
| | | C. pallens | 3.25 (76) |
| | | C. rigida | 2.29 (38) |
| | | C. rubra | 2.78 (46) |
| | | C. spiralis | 1.17 (9) |
| | | C. teretifolia | 1.54 (29) |

magnitude of seedfall events. Therefore, the seedfall values for each species were first standardised by their mean and then a weighted mean of quantiles across species was calculated. The 70th percentile across all species was then backtransformed to get the value for each individual species. The use of a threshold to represent a continuous response will always be somewhat arbitrary. However, given the precision of the predictions of the continuous models, and the intuitive requirements by managers to categorise years as either 'mast' or 'non-mast', this seems a reasonable approach. Logistic regressions are also very intuitive because the predictions are presented as the probability of a 'success' (i.e. a high seedfall year).

The logic of using a percentile threshold rather than an absolute threshold reflects the assumption that within each genus there are differences in the absolute magnitude of seeding between species, but that the standardised distribution of seeding events is the same between species. This assumption is supported by the high synchrony in the timing of high seedfall years both within species and between species of the same genus (Kelly et al. 2000; Schauber et al. 2002). Absolute threshold values probably depend on site fertility, plant size (*Chionochloa* particularly), and the differences between species in the mass of individual seeds (especially within *Nothofagus*).

Attempts to model these data using logistic mixed models failed because the software did not deliver credible results from the analysis. An alternative hierarchical method, in which each series was analysed independently and model averaging was then used to obtain the final model, was also not viable, because the data were too sparse: in some cases there was only one or two high seedfall years within a data series. Therefore, the data from each series were pooled and modelled using logistic regression, with the acknowledgement that there may be some small bias in the parameter estimates.

The logistic regression approach was also applied to the *Nothofagus* data as a second analysis, using the same model set as for the linear mixed-effects model approach. Again, the 70th percentile was used as the threshold seedfall value (Table 1).

All model parameters presented within this document follow the form of linear models:

$$g(Y_i) = \theta_0 + \sum_{j=1}^{p} \theta_j x_{ij} \tag{1}$$

where $\theta_0$ is the intercept, $\theta_j$ are the parameter values, and $x_{ij}$ are the observed predictors for predictor $j$ and observation $i$. $Y_i$ is the observation (0 or 1 for logistic models). The transformation $g$ varies according to the model.

An adequate fit of the global model (the model containing all the predictors found in the other models in the model set) is important for making valid inference from the analysis. A number of methods were used to assess goodness of fit. For the linear mixed-effects models, goodness of fit was assessed graphically (Pinheiro & Bates 2000). For the logistic regressions, the Hosmer-Lemeshow $\chi^2$ statistic (Dobson 2002) was used to assess goodness of fit, with five groups and three degrees of freedom. This test determines whether the frequencies of 'successes' and 'failures' within each group in the fitted model are significantly different from the frequencies observed in the data.

## Model averaging

Model averaging calculates a weighted average of the parameter values from the models in the model set to produce an averaged model. This technique takes into account model selection uncertainty in determining both the values of and the confidence limits on the parameters (Burnham & Anderson 2002).

The AIC weights ($w_i$) were used to calculate weighted averages of the parameters $\hat{\bar{\theta}}$ according to:

$$\hat{\bar{\theta}} = \sum_{i=1}^{R} w_i \hat{\theta}_i \qquad (2)$$

where $\hat{\theta}_i$ is the estimated value of parameter $\theta$ in model $i$, $w_i$ is the AIC weight for model $i$, and $R$ is the total number of models in the model set (Burnham & Anderson 2002). $\hat{\theta}_i$ was assumed to be zero for models in which a particular parameter was not included. The 95% confidence intervals were calculated according to:

$$\hat{\bar{\theta}}_i \pm z_{1-\alpha/2} SE(\hat{\bar{\theta}}_i) \qquad (3)$$

where

$$SE(\hat{\bar{\theta}}_i) = \sum_{i=1}^{R} w_i \sqrt{\mathrm{var}(\hat{\theta}_i \mid g_i) + \left(\hat{\theta}_i - \hat{\bar{\theta}}\right)^2} \qquad (4)$$

with $\mathrm{var}(\hat{\theta}_i \mid g_i)$ equal to the variance of the parameter estimate given the model (Burnham & Anderson 2002).

### 2.3.2   Rimu

The rimu analysis was based on only one dataset (Wanganui State Forest, $n = 33$; Norton & Kelly 1988) because the remaining datasets were either short in duration or, in the case of the Ianthe series, had been used to estimate a missing data point in the Wanganui series (Norton & Kelly 1988). This dataset was also used for the only published analysis of the relationship between climate and seedfall in rimu; therefore, there are no independent sources of information to a priori specify models of seedfall for rimu. The Wanganui State Forest seedfall data were log transformed and analysed using generalised least squares models, which allow autocorrelation within the residuals to be modelled (Pinheiro & Bates 2000).

### 2.3.3   Model validation

The purpose of model validation is to try to determine how well the model will predict new observations. The information theoretic approach is inherently validatory by nature, because the models are specified a priori and effectively tested on the data. However, two other techniques were also used to validate the model fits. The first is K-fold cross-validation, where the data used to fit the models are themselves used to validate the models. In this procedure, the data are divided randomly into $K$ nearly equal groups. For each $j$th group, the model is fitted to all groups $k \neq j$, and the parameter values are then used to predict the responses for the $j$th group (Davison & Hinkley 1997). The prediction error is then computed and averaged over all $K$ parts. For *Nothofagus* and *Chionochloa*, $K = 10$ was used. For rimu, leave-one-out cross-validation was used. This is a special case of K-fold cross-validation, in which $K$ equals the number of observations. Given the small sample size in the rimu analysis, it was felt that removing only one observation at a time would perturb the data sufficiently to cross-validate the model, while still allowing reasonable precision in each model fit.

Small amounts of additional data that were not used during the fitting process were also available to test the predictions of the models. One caveat about these data is that for *Nothofagus* in particular, they also included many

series that were excluded from the main analysis because of concerns over the small sampling effort. Therefore, we might expect a priori that these data would be more variable than the data used to fit the models. The rimu models were tested specifically on the seedfall data from Codfish Island (Whenuahou), where rimu seedfall is monitored for kakapo management.

## 2.4 PHENOLOGY, SELECTION OF ENVIRONMENTAL PREDICTORS AND A PRIORI MODEL SPECIFICATION

The selection of the initial set of predictors is an important part of the modelling process. The approach in this study has been to identify key developmental processes from the initiation of reproduction through to seedfall, and then to examine the climatic variables likely to influence each developmental process. Existing literature was used to guide the selection of potential predictors. Variable selection was constrained by the type of climate data collected at the stations used for the analysis. Monthly rainfall and daily temperature were the only data available at all of the sites.

The set of potential predictors was further constrained to exclude any predictors that would need to be measured during the season of seedfall. Climatic data are usually not available until at least 2–3 months after they are recorded; this prevents the inclusion of predictors that affect pollination or fruit maturation, because the predictions from such models would not be timely enough. This may be costly in terms of the model fit and our ability to interpret the relative importance of the predictors in an ecological context. However, alternative analyses that included these variables suggested that this cost is likely to be small (unpubl. data), except in the case of the rimu analysis (see section 3.3).

For *Nothofagus* and *Chionochloa*, analysis of a small subset of the data using mixed-effects models (following the procedure of Verbeke & Molenberghs 2000) allowed further refinement of the set of predictors. This, along with results from existing literature, led to the formation of a set of a priori models for the analysis of these datasets.

### 2.4.1 *Nothofagus*

Floral initials begin to form during the summer/autumn in the year prior to the seedfall event (Wardle 1984; Poole 1987). Flowering and fertilisation generally take place from late September through to early January (Wardle 1984). *Nothofagus* is wind pollinated. Ripe nuts fall from late January to early spring, although peak seedfall usually occurs from March to May (Wardle 1984; Alley et al. 1998).

The climate variables initially considered as predictors in the *Nothofagus* models and the timing of the developmental phases are shown in Fig. 2. A number of early writers observed that high seedfall years were preceded by years with dry warm summers (e.g. Poole 1955; Franklin 1977; Wardle 1984). The importance of temperature during the preceding summer is supported by analyses of the *Nothofagus solandri* series from Craigieburn and

Figure 2. *Nothofagus* reproductive phenology in relation to growing season, lag with respect to the year of seedfall, and the environmental factors likely to influence each phenological stage.
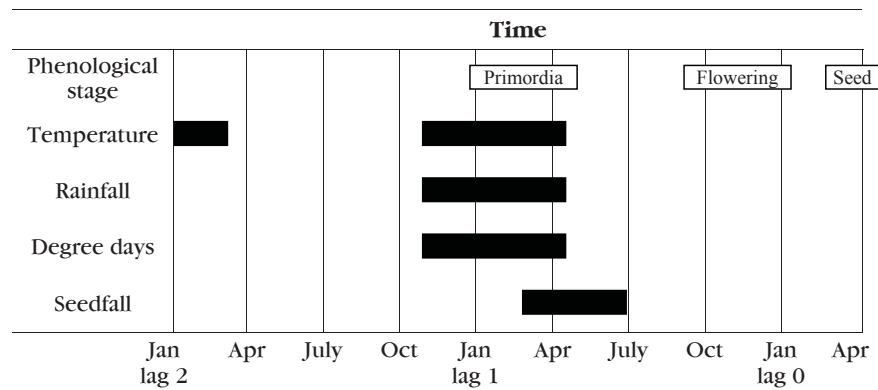


Mt Thomas in Canterbury (Allen & Platt 1990; Richardson et al. 2005); note that this period coincides with the development of the flower primordia. These analyses also suggest a limiting influence of high seedfall during previous years, perhaps as a consequence of resource depletion. Degree-days from November to April in the previous growing season were included as an overall measure of growing conditions during the season of primordial development. Maximum mean monthly summer temperature from 2 years preceding the seed year was also included because it is a substantial climatic correlate of lag1 seedfall, and may have either served as a climatic surrogate for previous seedfall and/or provided additional information in its own right (Richardson et al. 2005). Rainfall was excluded on the basis that the analysis of two of the data series showed that at best rainfall only played a very minor role in predicting seedfall. These preliminary analyses also indicated that the previous seedfall and summer temperature lag2 probably had non-linear effects that could be adequately modelled using degree 2 polynomials.

The model set was formulated with three broad hypotheses in mind. These were:

1. Seedfall in *Nothofagus* is synchronised between individuals by warm temperatures in the summer prior to seedfall.

2. Seedfall intensity is positively related to warm growing conditions in the growing season prior to the season of seedfall.

3. Seedfall in the current year is negatively related to seedfall in the previous year.

The models represent combinations of these hypotheses. All candidate models in the initial model set contained an intercept term; for the mixed-effects models, the intercept was modelled as a random effect nested within sites. Warm temperatures in the summer prior to seedfall were represented as January mean daily temperature ('Jan.dmean') or the maximum mean daily temperature recorded during the January–March period ('Jan.Mar.dmax'). The effects of previous years included log-transformed seedfall lag1 ('log. Seedfall.lag1') and the maximum mean daily temperature lag2 recorded between January and March, both modelled as polynomial terms. Growing conditions during the previous growing season were modelled using degree-days calculated from November through to April ('Nov.Apr.degreedays'). The predictors included in each model are shown in Table 2.

TABLE 2. PREDICTORS INCLUDED IN EACH OF THE MODELS OF SEEDFALL FOR *Nothofagus*. ALL MODELS CONTAIN AN INTERCEPT TERM. ● INDICATES INCLUSION OF THE PREDICTOR IN THE MODEL.

| MODEL | Jan.Mar. dmax.lag1 | Jan.dmean. lag1 | Poly(Jan.Mar. dmax.lag2, 2) | Poly(Seedfall. lag1, 2) | Nov.Apr. degreedays.lag1 |
|---|---|---|---|---|---|
| 1 | - | ● | - | - | - |
| 2 | ● | - | - | - | - |
| 3 | - | ● | ● | - | - |
| 4 | ● | - | ● | - | - |
| 5 | - | ● | - | ● | - |
| 6 | ● | - | - | ● | - |
| 7 | - | ● | ● | ● | - |
| 8 | ● | - | ● | ● | - |
| 9 | - | ● | - | - | ● |
| 10 | ● | - | - | - | ● |
| 11 | - | ● | ● | - | ● |
| 12 | ● | - | ● | - | ● |
| 13 | - | ● | - | ● | ● |
| 14 | ● | - | - | ● | ● |
| 15 | - | ● | ● | ● | ● |
| 16 | ● | - | ● | ● | ● |
| 17 | ● | ● | ● | ● | ● |

## 2.4.2 *Chionochloa*

The genus *Chionochloa* includes 24 species, 22 of which are endemic to New Zealand (Edgar & Connor 2000). The long-lived vegetative tillers of *Chionochloa* optionally produce a single inflorescence from late November through to early February (Rees et al. 2002). Flowering intensity the following year is correlated with warm summer temperatures during floral initiation (Mark 1968; McKone et al. 1998; Kelly et al. 2000; Rees et al. 2002). Seeds are dispersed during late summer–early autumn.

The initial set of predictors and their relationship with the timing of the phases of reproductive development was almost identical to that for *Nothofagus* (Fig. 3). The timing of initiation, flowering and seedfall are similar, and both genera are wind pollinated. Hence, the critical periods in which climate might affect reproductive output are also very similar. These predictors were refined through an analysis of three *C. pallens* datasets and previous analyses in the literature that detailed the primary climatic drivers of flowering in *Chionochloa*. The hypotheses directing the formulation of the models were identical to those for *Nothofagus* with the addition of:

4. Summer rainfall in the preceding year is positively associated with seedfall.

Summer temperatures were represented as the mean daily temperature during January and February ('Jan.Feb.dmean') and were modelled as degree 2 polynomials, as was lag1 November to April degree-days ('Nov. Apr.degreedays'). Summer rainfall was the total rainfall during January and February ('Jan.Feb.rain'). Previous seedfall was included as a binary variable ('High.seed'): 1 when seedfall exceeded the 70th quantile for a species, and zero otherwise. The a priori models are given in Table 3.

Figure 3. *Chionochloa*
reproductive phenology
in relation to growing
season, lag with respect
to the year of seedfall, and
the environmental factors
likely to influence each
phenological stage.



**Time**
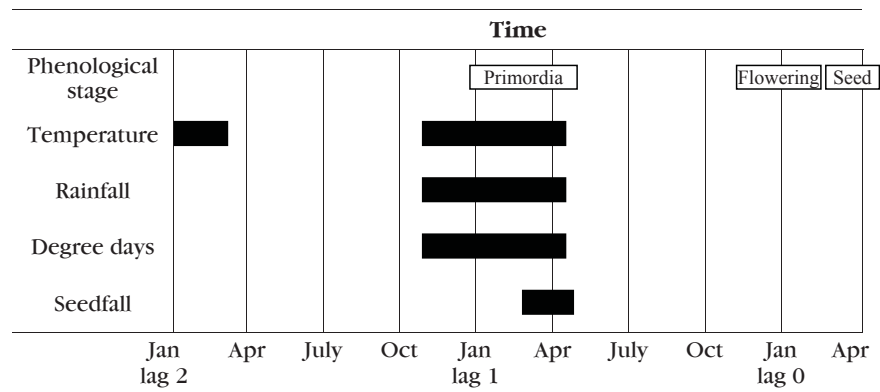
TABLE 3. PREDICTORS INCLUDED IN EACH OF THE MODELS OF SEEDFALL FOR *Chionochloa*. ALL MODELS INCLUDED AN INTERCEPT TERM. ● INDICATES INCLUSION OF THE PREDICTOR IN THE MODEL.

| MODEL | Poly(Jan.Feb. dmean. lag1, 2) | Poly(Nov.Apr. degreedays. lag1, 2) | Jan.Feb.rain. lag1 | Poly(Jan.Feb. dmean. lag2, 2) | High.seed. lag1 |
|---|---|---|---|---|---|
| 1 | ● | – | – | – | – |
| 2 | – | ● | – | – | – |
| 3 | ● | – | ● | – | – |
| 4 | – | ● | ● | – | – |
| 5 | ● | – | – | ● | – |
| 6 | – | ● | – | ● | – |
| 7 | ● | – | ● | ● | – |
| 8 | – | ● | ● | ● | – |
| 9 | ● | – | – | – | ● |
| 10 | – | ● | – | – | ● |
| 11 | ● | – | ● | – | ● |
| 12 | – | ● | ● | – | ● |
| 13 | ● | – | – | ● | ● |
| 14 | – | ● | – | ● | ● |
| 15 | ● | – | ● | ● | ● |
| 16 | – | ● | ● | ● | ● |
| 17 | ● | ● | ● | ● | ● |

## 2.4.3 Rimu

The phenology of fruit production in rimu is outlined in Norton & Kelly (1988) and Norton et al. (1988) (see Fig. 4). The production of seed from initiation to seedfall occurs over three growing seasons. It is thought that ovule and cone initiation occurs some time during the summer or autumn of growing season 1. Pollination follows in (November) December and January of growing season 2. Although uncertain, fertilisation of the ovules may occur 12 months later, during growing season 3. Ripe seed falls a short time later in the autumn.

Figure 4.   Rimu (*Dacrydium cupressinum*) reproductive phenology in relation to growing season, lag with respect to the year of seedfall, and the environmental factors likely to influence each phenological stage.
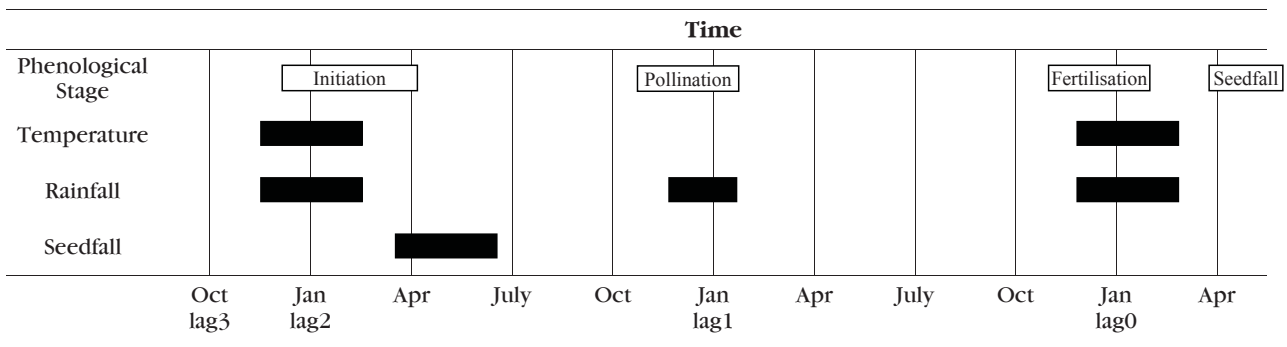
Temperature accompanied by long day length is the most common factor initiating flowering in mast species around the world (Kelly & Sork 2002). In addition, initiation of cone production in conifers can be increased by drought, because dry years result in elevated levels of gibberellins, the hormones responsible for cone initiation (Pharis & King 1985). Mean daily temperature and total rainfall from December to February during the period of initiation were included in the variable set. There is evidence from a number of studies that high seed production during the year of initiation can also limit the reproductive output (reviewed by Kelly & Sork 2002). Consequently, lag2 seedfall was also included in the variable set.

Pollination failure in rimu is probably caused by wet weather (McEwen 1983, cited in Norton et al. 1988). The total number of days on which it rains during the pollination period (December lag2–January lag1) is likely to be more important than the absolute amount of rain that has fallen. The number of wet days was used for December, but unfortunately the record for wet days (rain > 1 mm) was not complete for January, so total rainfall was used instead.

To complete the set of possible predictors, monthly mean temperature and monthly total rainfall during the summer of fertilisation/fruit maturation were also included. This gave 15 possible predictors in the initial set: seedfall.lag2, monthly mean temperature and total rainfall for Dec.lag3 to Feb.lag2 and Dec.lag1 to Feb.lag0, number of wet days for Dec.lag3, and total rainfall for Jan.lag1. As mentioned previously, it was not appropriate to propose a priori models for the analysis of rimu seedfall, because all previous information on the relationship between climate and rimu seedfall was derived from an analysis of the Wanganui State Forest dataset by Norton & Kelly (1988). Therefore, the final models were obtained by post-hoc stepwise model fitting procedures.

# 3. Results

## 3.1 *Nothofagus*

The global mixed-effects model gave an adequate fit to the data, with a coefficient of determination of 0.64 estimated at the site level. There was also no significant residual autocorrelation, indicating that the model terms were sufficient to account for this structure in the data. The global model was a priori rejected from the model set because there was some parameter redundancy: Jan.Mar.dmax.lag1 and Jan.dmean.lag1 were highly correlated, because the maximum temperature often occurred in January.

Models 8 and 16 were clearly superior to all others (high $w_i$), although neither received unilateral support (Table 4). The fit of Model 16 as estimated by the log-likelihood was similar to Model 8. Since Models 16 and 8 differ by only one parameter, this suggests that the shared parameters are important but the additional parameter in Model 16 is not. Consequently, Model 16 can be discarded as a serious contender for the Kullback-Leibler best model. The cross-validated coefficient of determination for Model 8 was 61.5%; this dropped to only 42.5% when predictions were based on fixed effects only (i.e. at the population level, excluding the random effects of site). Model 8 contained all the predictors in the model set except for the lagged degree-day term. It is interesting to note that models without the lagged seedfall terms generally performed poorly, with six of the eight bottom-ranked models not containing these terms.

Model 8 was biased towards classifying seedfall events as less than the 70th percentile for each species, i.e. there was a tendency to under-predict high

TABLE 4. SUPPORT FOR THE A PRIORI SET OF LINEAR DIFFERENCE MODELS FOR *Nothofagus*. MODEL NUMBER REFERS TO THE MODELS OUTLINED IN TABLE 2.

| MODEL | df | LOG-LIKELIHOOD | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|
| 8 | 8 | –540.1 | 1096.7 | 0.00 | $6.39 \times 10^{-1}$ |
| 16 | 9 | –539.6 | 1097.8 | 1.14 | $3.61 \times 10^{-1}$ |
| 4 | 6 | –553.3 | 1118.9 | 22.22 | $9.55 \times 10^{-6}$ |
| 12 | 7 | –553.1 | 1120.6 | 23.96 | $4.02 \times 10^{-6}$ |
| 6 | 6 | –554.5 | 1121.4 | 24.72 | $2.74 \times 10^{-6}$ |
| 14 | 7 | –554.5 | 1123.4 | 26.73 | $1.00 \times 10^{-6}$ |
| 15 | 9 | –553.7 | 1126.1 | 29.43 | $2.59 \times 10^{-7}$ |
| 7 | 8 | –558.4 | 1133.4 | 36.72 | $6.78 \times 10^{-9}$ |
| 11 | 7 | –564.3 | 1142.9 | 46.27 | $5.73 \times 10^{-11}$ |
| 3 | 6 | –567.3 | 1147.0 | 50.29 | $7.68 \times 10^{-12}$ |
| 13 | 7 | –571.7 | 1157.9 | 61.18 | $3.31 \times 10^{-14}$ |
| 5 | 6 | –574.9 | 1162.1 | 65.45 | $3.92 \times 10^{-15}$ |
| 2 | 4 | –583.3 | 1174.8 | 78.13 | $6.92 \times 10^{-18}$ |
| 10 | 5 | –583.3 | 1176.8 | 80.11 | $2.57 \times 10^{-18}$ |
| 9 | 5 | –595.5 | 1201.2 | 104.52 | $1.28 \times 10^{-23}$ |
| 1 | 4 | –596.7 | 1201.6 | 104.95 | $1.04 \times 10^{-23}$ |

seedfall events relative to low seedfall events (cross-validated percentage of correct classifications: low = 90.2%, $n = 170$; high = 45.0%, $n = 94$; total correct = 76.5%, $n = 264$). These predictions were, nonetheless, significantly better than the random expectation of correct prediction (low = 70%, high = 30%, total correct = 58%; $\chi^2 = 44.3$, df = 3, $P < 0.001$).

Model averaging was applied to the model set in an attempt to find a model that gave more robust predictions of seedfall. The cross-validated coefficient of determination for the averaged model was 42.2%. The average model was marginally more successful than Model 8 at correctly classifying seedfall events as larger or smaller than the 70th percentile (cross-validated percentage of correct classifications: low = 86.4%, $n = 184$; high = 56.4%, $n = 80$; total correct predictions = 77.3%, $n = 264$). However, there was still a bias towards under-classifying high seedfall years.

The ability of the averaged model to correctly classify low and high seedfall events appears to be very sensitive to the value selected as the threshold for defining a high seedfall year (Fig. 5). This bias probably reflects a combination of two things. First, the distribution of seedfall is leptokurtic: there are many low observations and then a long tail containing the few high observations. Since the threshold is defined to lie within the long tail, variability in the predictions of the bulk of the low observations has no effect on whether the prediction is classified as a high or low year. However, this is not the case for the high seedfall years. Consequently, the model is inevitably biased toward correctly classifying low seedfall events and being sensitive to error in the predictions of high seedfall events. This can be seen in Fig. 5, where correct classification of events above the threshold becomes comparable with those below as the threshold approaches the median (74 seeds/m$^2$). Second, high seedfall events are more often associated as positive residuals than low seedfall events; consequently, the model tends to under-predict high seedfall events and over-predict low seedfall events. It should be emphasised

Figure 5. Sensitivity of the average *Nothofagus* linear mixed-effects model to the choice of threshold value in terms of its ability to correctly classify seedfall events as above or below the threshold. Points for each threshold are based on 500 bootstrapped samples from a dataset of 240 observations.
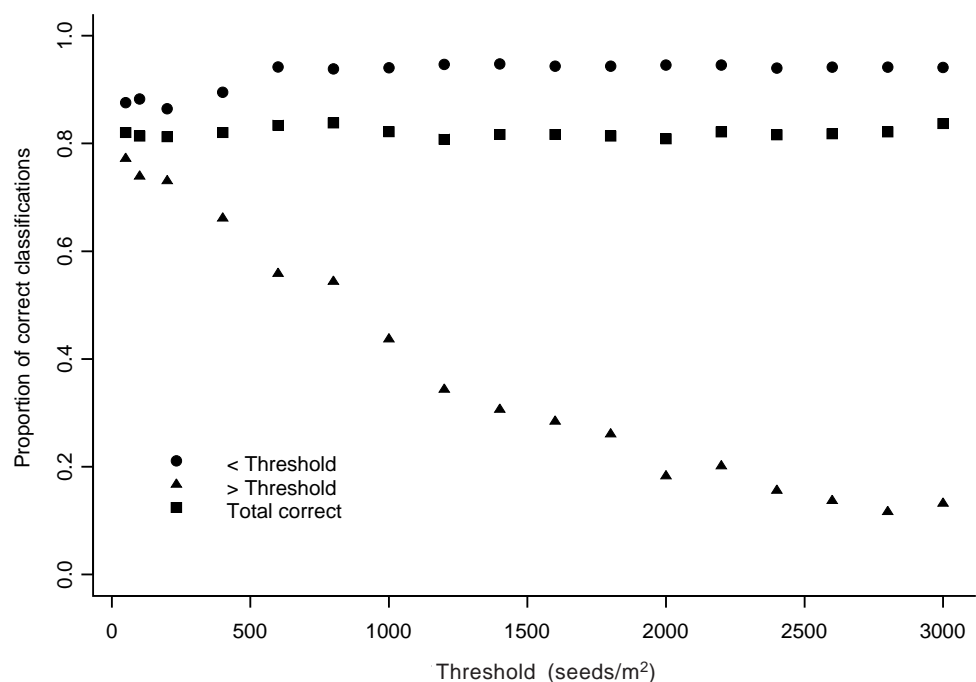
that there is currently no clear understanding of what constitutes a useful seed intensity threshold in *Nothofagus* at which action to manage pests is required. However, we should be mindful of the fact that although lower thresholds result in more reliable predictions, they are also less biologically meaningful and hence less useful as a decision point for management, because low seedfall years add few additional nutrients into the system.

In the averaged model, the large coefficient for maximum mean monthly temperature from January to March in the year prior to seedfall (Jan.Mar.dmax.lag1) suggests that seedfall is very sensitive to changes in this predictor (Table 5). This supports the expectation that summer temperature during primordial initiation is a key determinant of future seedfall. Seedfall in the year prior to the seedfall event has a large negative non-linear effect on seedfall. The rate at which previous seedfall inhibits seedfall accelerates as the amount of seedfall increases (Fig. 6). The opposite pattern is observed for the maximum mean daily temperature from January to March 2 years prior to the seedfall event (Jan.Mar.dmax.lag2): the rate of change in seedfall with respect to Jan.Mar.dmax.lag2 is highest when Jan.Mar.dmax.lag2 increases from low levels (Fig. 6). The pathway by which Jan.Mar.dmax.lag2 inhibits seedfall is not clear, but the fact that it is negatively related to lag1 seedfall may mean that it is confounded with the resource dynamics surrounding previous seedfall rather than having a direct effect on seedfall itself. However, Piovesan & Adams (2001) argue that *Fagus* trees are primed for floral induction by cool moist summers 2 years prior to seedfall because of an increased build-up of carbohydrates under these conditions. The contribution to the model of November to April degree-days and January daily mean temperature, both at lag1, was small, with both confidence intervals including zero.

TABLE 5.   COEFFICIENTS AND 95% CONFIDENCE INTERVALS FOR THE PARAMETERS INCLUDED IN THE K-L BEST MODEL AND FOLLOWING MODEL AVERAGING FOR THE LINEAR MIXED MODELS APPLIED TO *Nothofagus* SEEDFALL.

| PREDICTOR | MEAN | LOWER 95%CI | UPPER 95%CI |
|---|---|---|---|
| **K-L best model (Model 8)** | | | |
| (Intercept) | 4.434 | 3.360 | 5.508 |
| Jan.Mar.dmax.lag1 | 1.484 | 1.282 | 1.686 |
| Jan.Mar.dmax.lag2 | −0.677 | −0.924 | −0.431 |
| Jan.Mar.dmax.lag2$^2$ | 0.160 | 0.029 | 0.292 |
| log.Seedfall.lag1 | 0.445 | 0.164 | 0.725 |
| log.Seedfall.lag1$^2$ | −0.067 | −0.096 | −0.037 |
| **Average model** | | | |
| Intercept | 4.422 | 3.340 | 5.505 |
| Jan.dmean.lag1 | 0.848 | −0.814 | 2.510 |
| Jan.Mar.dmax.lag1 | 1.442 | 1.180 | 1.705 |
| Nov.Apr.degreedays.lag1 | 0.001 | −0.001 | 0.004 |
| Jan.Mar.dmax.lag2 | −0.681 | −0.930 | −0.433 |
| Jan.Mar.dmax.lag2$^2$ | 0.164 | 0.155 | 0.173 |
| Log(Seedfall.lag1+1) | 0.449 | 0.166 | 0.732 |
| Log(Seedfall.lag1+1)$^2$ | −0.067 | −0.068 | −0.066 |

Figure 6. The functional form of the fitted relationship between *Nothofagus* seedfall and seedfall during the previous season (Seedfall.lag1) and the maximum mean daily temperature from January to March 2 years previously (Jan.Mar.dmax.lag2). Seedfall has been scaled to be a proportion of its maximum value. Seedfall.lag1 has also been rescaled and then expressed as deviations from its mean value.
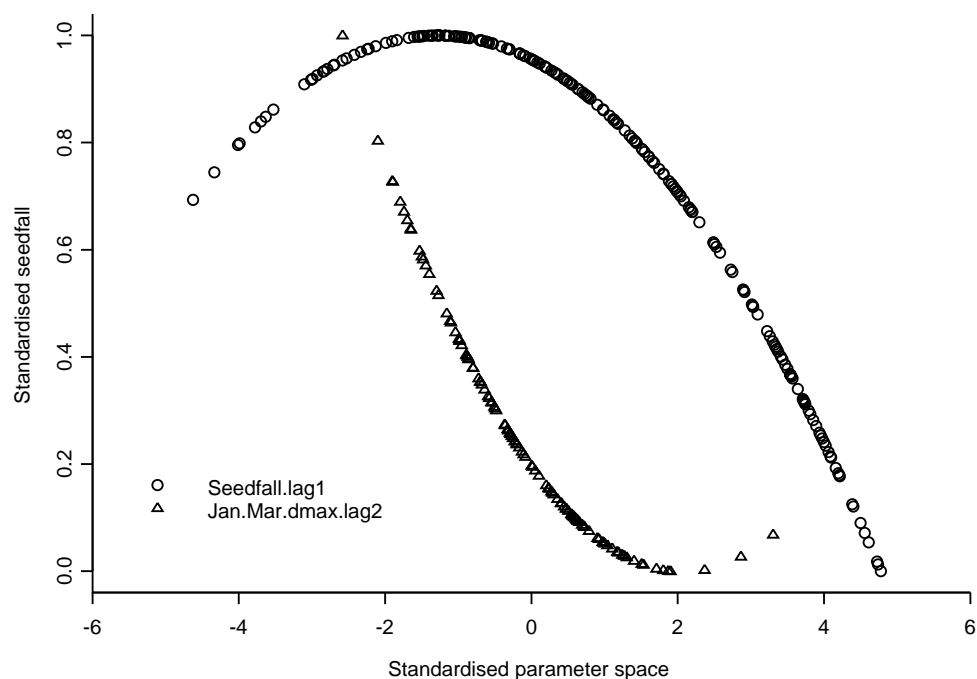
## Logistic model

To address the poor ability of the linear mixed-effects models to correctly classify seedfall events as being high or low, a series of logistic regression models were fitted using the same predictors and model set but with the response transformed into a binary variable according to whether seedfall exceeded the 70th percentile on a species-specific basis. Logistic models have the advantage that the predicted response variable is a probability of a 'success': in this case defined as a seedfall event greater than the threshold. To convert predictions from the logit scale to probabilities of success ($p$): $p = 1/(1 + \exp(-\text{Prediction}))$.

The global model (Model 17) fitted the data well ($\chi^2 = 0.90$, df $= 3$, $P > 0.1$) but, as with the previous analysis, this model was excluded from the final model set due to redundancy in the parameters.

Model 15 had very strong support, followed by Model 16 (Table 6). These two models differed in the summer initiating variable (Jan.dmean.lag1 and Jan.Mar.dmax.lag1 respectively). Models were said to predict a high seedfall year if the probability of 'success' was greater than 0.5. Model 15 gave good predictions of the probability of a high seedfall year (cross-validated percentage of correct classification: high $= 73.8\%$; low $= 84.8\%$; total $= 81.4\%$; cf. random, $\chi^2 = 92.7$, df $= 3$, $P < 0.001$), although there was a slight bias toward classifying events as low seedfall years.

Applying model averaging, the average model performed well, with the cross-validated fits correctly classifying seedfall events 79.1% of the time. Prediction error was more balanced between high and low seedfall years (high $= 80.0\%$, $n = 80$; low $= 78.8\%$, $n = 184$; cf. random, $\chi^2 = 103.0$, df $= 3$, $P < 0.001$) than with Model 15. Parameter values for Model 15 and the average model are given in Table 7. While the average model had a slightly, but non-significantly, higher total error rate ($\chi^2 = 0.90$, df $= 1$, $P > 0.1$), the errors were more balanced between high and low seedfall years; for this reason it should be the preferred model.

TABLE 6.  SUPPORT FOR THE A PRIORI SET OF LOGISTIC REGRESSION MODELS FOR *Nothofagus*. MODEL NUMBER REFERS TO THE MODELS OUTLINED IN TABLE 2.

| MODEL | df | DEVIANCE | AICc | ΔAICc | $w_i$ |
|-------|----|----------|------|-------|-------|
| 15 | 7 | 193.9 | 208.3 | 0.00 | $8.47 \times 10^{-1}$ |
| 16 | 7 | 197.4 | 211.9 | 3.54 | $1.44 \times 10^{-1}$ |
| 8 | 6 | 206.3 | 218.7 | 10.35 | $4.78 \times 10^{-3}$ |
| 7 | 6 | 207.6 | 220.0 | 11.64 | $2.51 \times 10^{-3}$ |
| 11 | 5 | 212.0 | 222.3 | 13.96 | $7.89 \times 10^{-4}$ |
| 12 | 5 | 212.7 | 222.9 | 14.58 | $5.79 \times 10^{-4}$ |
| 4 | 4 | 219.1 | 227.3 | 18.98 | $6.41 \times 10^{-5}$ |
| 3 | 4 | 222.5 | 230.7 | 22.38 | $1.17 \times 10^{-5}$ |
| 14 | 5 | 242.0 | 252.2 | 43.87 | $2.53 \times 10^{-10}$ |
| 6 | 4 | 244.6 | 252.8 | 44.43 | $1.90 \times 10^{-10}$ |
| 13 | 5 | 246.8 | 257.0 | 48.73 | $2.22 \times 10^{-11}$ |
| 5 | 4 | 253.3 | 261.5 | 53.18 | $2.40 \times 10^{-12}$ |
| 2 | 2 | 271.0 | 275.0 | 66.72 | $2.75 \times 10^{-15}$ |
| 10 | 3 | 269.4 | 275.5 | 67.14 | $2.23 \times 10^{-15}$ |
| 9 | 3 | 272.6 | 278.7 | 70.40 | $4.37 \times 10^{-16}$ |
| 1 | 2 | 276.5 | 280.6 | 72.23 | $1.75 \times 10^{-16}$ |

TABLE 7.  COEFFICIENTS AND 95% CONFIDENCE INTERVALS FOR THE PARAMETERS INCLUDED IN THE K-L BEST MODEL AND FOLLOWING MODEL AVERAGING FOR LOGISTIC REGRESSION MODELS APPLIED TO THE *Nothofagus* DATA. THE PARAMETERS RELATE TO THE RESPONSE ON THE LOGIT SCALE.

| PREDICTOR | PARAMETER ESTIMATE | LOWER 95% CI | UPPER 95% CI |
|-----------|--------------------|--------------|--------------|
| **K-L best model (Model 15)** | | | |
| (Intercept) | -2.263 | -3.282 | -1.244 |
| Jan.Mar.dmax.lag1 | 1.286 | 0.902 | 1.670 |
| Jan.Mar.dmax.lag2 | -1.039 | -1.432 | -0.647 |
| Jan.Mar.dmax.lag2$^2$ | 0.297 | 0.097 | 0.498 |
| log.Seedfall.lag1 | 0.772 | 0.350 | 1.193 |
| log.Seedfall.lag1$^2$ | -0.086 | -0.131 | -0.041 |
| **Average model** | | | |
| (Intercept) | -3.181 | -4.382 | -1.981 |
| Jan.dmean.lag1 | 0.796 | 0.213 | 1.379 |
| Jan.Mar.dmax.lag1 | 0.951 | -0.719 | 2.621 |
| Nov.Apr.degreedays.lag1 | 0.008 | 0.003 | 0.013 |
| Jan.Mar.dmax.lag2 | -1.295 | -1.747 | -0.843 |
| Jan.Mar.dmax.lag2$^2$ | 0.394 | 0.379 | 0.409 |
| Log.Seedfall.lag1 | 0.934 | 0.447 | 1.421 |
| Log.Seedfall.lag1$^2$ | -0.103 | -0.108 | -0.098 |

## 3.2 Chionochloa

Attempts to model *Chionochloa* flowering intensity directly resulted in poorly fitting models. The variability of *Chionochloa* flowering is much more extreme than flowering of either *Nothofagus* or rimu. *Chionochloa* species fill three of the top five places in a list of the most extreme (i.e. variable) mast seeders in the world (based on coefficients of variation; Kelly et al. 2000), having many low seedfall years punctuated by occasional extreme seedfall years. Consequently, it was decided that the only reasonable approach to modelling seedfall in *Chionochloa* that would generalise across sites and species was to convert the seedfall data to a binary variable, with species-specific thresholds set at the 70th percentile level using the values outlined in Table 1.

The global model gave an adequate fit to the data ($\chi^2 = 5.53$, df = 3, $P > 0.1$). There was little to discriminate between the top two models in terms of their fit to the data (Table 8). These two models differed by one parameter, Jan.Feb.rain.lag1, which gave only a modest decrease in deviance in Model 15 at the cost of one extra parameter. Model 13 (the K-L best model) accounted for only 36.2% of the variation in the data. This model correctly classified high and low seedfall years 72.6% of the time ($n = 307$; cf. random $\chi^2 = 32.3$, df = 3, $P < 0.001$). While prediction of low seedfall years was very good (86.0% correct, $n = 214$), classification of high seedfall years was relatively poor (41.9% correct, $n = 93$).

The average model also performed well, correctly classifying high and low seed years 76.2% of the time ($n = 307$; cf. random $\chi^2 = 79.3$, df = 3, $P < 0.001$). The model predictions were more balanced than with Model 13, predicting low seedfall years (79.0%, $n = 214$) only slightly more than high seedfall years

TABLE 8. SUPPORT FOR THE A PRIORI SET OF LOGISTIC REGRESSION DIFFERENCE MODELS FOR *Chionochloa*. MODEL NUMBER REFERS TO THE MODELS OUTLINED IN TABLE 3.

| MODEL | df | DEVIANCE | AICc | ΔAICc | $w_i$ |
|-------|----|----------|------|-------|-------|
| 13 | 6 | 240.3 | 252.6 | 0.00 | 0.47 |
| 15 | 7 | 238.4 | 252.8 | 0.15 | 0.43 |
| 17 | 9 | 237.1 | 255.7 | 3.07 | 0.10 |
| 11 | 5 | 254.2 | 264.4 | 11.82 | $1.01 \times 10^{-1}$ |
| 9 | 4 | 257.7 | 265.9 | 13.25 | $6.20 \times 10^{-4}$ |
| 5 | 5 | 256.9 | 267.1 | 14.50 | $3.31 \times 10^{-4}$ |
| 7 | 6 | 255.9 | 268.1 | 15.52 | $1.99 \times 10^{-4}$ |
| 14 | 6 | 273.5 | 285.8 | 33.20 | $2.88 \times 10^{-8}$ |
| 16 | 7 | 272.9 | 287.2 | 34.61 | $1.42 \times 10^{-8}$ |
| 6 | 5 | 288.8 | 299.0 | 46.36 | $3.99 \times 10^{-11}$ |
| 10 | 4 | 292.2 | 300.3 | 47.67 | $2.07 \times 10^{-11}$ |
| 12 | 5 | 290.4 | 300.6 | 48.01 | $1.75 \times 10^{-11}$ |
| 8 | 6 | 288.7 | 300.9 | 48.32 | $1.50 \times 10^{-11}$ |
| 3 | 4 | 298.4 | 306.6 | 53.95 | $9.00 \times 10^{-13}$ |
| 1 | 3 | 300.9 | 306.9 | 54.32 | $7.45 \times 10^{-13}$ |
| 2 | 3 | 330.8 | 336.9 | 84.29 | $2.31 \times 10^{-19}$ |
| 4 | 4 | 329.9 | 338.0 | 85.43 | $1.31 \times 10^{-19}$ |

(70.0%, $n = 93$). When applied to a small novel dataset, this position was reversed (high = 85%, $n = 20$; low = 70.2%, $n = 47$), but the average correct classification was similar (74.6%).

Details of the parameters for the averaged model are given in Table 9. High seedfall during the previous year is strongly negatively associated with the probability of high seedfall in the following year. This pattern is consistent with resource-based models of mast seeding for *Chionochloa*, in which flowering results in short-term depletion of the resource reserves within a plant (Rees et al. 2002). However, as with *Nothofagus*, there is little support for a large influence of growing degree-days in the year prior to seedfall on reproductive effort, even though leaf growth is known to increase with temperature in *Chionochloa* (Espie et al. 1992). There is, however, strong support for an effect of summer temperature lag1 and lag2, although the effect is slightly different between the two: summer temperature at lag1 is positively but non-linearly (Fig. 7) related to the probability of a high seedfall year, reaching a maximum at very high temperatures (> 1.5°C above the mean); in contrast, increasing summer temperature lag2 has an increasingly negative effect on reproductive effort (Fig. 7). As with *Nothofagus*, it is not absolutely clear whether this is a direct effect, or whether it is indirectly related due to the effect of summer temperature at lag1 on reproductive effort at lag1. Flowering in *Chionochloa* seems most likely to be driven by a synchronising agent, summer temperature in the year prior to flowering, mediated by a resource-linked constraint of the plant's recent reproductive history.

TABLE 9. COEFFICIENTS AND 95% CONFIDENCE INTERVALS FOR THE PARAMETERS INCLUDED IN THE K-L BEST MODEL AND FOLLOWING MODEL AVERAGING FOR LOGISTIC REGRESSION MODELS APPLIED TO THE *Chionochloa* DATA. THE PARAMETERS RELATE TO THE RESPONSE ON THE LOGIT SCALE.

| PARAMETER | PARAMETER ESTIMATE | LOWER 95%CI | UPPER 95%CI |
|---|---|---|---|
| **K-L best model (Model 13)** | | | |
| (Intercept) | -0.726 | -0.894 | -0.557 |
| Jan.Feb.dmean.lag1 | 1.993 | 1.765 | 2.221 |
| Jan.Feb.dmean.lag1$^2$ | -0.401 | -0.507 | -0.294 |
| Jan.Feb.dmean.lag2 | -0.913 | -1.088 | -0.737 |
| Jan.Feb.dmean.lag2$^2$ | -0.328 | -0.448 | -0.208 |
| High.seed.lag1 | -1.938 | -2.297 | -1.579 |
| **Average Model** | | | |
| (Intercept) | -0.890 | -1.549 | -0.231 |
| Jan.Feb.dmean.lag1 | 2.043 | 1.330 | 2.756 |
| Jan.Feb.dmean.lag1$^2$ | -0.406 | -0.444 | -0.368 |
| Nov.Apr.degreedays.lag1 | -0.001 | -0.003 | 0.001 |
| Nov.Apr.degreedays.lag1$^2$ | 0.000 | 0.000 | 0.000 |
| Jan.Feb.rain.lag1 | 0.001 | -0.001 | 0.003 |
| Jan.Feb.dmean.lag2 | -0.908 | -1.432 | -0.384 |
| Jan.Feb.dmean.lag2$^2$ | -0.329 | -0.343 | -0.316 |
| High.seed.lag1 | -1.968 | -3.026 | -0.910 |

Figure 7. The functional form of the fitted relationship between *Chionochloa* seedfall and the mean daily temperature during January and February 1 and 2 years previously (Jan.Feb.dmean.lag1 and Jan.Feb.dmean.lag2 respectively). Seedfall has been scaled to be a proportion of its maximum value.
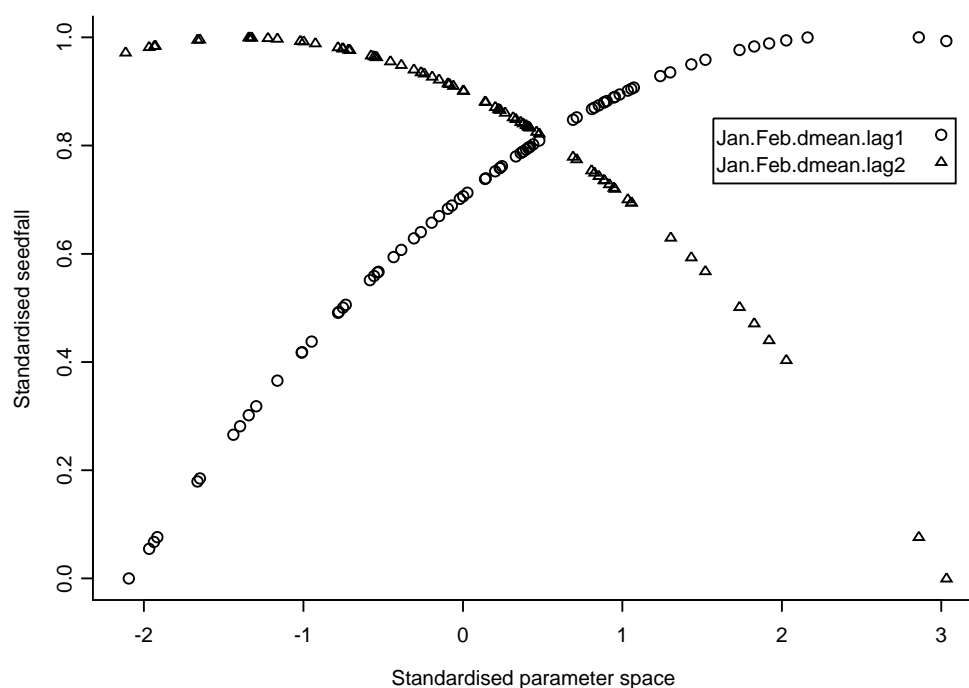


## 3.3 RIMU

Constraining the predictor set to only include variables outside the year of seedfall gave a very poor model, with a cross-validated coefficient of determination of only 31.7% (Table 10, Model 1). The reason for this poor fit seems to be that a cold wet January in the year of seedfall was associated with lower seed yields. This is apparently the time at which fertilisation takes place (Norton et al. 1988). A model in which the predictor set was not constrained gave a much better fit to the data (cross-validated $r^2 = 0.62$;

TABLE 10. COEFFICIENTS AND 95% CONFIDENCE LIMITS FOR THE PARAMETERS INCLUDED IN THE RIMU (*Dacrydium cupressinum*) MODELS.

Model 1 is the model constrained to exclude all predictors from the growing season in which seedfall occurs. Model 2 includes those predictors.

| PREDICTOR | VALUE | SE | LOWER 95% CI | UPPER 95% CI |
|---|---|---|---|---|
| **Model 1** | | | | |
| (Intercept) | 4.088 | 0.305 | 3.490 | 4.685 |
| temp.Jan.lag2 | −1.038 | 0.238 | −1.505 | −0.571 |
| Dec.rain.lag3 | −0.003 | 0.001 | −0.006 | 0.000 |
| **Model 2** | | | | |
| (Intercept) | 6.224 | 0.522 | 5.200 | 7.248 |
| temp.Jan.lag0 | 0.817 | 0.173 | 0.479 | 1.155 |
| log.Seedfall.lag2 | −0.432 | 0.112 | −0.651 | −0.213 |
| Dec.rain.lag3 | −0.005 | 0.001 | −0.008 | −0.003 |
| Jan.rain.lag2 | 0.002 | 0.001 | 0.000 | 0.004 |
| Jan.rain.lag0 | −0.003 | 0.001 | −0.005 | −0.001 |
| Feb.rain.lag2 | 0.003 | 0.001 | 0.001 | 0.005 |
| Dec.wetday.lag2 | 0.118 | 0.054 | 0.012 | 0.225 |
| Jan.rain.lag1 | −0.002 | 0.001 | −0.004 | 0.000 |

Table 10, Model 2). However, including these variables severely limits the utility of the model, because by the time the information is available to calculate the predictions, the seeds will already be falling. There were too few data to make sensible statements about the model's ability to predict high and low seedfall years.

The unconstrained model (Model 2, Table 10) predicts that high seedfall events will be associated with warm dry conditions during the fertilisation period and generally wetter conditions during the summer of initiation (lag2), and will be inhibited by high seedfall 2 years before the seedfall event of interest. Interestingly, Norton & Kelly (1988) noted that their correlation analysis showed that cold January temperatures during the year of initiation were associated with high seedfall in this dataset. This analysis is supported by Model 1, but not by Model 2. In Model 2, monthly mean daily temperature for January in the season of seedfall is a predictor of seedfall. Thus, January temperature and seedfall, both at lag2, are confounded as predictors: either or both variables could be important. Seedfall.lag2 seems more likely to be important, however, because of the more obvious inhibitory pathway via the plant's internal resource dynamics. It is more difficult to explain why cold temperatures during cone initiation might lead to higher seedfall, although one possibility could be a greater net carbon balance during cool moist periods, as found for *Nothofagus* and *Chionochloa*.

Models 1 and 2 were used to generate predictions from climate data from Invercargill aerodrome to validate the models against data collected from Codfish Island (Whenuahou), off the northwestern coast of Stewart Island/Rakiura. Model 1 gave a fairly poor fit to the data ($r^2 = 0.32$, $n = 6$; Fig. 8) and failed to predict the extreme seedfall year of 2002 (predicted seedfall = 175 seeds/m$^2$, observed = 663 seeds/m$^2$). In contrast, predictions from the unconstrained model (Model 2) were very good ($r^2 = 0.87$, $n = 5$; Fig. 8), with the prediction for 2002 of 484 seeds/m$^2$ approaching that of the true value (and very close on the log scale). More data would be needed to critically evaluate these models.

Figure 8. Rimu (*Dacrydium cupressinum*) seedfall predictions using Model 1 and Model 2 against the observed seedfall on Codfish Island (Whenuahou). The axes are log transformed seed/m$^2$.
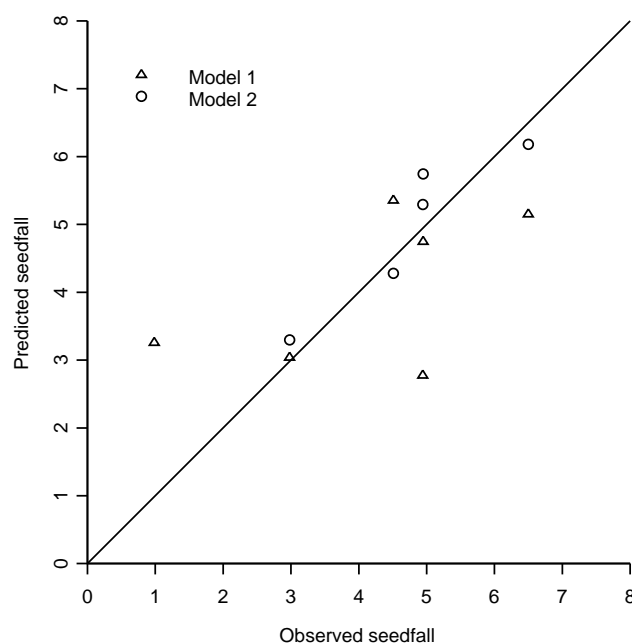
## 3.4    PREDICTIONS FOR 2004/05

At the time of writing this report (June 2004), predictions of *Nothofagus* and *Chionochloa* seedfall for the Te Anau Basin in the 2004/05 year were made using the Takahe Valley climate data and seedfall/flowering records collected locally[1].

### 3.4.1    *Nothofagus*

The model predicted that there was a low to moderate probability that 2004/05 would be a high seedfall year in the Te Anau Basin. The probabilities that the Princhester Creek site and the Eglinton would exceed the 70th percentile were 0.56 and 0.55 respectively. For Takahe Valley, the probability was only 0.27. The Takahe Valley site experienced a moderate seedfall year in 2003/04, which largely accounts for the low expectation of a high seedfall year in 2004/05 for this site compared with the others.

### 3.4.2    *Chionochloa*

The model predicted that for the lower altitude sites in Takahe Valley (900–1000 m a.s.l) containing *C. rubra* and *C. spiralis* there was a high probability that 2004/05 would be a high seedfall year (0.89 and 0.73 respectively). For the remainder of the species (*C. pallens*, *C. crassiuscula*, *C. teretifolia* and *C. rigida*, c. 1160–1190 m a.s.l), there was a low to moderate probability of a high seedfall year (range of predictions = 0.4–0.44).

### 3.4.3    Rimu

The constrained model (Model 1) predicted that 2004/05 would be a low to moderate seedfall year for rimu on Codfish Island (Whenuahou) (67 seeds/m$^2$; 95% confidence limits = 4–1509 seeds/m$^2$). The early to mid-summer of 2002/03 (during cone initiation) was only slightly colder than average, but had higher than average rainfall. This prediction should be treated with caution, however, given the caveats on the constrained model. It was not be possible to make predictions from the unconstrained model (Model 2) until the January 2005 climate data were available.

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[1]   Subsequent observation showed that seedfall in the 2004/05 year was as follows:

*Nothofagus*—Princhester Creek, Eglington and Takahe Valley all exceeded their 70th seedfall percentile (Glen Greaves, DOC, pers. comm.).

*Chionochloa*—three of the six species monitored in Takahe Valley (*C. rigida*, *C. rubra* and *C. pallens*) exceeded their 70th percentile (Bill Lee, Landcare Research, pers. comm.).

Rimu—seedfall on Codfish Island (Whenuahou) was 1954 seeds/m$^2$ (Daryl Eason, DOC, pers. comm.).

# 4. Discussion

## 4.1 UNCERTAINTY IN THE PREDICTIONS

The quality of models and the predictions made are strongly influenced by the quality of the data used to generate them. One limitation of this study is that climate could only be modelled at a coarse scale. The network of New Zealand climate stations is sparse compared with the fine-scale topographical features that are likely to influence seedfall at a local level. The climate stations used in this study were up to 65 km from the site of seedfall collection. The effects of distance are probably most pronounced along the steep environmental gradients found in the Southern Alps, where many of the predictions are required. Although the climate data were expressed as deviations from the mean, which should ameliorate those absolute differences to some degree, we cannot expect to make especially fine-scale predictions. Two adjacent valleys or aspects of the same valley could, on rare occasions, behave differently, but the resolution of the climate data would not be sufficient to make predictions that would address this. Prediction could probably be enhanced by the presence of local weather stations.

To counter the problem of localised conditions, site-specific models appear quite attractive, as they can be tailored to the particular environmental peculiarities of a site and so avoid the generalisations necessary for fitting a site-independent model. However, many of the available data are inadequate to develop such models. High seedfall years are infrequent and therefore require a lot of data to successfully identify and parameterise models. Small datasets generally result in low precision of the parameter estimates, ultimately leading to low predictive power.

It may be possible to exploit the relatively high degree of reproductive synchrony between species and between sites by these masting species (Schauber et al. 2002) to give added certainty to the semi-quantitative predictions made by the models (i.e. is it going to be a high seedfall year or not?). Predictions can be made for and compared across a number of sites. If they all agree, or the large majority agree, we can be very confident of the results; if, on the other hand, there is considerable variation in the predictions, this should alert managers to the need to examine the predictions more carefully. If the predictions agree regionally, then it may be that the models are predicting local high seedfall events; however, if there is considerable variation at this level also, then managers should proceed cautiously, and perhaps directly monitor the situation in the field where appropriate.

## 4.2    SPECIES-SPECIFIC PREDICTIONS AND THE USE OF THRESHOLDS

The intensity of a seeding event is almost certainly species-specific. For *Chionochloa*, the different species vary greatly in tussock size and the fertility of the underlying substrate on which they grow. In *Nothofagus,* the size of seeds differs markedly between species (Ledgard & Cath 1983), which will, in turn, affect the nutrient input required to produce each seed. It would seem, therefore, that species is a notable omission from the a priori models specified in this study. However, this omission was deliberate. Given the available data, many of the species are confounded by site effects because there is only one dataset for that particular species. Thus, it could in fact be misleading to model this as a species effect. The linear mixed-effects model for *Nothofagus* modelled the intercept term as a random effect grouped by series, which encapsulates variation in the mean seedfall per species. However, this approach is not useful for making predictions about new data series not used when fitting the model, because 'species' is not specifically modelled. The logistic models dealt with the species issue by using species-specific thresholds. At first glance, it could be argued that using a threshold derived from unreplicated species data is as equally site- rather than species-dependent as including a species parameter in the model. It is different, however, because it does not depend on the absolute value of the seedfall event but, rather, the relative ranking of the seedfall events. This is independent of the site mean, and relies on the shape of the probability distribution of seedfall events being similar between species, which is a much more tenable assumption given the apparent reproductive synchrony within genera (Schauber et al. 2002).

The logistic regressions used a threshold set at the 70th percentile of seedfall to categorise high and low seedfall years. The setting of the threshold at this level was a matter of judgment; since seedfall is a continuous variable, setting any threshold is arbitrary (Kelly 1994). It is likely that the optimum threshold to achieve the desired management outcomes will vary between systems, depending on the particular characteristics of the site. Therefore, this choice could and should be revisited to establish limits for individual systems once we understand more about the biological significance of seedfall magnitude.

## 4.3 RIMU PREDICTIONS

Timely and accurate prediction of seedfall was a critical goal of this study. Neither of the models developed for rimu satisfy both of these criteria. The constrained model (Model 1) fails because it does not include the temperature during the fertilisation period (the summer of seedfall), which appears to explain a major component of the variance in the data; in particular, cool temperatures seem to account for extremely low fruit set in years in which fruit set might otherwise have been moderate. Hence, this model has poor predictive ability. The unconstrained model (Model 2) fails because it includes climatic variables from the fertilisation period, meaning that the predictions cannot be timely: ripe seed falls from the trees in the autumn following fertilisation; therefore, at best, predictions might be available 1–2 months in advance of seedfall.

The rimu model almost certainly involves some element of overfitting, and its applicability to other sites is questionable given only one dataset was available for the analysis. However, despite these expected handicaps, the unconstrained model gave very good prediction of seedfall at Codfish Island (Whenuahou). Admittedly, five data points are inadequate for a thorough test of the model's generality; however, the results are encouraging.

## 4.4 USE OF THE MODELS WITHIN A LARGER FRAMEWORK

The ability to predict seedfall of *Nothofagus* and *Chionochloa* is desirable for the management of these systems, as the predictions can be used to crudely predict the likelihood of rodent outbreaks; thus a prediction is being used to make a prediction. Clearly there are dangers in this approach, because the function that maps seedfall to rodent density is imperfectly understood, i.e. we do not completely understand what aspect of mast ecology drives rodent outbreaks. For *Nothofagus* forests, supra-abundance of seed is an appealing hypothesis (King 1983); however, it has also been suggested that mice in particular may, at least initially, be responding to increases in the number of leaf litter invertebrates that feed on the beech flowers (Fitzgerald et al. 1996; Alley et al. 2001), as the nutrient input into flowers is at least equal to that of the seeds (Alley et al. 1998). Should the second hypothesis be true, there is a danger that by focusing on the seeds, the importance of mast flowering events that do not translate into high seedfall will be ignored. The *Nothofagus* models predict total seedfall, not flowering, although in most cases it would be sensible to assume a close but imperfect correlation between the two. Managers should also be aware that smaller rodent outbreaks may occur outside mast years (M.G. Efford, University of Otago, pers. comm.).

The details of the dynamics of multi-trophic systems are important because they remind us of the uncertainty in using climatic variables to predict rodent density via the models of seedfall. Prediction failure could occur if either the climate model fails to accurately predict seedfall or if seedfall fails to accurately predict rodent density. For this reason alone, the models

should be embedded within a wider management framework that allows rapid intervention in the system should the chain of prediction fail at any point, or pullback should intervention prove unnecessary. This is particularly important for systems with high conservation values. Logically, the best way to provide this information is to directly measure rodent abundance using current best practice. The strength of the models is that they can predict high seedfall years in advance with a much higher success rate than if we made random predictions. Their weakness is that, because they are only models, they are imperfect representations of reality, and the predictions are only as good as the data used to generate them.

## 4.5 IMPORTANCE OF SEEDFALL MONITORING

The addition of previous seedfall to the models greatly improved their fit to the data. Previous seedfall is negatively correlated with future seedfall, which may, in part, reflect the internal resource dynamics within the plant. It may also partly reflect the structure of the data, in which there are few instances of double mast years due to the vagaries of the climate; high seedfall years should follow low seedfall years because they are rare events. Irrespective of the reason, the success of previous seedfall as a predictor presents a strong argument to support and extend existing seedfall monitoring programmes in areas where seedfall predictions are required.

Standardisation of the collection protocol would maximise the quality of the data that are collected. It is beyond the scope of this study to make specific recommendations on what this protocol should be, but a number of important issues need to be considered. First, sites should be selected that are representative of the forest or grassland habitat for which predictions are to be made. Second, there are a large number of issues surrounding the design of the sampling protocol, including what data to collect, when to collect it, how many sampling units are required, the design of those sampling units (e.g. trays), and where to locate them within the site (e.g. under isolated trees, in pure stands or along transects). Finally, a key issue is data management: the data should be stored in a system that allows easy retrieval by those requiring access to it.

# 5.    Recommendations

Models for the prediction of seedfall in *Nothofagus*, *Chionochloa* and rimu have been developed. For successful implementation of these models, the following points should be considered:

1.  For *Nothofagus*, the logistic regression model gives the best prediction of high seedfall years, although this model is clearly insufficient if predictions on the scale of seeds/m$^2$ are required. For *Nothofagus* and *Chionochloa*, the average models give more balanced predictions (i.e. similar probabilities of failing to predict both high and low seedfall years) than the Kullback-Leibler best model as selected by AIC$_c$. This is perhaps more important in a conservation management setting, where the ability to accurately predict high years is critical.

2.  For rimu, the unconstrained model (Model 2) is recommended for making accurate predictions about seedfall. Unfortunately, because of the critical importance of climate during fertilisation of the ovules, the predictions cannot be both timely and accurate. At the earliest, predictions from the unconstrained model will be available in February of the year of seedfall. Ripe rimu fruits begin to fall from late March through to May.

3.  The models should be implemented within a wider management framework that allows failure in the model predictions to be detected early and rapid intervention where necessary. In practice, in systems where rodents are a concern, this will mean direct monitoring of rodent populations. This is critical where important conservation values are at risk should the models fail to accurately predict a high seedfall year.

4.  Ongoing seedfall monitoring is an essential requirement at sites in which predictions are to be made. Models that did not include previous seedfall as a predictor performed relatively poorly. Seedfall monitoring should follow a standard seedfall monitoring protocol.

5.  There is a critical shortage of sites at which rimu seedfall is monitored. The number of sites monitored needs to be expanded, to develop more robust models of seedfall in rimu.

# 6.    Acknowledgements

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# Appendix 1

## DATA USED IN THE ANALYSIS

| SPECIES | SITE | EASTING | NORTHING | ALTITUDE (m) | YEAR MIN | YEAR MAX | NO. | SOURCE OR OWNER |
|---------|------|---------|----------|--------------|----------|----------|-----|-----------------|
| *Chionochloa macra* | Mt Hutt | 2392820 | 5740560 | 1070 | 1990 | 2000 | 11 | Dave Kelly[a] |
| *Chionochloa conspicua* | Camp Creek | | | 900 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa pallens* | Camp Creek | | | 900 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa pallens* | Camp Creek | | | 1250 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa pallens* | Camp Creek | | | 1650 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa pallens* | Camp Creek | | | 1250 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa pallens* | Camp Creek | | | 1430 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa crassiuscula* | Camp Creek | | | 1250 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa crassiuscula* | Camp Creek | | | 1650 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa flavescens* | Camp Creek | | | 1250 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa flavescens* | Camp Creek | | | 1430 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa pallens* | Mt Hutt | 2392820 | 5740560 | 1070 | 1986 | 2003 | 18 | Dave Kelly[a] |
| *Chionochloa oreophila* | Camp Creek | | | 1430 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa oreophila* | Camp Creek | | | 1650 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa rubra* | Camp Creek | | | 1100 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa rubra* | Camp Creek | | | 1100 | 1979 | 2000 | 22 | Ian Payton[b] |
| *Chionochloa rigida* | Old Man Range | 2215140 | 5533470 | 1220 | 1961 | 1974 | 14 | Payton & Mark (1979) |
| *Chionochloa pallens* | Takahe Valley | 2088600 | 5534600 | 1190 | 1973 | 2003 | 31 | Bill Lee[c] |
| *Chionochloa crassiuscula* | Takahe Valley | 2088600 | 5534500 | 1160 | 1973 | 2003 | 31 | Bill Lee[c] |
| *Chionochloa teretifolia* | Takahe Valley | 2088500 | 5534800 | 1160 | 1973 | 2003 | 31 | Bill Lee[c] |
| *Chionochloa rigida* | Takahe Valley | 2090500 | 5534300 | 1160 | 1973 | 2003 | 31 | Bill Lee[c] |
| *Chionochloa rubra* | Takahe Valley | 2090600 | 5533400 | 900 | 1973 | 2003 | 31 | Bill Lee[c] |
| *Chionochloa spiralis* | Takahe Valley | 2091700 | 5532700 | 1000 | 1993 | 2003 | 11 | Bill Lee[c] |
| *Dacrydium cupressinum* | Wanganui State Forest, Harihari | 2302350 | 5790250 | 15 | 1954 | 1986 | 33 | Norton & Kelly (1988) |
| *Dacrydium cupressinum* | Ianthe State Forest | 2320100 | 5800600 | 20 | 1970 | 1980 | 11 | James & Franklin (1978) |
| *Dacrydium cupressinum* | Pureora State Forest | | | 0 | 1961 | 1967 | 7 | Beveridge (1973) |
| *Dacrydium cupressinum* | Codfish Island (Whenuahou) | | | 0 | | | 0 | Graeme Elliott[d] |
| *Nothofagus fusca* | Rahu | 2422890 | 5888600 | 290 | 1964 | 1976 | 13 | Wardle (1984)/ Franklin (1977) |
| *Nothofagus truncata* | Orongorongo Valley | 2674860 | 5982500 | 130 | 1968 | 2002 | 35 | Peter Berben/ Phil Cowan[e] |
| *Nothofagus menziesii* | Landsborough | 2214600 | 5689800 | 320 | 1997 | 2002 | 6 | DOC (see Graeme Elliott[d]) |
| *Nothofagus solandri* | Craigieburn | 2406500 | 5786000 | 900 | 1998 | 2002 | 5 | DOC (see Graeme Elliott[d]) |
| *Nothofagus menziesii* | Hollyford | 2125000 | 5594000 | 250 | 1975 | 1979 | 3 | DOC (see Graeme Elliott[d]) |
| *Nothofagus solandri* | Dart | 2140000 | 5601000 | 420 | 1999 | 2002 | 4 | DOC (see Graeme Elliott[d]) |

| SPECIES | SITE | EASTING | NORTHING | ALTITUDE (m) | YEAR | | | SOURCE OR OWNER |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | | | | MIN | MAX | NO. | |
| *Nothofagus menziesii* | Dart | 2140000 | 5601000 | 420 | 1999 | 2002 | 4 | DOC (see Graeme Elliott[d]) |
| *Nothofagus fusca* | Dart | 2140000 | 5601000 | 420 | 1999 | 2002 | 4 | DOC (see Graeme Elliott[d]) |
| *Nothofagus solandri* | Rotoiti | 2498000 | 5933000 | 680 | 1997 | 2002 | 6 | DOC (see Graeme Elliott[d]) |
| *Nothofagus menziesii* | Rotoiti | 2498000 | 5933000 | 680 | 1997 | 2002 | 6 | DOC (see Graeme Elliott[d]) |
| *Nothofagus fusca* | Rotoiti | 2498000 | 5933000 | 680 | 1997 | 2002 | 6 | DOC (see Graeme Elliott[d]) |
| *Nothofagus fusca* | Station Creek, Maruia | 2448560 | 5889400 | 400 | 1969 | 1976 | 8 | Franklin (1977) |
| *Nothofagus solandri* | Craigieburn | 2403820 | 5784830 | 1050 | 1965 | 2002 | 38 | Rob Allen[b] |
| *Nothofagus solandri* | Craigieburn | 2403370 | 5784680 | 1340 | 1965 | 2002 | 38 | Rob Allen[b] |
| *Nothofagus solandri* | Mt Thomas State Forest | 2451560 | 5780060 | 470 | 1966 | 2002 | 37 | Rob Allen[b] |
| *Nothofagus menziesii* | Rahu | 2422890 | 5888600 | 290 | 1964 | 1976 | 13 | Franklin (1977) |
| *Nothofagus menziesii* | Alton | 2091150 | 5451100 | 240 | 1964 | 1976 | 13 | Franklin (1977) |
| *Nothofagus solandri* | Mt Misery | 2482300 | 5920400 | | 1974 | 1999 | 26 | Pete Wilson[f] |
| *Nothofagus menziesii* | Mt Misery | 2482300 | 5920400 | | 1974 | 1999 | 26 | Pete Wilson[f] |
| *Nothofagus fusca* | Mt Misery | 2482300 | 5920400 | | 1974 | 1999 | 26 | Pete Wilson[f] |
| *Nothofagus menziesii* | Lillburn | 2091100 | 5451280 | 260 | 1964 | 1969 | 6 | Franklin (1977) |
| *Nothofagus menziesii* | Rowallan | 2091150 | 5451100 | 240 | 1964 | 1982 | 19 | Wardle (1984)/ Franklin (1977) |
| *Nothofagus menziesii* | Princhester Creek, Takitimu Mts | 2114600 | 5499900 | 640 | 1970 | 2002 | 33 | DOC Te Anau[g] |
| *Nothofagus menziesii* | Lake Eyles | 2077000 | 5536000 | 880 | 1979 | 1987 | 9 | DOC Te Anau[g] |
| *Nothofagus solandri* | Takahe Valley | 2093000 | 5532000 | 880 | 1979 | 2002 | 24 | DOC Te Anau[g] |

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