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**Article:**

Rees, M., Kelly, D. and Bjørnstad, O.N. (2002) Snow tussocks, chaos, and the evolution of mast seeding. *American Naturalist*, 160 (1). pp. 45-59. ISSN 0003-0147

<https://doi.org/10.1086/340603>

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# Snow Tussocks, Chaos, and the Evolution of Mast Seeding

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Submitted October 26, 2001; Accepted January 10, 2002

**ABSTRACT:** One hitherto intractable problem in studying mast seeding (synchronous intermittent heavy flowering by a population of perennial plants) is determining the relative roles of weather, plant reserves, and evolutionary selective pressures such as predator satiation. We parameterize a mechanistic resource-based model for mast seeding in *Chionochloa pallens* (Poaceae) using a long-term individually structured data set. Each plant's energy reserves were reconstructed using annual inputs (growing degree days), outputs (flowering), and a novel regression technique. This allowed the estimation of the parameters that control internal plant resource dynamics, and thereby allowed different models for masting to be tested against each other. Models based only on plant size, season degree days, and/or climatic cues (warm January temperatures) fail to reproduce the pattern of autocovariation in individual flowering and the high levels of flowering synchrony seen in the field. This shows that resource-matching or simple cue-based models cannot account for this example of mast seeding. In contrast, the resource-based model pulsed by a simple climate cue accurately describes both individual-level and population-level aspects of the data. The fitted resource-based model, in the absence of environmental forcing, has chaotic (but often statistically periodic) dynamics. Environmental forcing synchronizes individual reproduction, and the models predict highly variable seed production in close agreement with the data. An evolutionary model shows that the chaotic internal resource dynamics, as predicted by the fitted model, is selectively advantageous provided that adult mortality is low and seeds survive for more than 1 yr, both of which are true for *C. pallens*. Highly variable masting and chaotic dynamics appear to be advantageous in this case because they reduce seed losses to specialist seed predators, while balancing the costs of missed reproductive events.

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*Keywords:* synchrony, predator satiation, resource matching, seed bank, time-series analysis.

Mast seeding—synchronous highly variable seed production among years by a population of perennial plants (Janzen 1971; Kelly 1994)—is a widespread, much discussed, but still puzzling phenomenon. Questions still remain at both the evolutionary and mechanistic levels. From an evolutionary viewpoint, mast seeding carries certain inescapable costs. Principal among these are higher density-dependent mortality (e.g., Hett 1971), lost opportunities for reproduction (Waller 1979), and lower population reproductive rates. Therefore, to counter these costs, we should expect to find some economy of scale, which makes occasional large reproductive efforts more efficient than smaller more regular efforts (Norton and Kelly 1988). Intriguingly, however, while masting is prevalent in nature, the null hypothesis that there is no evolutionary benefit from masting but plants merely mirror fluctuation in the environment (Busgen and Munch 1929) has proved hard to refute. This null hypothesis (also known as resource matching [RM]; Kelly 1994) posits a link between resources available to plants each year (determined by favorable conditions such as warm, sunny, moist weather) and flowering effort in that year. The difficulty in refuting RM is that adaptive explanations of masting may require some cue from the environment to synchronize reproduction among plants (although synchronization through pollen limitation is a possible alternative; Satake and Iwasa 2000). The best candidate cues are weather variables that correlate with resource abundance and primary production (Norton and Kelly 1988).

Mast seeding is also puzzling on a mechanistic level. The problem is to understand how plants can vary their reproductive effort widely among years in a synchronized way across individuals. The variation in population-level reproduction (as measured by the coefficient of variation [standard deviation/mean] of total population flowering or seed crop,  $CV_p$ ) is affected by both the variation among years by each individual plant (the CV for each plant,  $CV_i$ ) and the synchrony among plants,  $S$  (Herrera 1998). For plants to increase their  $CV_p$ , some form of internal resource dynamics is required where resources are accumulated and

then expended in large intermittent flowering efforts (Janzen 1971). Flowering is reduced or absent in the years following the depletion of individual's energy reserves until resources are built up again. Previous findings of negative lag 1 or 2 autocorrelations in seed production time series (Norton and Kelly 1988; Sork et al. 1993; Koenig et al. 1994; Koenig 1999) suggest that internal resource dynamics are important in nature, yet as discussed above, evidence is equivocal.

Several recent articles have modeled the internal resource dynamics of plants to understand masting dynamics (Yamauchi 1996; Isagi et al. 1997; Satake and Iwasa 2000). Internal resource dynamics can produce high variability in individual reproductive output (i.e., high  $CV_i$ ) if individuals deplete a large proportion of their resources upon deciding to reproduce (Isagi et al. 1997; Satake and Iwasa 2000). However, this type of overcompensatory internal dynamics cannot synchronize the behavior of different individuals as required, for instance, to satiate predators. To induce the type of synchrony seen in many masting species, one of two additional mechanisms may be invoked: first, synchrony arises from each plant responding to a common weather cue (note that this can either be incidental synchrony, as in the resource-matching hypothesis, or entrainment on a weather cue as a result of selection under an economy of scale); or second, synchrony arises as a consequence of internal resource dynamics interacting with pollen limitation (Satake and Iwasa 2000). To test what conditions are necessary to produce pronounced masting (high  $CV_p$  and high synchrony), we thus consider three possible combinations of factors; the first is cueing or resource matching—reproduction is related solely to a cue or some measure of the quality of the environment (Busgen and Munch 1929). There is no requirement for internal resource dynamics to exaggerate reproductive variation. The second is cueing plus energy stores—reproduction is dependent on cueing or resource matching but also dependent on the energy stores of the plant. The third is pollen coupling plus energy stores—reproduction is dependent on the energy stores and is synchronized through pollen coupling (Isagi et al. 1997; Satake and Iwasa 2000).

In this article, we analyze time-series data to test the factors responsible for the masting behavior of the grass *Chionochloa pallens*. This species from the alpine zone in New Zealand is one of the most dramatic mast-seeding plants (Kelly et al. 2000). The task of understanding its reproductive ecology is simplified by previous studies of wind pollination in this species showing almost no effect of flower crop on seed set (Kelly and Sullivan 1997; Tisch and Kelly 1998; Kelly et al. 2001). Therefore, the pollen-coupling model is not relevant, and the question becomes the relative roles of resource tracking and internal resource

dynamics in the masting behavior. Our task, as well as that of most other masting studies, is complicated by the fact that the internal energy state of individuals is not measured. In order to address the masting dynamics, we therefore develop new methods to reconstruct the internal resource state of individuals, as well as fitting theoretical resource-based models to time-series data on flowering. These methods are likely to prove useful for understanding the factors responsible for masting by other plant species with variable reproduction.

## Methods

### *Biology of Chionochloa pallens*

*Chionochloa pallens* (Poaceae) has a number of advantages as a model system for masting. Plants are long-lived and show extremely variable flowering, yet plants are small enough for complete flower counts to be readily and accurately performed. Flowering is strongly correlated with a simple climatic cue, the effects of masting on predator satiation and pollination efficiency are well understood, and good individual plant-level data sets exist.

The genus *Chionochloa* includes 22 species endemic to New Zealand, most of which are alpine tussocks (bunchgrasses), which variously dominate the vegetation in mountainous regions above the tree line (Connor 1991). For general background to the ecology of the genus and details on their mast-seeding behavior, see Mark (1969), Mark and Dickinson (1997), and Kelly et al. (2000). Most species, including *C. pallens*, grow as individual tufts around 0.5–1.5 m tall and 15–50 cm in basal diameter. Individuals are discrete with no evidence of rhizomatous spread (Connor 1991) and are very long-lived (>100 yr). Each plant consists of hundreds to thousands of long-lived tillers, each of which grows vegetative leaves for some years before optionally producing a single inflorescence (culm). In a heavy flowering year, a single plant can have hundreds of flowering tillers. The tiller dies after flowering but usually first produces a lateral offshoot to replace itself. This new tiller is not competent to flower for perhaps 3–5 yr depending on resource levels, but even in the heaviest flowering years only a small percentage of tillers (<20%) are consumed by flowering, so a shortage of competent tillers should not limit flowering. However, heavy flowering years do deplete the plant's stores of nonstructural carbohydrates (Payton and Brasch 1978).

Levels of flowering at the population level vary extremely widely from year to year, with 16 published data sets from 11 *Chionochloa* species having  $CV_p$  (using sample standard deviation/mean) between 3.08 and 1.51 with a mean of 1.90, which are the highest reported worldwide. Flowering is synchronous among plants at a site and

among sites, both within and between *Chionochloa* species (Kelly et al. 2000). Flower bud initiation is triggered by warm temperatures in the austral summer (January or January to February) the year before flowering; floral buds are recognizable by April, and inflorescences elongate the following December (Mark 1965b, 1968, 1969; McKone et al. 1998, 2001; Kelly et al. 2000). Anthesis occurs around January (McKone et al. 2001). Like other grasses, *Chionochloa* species are wind pollinated, and all eight tested species (including *C. pallens*) are self-compatible (Connor 1967; McKone et al. 1997). Seeds take about 6 wk to ripen, and the dry, gravity-dispersed single-seeded caryopsis is shed before winter.

There has been little work on the size of the persistent seed bank in *Chionochloa* spp. Spence (1990) buried to a depth of 1 cm seeds of *Chionochloa macra* collected during a very low flowering year and found that only 6% were still dormant and viable 1 yr later, whereas 75% had germinated. In contrast, Mark (1969) reports that seeds of *Chionochloa rigida* had an initial flush of germination (20% in the first 50 d) followed by intermittent germination over a period of about 4 yr.

A number of possible economies of scale could provide selective benefits to mast-seeding plant species, of which the most frequently observed are satiation of seed predators and increased pollination efficiency (Kelly 1994). The possible benefits gained by *C. pallens* as a result of predator satiation and pollination have been well explored. Improved pollination efficiency provides very little benefit from mast seeding in *C. pallens*, mainly because only in the very lowest flowering years does pollination success decrease (Kelly and Sullivan 1997). This lack of effect has been confirmed both by empirical tests that manipulated flower densities in the field (Tisch and Kelly 1998) and by modeling (Kelly et al. 2001). Pollination seems to be efficient even at low flowering densities because plants are capable of self-pollination within a solitary inflorescence.

In contrast, *Chionochloa* has been shown to gain major benefits from predator satiation. Flowers and developing seeds are attacked by three widespread specialist invertebrates: a chloropid fly (*Diplotoxa similis*, Diptera: Chloropidae), an undescribed cecidomyiid (Diptera: Cecidomyiidae), and a moth (*Megacraspedus calamogonus*, Lepidoptera: Gelechiidae). All three species of insect have been recorded from a wide range of *Chionochloa* host species, including *C. pallens* (McKone et al. 2001). Each of the insects alone can destroy more than 50% of florets. The three species often co-occur, and total levels of predation can exceed 90% (Kelly et al. 1992; Kelly and Sullivan 1997; Sullivan and Kelly 2000). However, mast flowering is effective in reducing levels of predation in *C. pallens* from around 80% losses in years with lower flowering effort than the previous year, down to less than 10% pre-

duction in years with much higher flowering effort than the previous year (Kelly and Sullivan 1997).

As well as flowering following warm summers, some *Chionochloa* species also flower heavily after being burned in wildfires (Payton and Brasch 1978; Payton and Mark 1979) despite having reduced carbohydrate levels at that time. Payton and Mark (1979) showed that in *C. rigida*, plants invariably flowered heavily in the year after fire, and it then took 14 yr of reduced growth and flowering for biomass levels to recover to prefire levels. There are anecdotal reports of other *Chionochloa* species also flowering after fire, although *Chionochloa rubra* does not show this response (Bycroft 1999). Flowering postfire could represent an economy of scale that would favor mast seeding (Kelly 1994). However, before the arrival of humans, natural wildfires were extremely rare in New Zealand (McGlone 2001), so we do not consider fire further in this article.

Seedlings can often be found where there has been little disturbance, but growth rates are very slow, with 6-yr-old seedlings being <5 cm tall and having less than seven tillers (Mark 1969). Seedling establishment in *Chionochloa* is inhibited by competition with established vegetation (including adults) and by introduced mammalian herbivores (Rose and Platt 1992; Lee et al. 1993). Removal of the vegetation cover by fire can enhance establishment (Mark 1965a; Yeates and Lee 1997).

#### *Study Site and Field Methods*

Individual plant flowering data were available for *C. pallens* from Mount Hutt, Canterbury, New Zealand. The site (43°32'S, 171°33'E) was at 1,070 m elevation in secondary subalpine grassland that developed following anthropogenic fires below the original tree line (~1,350 m). A number of other studies of *Chionochloa* biology have used this site (McKone 1990; Kelly et al. 1992, 2001; Kelly and Sullivan 1997; McKone et al. 1997, 1998, 2001; Sullivan and Kelly 2000). The site was a southeast-facing slope dominated by a mixture of *C. pallens* (94% of the tussock cover) and *C. macra* (6%). Records of *C. pallens* flowering at this site began in 1986, but data on an individual plant level did not commence until 1990. Three permanent transects, each 20 m long, were marked with steel pegs, and all *C. pallens* that touched the line were mapped ( $n = 81$ ). Each February from 1990 to 2001 the number of inflorescences were counted on each mapped plant.

In *C. pallens*, each inflorescence is ~0.5–1.0 m tall and carries ~35 spikelets, each bearing approximately five single-seeded florets. There is variation among years in the number of spikelets per inflorescence and the number of florets per spikelet (yearly means for *C. pallens* at Mount Hutt from 1986 to 2000 varied over a twofold range in

both cases). However, variation in the number of inflorescences per tussock (percentage of tillers that flower) is so much more extreme (>1,300-fold) that this latter variable accounted for 96% of the variation among years in florets per tussock (Kelly et al. 1992). Therefore, we use the number of inflorescences as our measure of flowering effort.

Mount Hutt experiences a cool-temperate humid climate. Annual rainfall is around 2,000 mm/yr, evenly distributed through the year, so there are probably very few periods when soil moisture is limiting. Air temperatures were measured on the *C. pallens* site from May 1995 with a CR21X micrologger (Campbell Scientific, Logan, Utah). Annual mean temperature from 1996 to 2000 was 7.0°C; the warmest month was February (mean = 12.6°C), and the coldest was July (1.2°C). Daily air temperatures at Mount Hutt were highly correlated with daily values from Christchurch (10 m elevation, 87 km to the east, mean difference of 6.0°C); therefore, for periods before May 1995, Mount Hutt temperature was estimated from Christchurch data.

At this moist alpine site, growth and photosynthesis are likely to be limited by temperature. Leaf growth has been shown to increase with temperature in *Chionochloa* species (Espie et al. 1992). To estimate accumulation of resources by *Chionochloa*, we used season-growing degree days from mean air temperature data, using a threshold of 6°C below which no growth was assumed to occur. This relationship is similar to that used in agricultural settings but with the threshold lowered by 2°C to suit the physiology of alpine plants. The growing season was defined as November to March inclusive, a period that included >80% of the whole-year (July to June) growing degree days.

#### Description of Time Series

In any masting species, there are two critical aspects of the pattern of reproduction that are of interest. The first is the temporal variability from year to year, while the second is the degree of synchrony in reproduction between individuals within the population. Temporal variability was assessed using the population-level coefficient of variation  $CV_p = \sigma/\mu$ . To assess synchrony, we calculated the average correlation coefficient,  $r_{i,j}$ , between the time series of reproductive output of all distinct pairs of individuals within the population,

$$S = \frac{1}{n(n-1)} \sum_i \sum_{j \neq i} r_{i,j}. \quad (1)$$

This approach has the advantages of being simple to bootstrap and so to obtain confidence intervals (Bjørnstad et al. 1999). We constructed a bootstrapped 95% confidence

interval by randomly selecting individuals with replacement and recalculating  $S$ . This procedure was repeated 1,000 times to produce the confidence interval.

To explore the cueing or resource-tracking hypotheses, we developed a series of regression models to predict the reproductive output from the average January temperature the previous year and the growing degree days in the previous growing season. The dependence of flowering on January temperature was modeled as either a continuous relationship or a threshold. Plant size was included in all models as a covariate. As reproductive output cannot be negative, a log-link function was used, and to allow for the dispersion in the count data, the negative binomial distribution was used for the error (Lawless 1987). We then simulated the reproductive output of each individual using the appropriate regression model incorporating the estimated error variance. This procedure was repeated 1,000 times to obtain the expected distribution of reproductive synchrony,  $S$ , and  $CV_p$ .

#### Resource-Based Models of Masting: Dynamics and Estimation

Here, we briefly describe the resource-based models of masting (Isagi et al. 1997; Satake and Iwasa 2000). The models assume that an individual has  $S(t)$  energy in store at the beginning of year  $t$ . Each year, plants receive  $P_s$  units of energy from photosynthesis. If the resultant energy store ( $S(t) + P_s$ ) exceeds a critical level,  $L_T$ , then the plant reproduces; otherwise, it saves all its energy for the following year. The energy expended on flowering is assumed to be proportional to the excess, namely  $a[S(t) + P_s - L_T]$ . Plants that flower may be pollinated and in turn produce fruit. The cost of fruit is assumed to be proportional to the cost of flowers (by a factor  $R_c$ ). With these assumptions, the energy dynamics of an individual can be written

$$S(t+1) = \begin{cases} S(t) + P_s & \text{if } S(t) + P_s \leq L_T \\ S(t) + P_s - a(R_c + 1)[S(t) + P_s - L_T] & \text{if } S(t) + P_s > L_T \end{cases}. \quad (2)$$

The associated flowering dynamics is

$$F(t+1) = \begin{cases} a(R_c + 1)[S(t) + P_s - L_T] & \text{if } S(t) + P_s > L_T \\ 0 & \text{if } S(t) + P_s \leq L_T \end{cases}. \quad (3)$$

The equilibrium energy budget of a plant is given by

$$\tilde{S} = \frac{P_s}{a(R_c + 1)} - P_s + L_T. \quad (4)$$

This equilibrium is stable providing  $a(R_c + 1) < 2$  (Satake and Iwasa 2000). If the stability condition is violated, then

the system shows chaotic dynamics but at times with a strong statistical periodicity; the bifurcation diagram is shown in Satake and Iwasa (2000).

The main problem in applying this model is that while reproductive expenditure and energy accumulation are relatively easy to measure (at least through proxies such as flower counts and degree days), it is extremely difficult to estimate the energy stores of a plant without destructive sampling. To get around this problem, we need a way of reconstructing the energy budget of a plant given the energy it receives each year,  $P_s$ , and its reproductive output. To do the reconstruction, we rewrite the recursive equation (2) as

$$S(t) = \tilde{S} + D(0) + \sum_{j=0}^t cP_s(j) - \sum_{j=0}^t F(j), \quad (5)$$

where  $D(0)$  is the unknown deviation from the equilibrium energy budget at time 0. The conversion factor,  $c$ , includes the conversion of energy units into “flower units” and the proportion of photosynthate devoted to reproduction (relative to maintenance, etc). Note that we allow the parameter  $P_s$  to vary through time to reflect annual weather variation and that the approach can be extended to allow for fixed rather than proportional maintenance cost (see app. A). We can reconstruct the time series,  $D(t)$ , of how the energy store deviates from its equilibrium value ( $D(t) = S(t) - \tilde{S}$ ) by rewriting (5) as

$$\sum_{j=0}^t F(j) = D(0) + c \sum_{j=0}^t P_s(j) - D(t), \quad (6)$$

from which it is clear that  $D(t)$  is the residual from the regression of cumulative number of flowers on cumulative energy input. Note that this reconstruction still works if  $P_s$  is measured through a proxy (in our case, the number of degree days) because the slope,  $c$ , will accommodate additional conversion constants.

The reconstruction does not allow us to estimate the equilibrium energy budget,  $\tilde{S}$ . Fortunately, equation (2) can be rewritten in terms of the deviations from the energy equilibrium,  $\tilde{S}$ , according to

$$D(t+1) = \begin{cases} D(t) + P_s & \text{if } D(t) + \frac{P_s}{a(R_c + 1)} \leq 0 \\ D(t) + P_s - a(R_c + 1) \left[ D(t) + \frac{P_s}{a(R_c + 1)} \right] & \text{if } D(t) + \frac{P_s}{a(R_c + 1)} > 0 \end{cases}. \quad (7)$$

From equation (7), it is obvious that the dynamics of the

system are perfectly defined even when  $\tilde{S}$  is not known; conditional on reproduction taking place, the reproductive output in year  $t+1$  is

$$F(t+1) = a(R_c + 1)D(t) + P_s, \quad (8)$$

which is a linear function in  $D(t)$ . The key parameter combination of interest for the resource-depletion model is  $a(R_c + 1)$  (Satake and Iwasa 2000), which we refer to as the resource-depletion coefficient and hereafter label  $A$ . From equation (8), it can be seen that  $A$  can be estimated as the slope of the regression of  $F(t+1)$  on  $D(t)$  for the subset of the data for which the energy store exceeds a critical threshold. Given a known threshold, this is simply a standard linear regression problem. However, since we do not know the threshold, we need to estimate both the threshold and the slope simultaneously. Fortunately, this is a standard piecewise linear regression problem (Tong 1990). We use maximum likelihood to estimate three parameters (threshold, slope, and mean number of inflorescences produced when a plant is below the threshold) and profile likelihood (e.g., Hilborn and Mangel 1997) to erect confidence intervals (assuming the likelihood is  $\chi^2$  distributed with three degrees of freedom). To test whether this approach, first, allows accurate estimation of  $A$  and, second, can distinguish between the resource-based models and RM, we performed an extensive simulation study using both resource-based and RM models (see app. B).

#### *Models for the Evolution of Masting Behavior*

To explore how resource dynamics, cueing, and predator satiation interact to determine the optimal flowering dynamics (as controlled by  $A$ ), we developed a stochastic simulation model. In the model, each plant has resource dynamics determined by equation (2); the probability that an established plant dies is  $p_d$ , and following the death of an established plant, the identity of the successful recruit is determined by lottery competition between seedlings. New recruits are given an initial energy store of  $L_T$ . We assume there are potentially good years for reproduction (e.g., whether previous year’s summer temperatures were warm enough to allow bud formation), which occur with probability,  $p_{\text{good}}$ , and these occur independently at random. In years that are not suitable for reproduction, no plants reproduce. Following reproduction, plants produce seeds according to equation (3), and a fraction of the seeds produced are destroyed by predation. The proportion of seeds that escape predation was determined by the ratio of successive total seed crops using the empirical relationship presented in Kelly and Sullivan (1997; fig. 1). Following predation, a fraction of the seeds,  $g$ , germinate and compete for establishment sites. Those seeds that do not

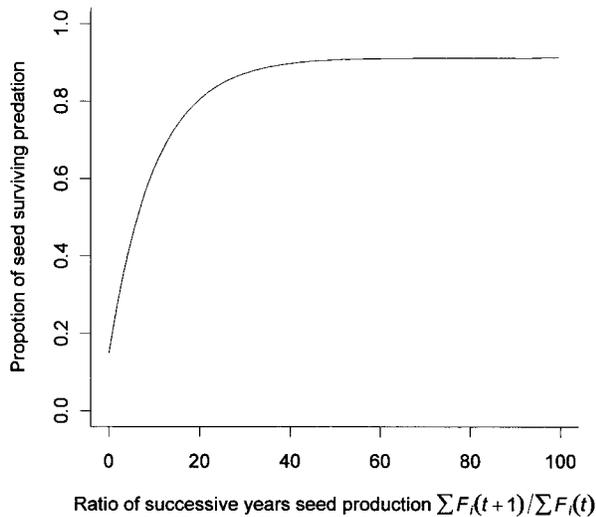


Figure 1: Empirical relationship between the proportion of seed escaping seed predators and the size of successive seed crops, from Kelly and Sullivan (1997).

germinate enter the seed bank where the probability of dying is  $d$  (see Rees and Long 1992 for examples of this type of seed bank model). To determine the optimal strategy, we competed 50 genotypes with different values of  $A$  equally spaced between 0 and 10. If any genotype had a frequency of  $<0.001$  in the seed bank, it was reintroduced at this frequency to prevent extinction. All simulations were run for 100,000 yr.

## Results

### Description of the Time Series

Flowering in *Chionochloa pallens* is highly variable between years and synchronized within the population (fig. 2a). The relationship between flowering this year and flowering last year is highly nonlinear and low dimensional, demonstrating that plants rarely flower 2 yr in succession, and if they do, the number of flowers produced is low (fig. 2b). The population-level  $CV_p$  was 1.88 (bootstrapped 95% confidence interval: 1.13–2.80), and the estimated level of synchrony,  $S$ , was 0.77 (bootstrapped 95% confidence interval: 0.69–0.84).

The critical January temperature for flowering was  $\approx 11.5^\circ\text{C}$  at Mount Hutt, below which very few inflorescences were produced (fig. 3a). There were also positive relationships between plant size, degree days, and the number of inflorescences produced (fig. 3b, 3c). All three relationships were highly significant ( $P < .001$ , using a negative binomial generalized linear model with log-link

function) when analyzed separately or included in a multiple regression. It is also noteworthy, however, that low flowering can occur in the second warm year if two warm years occur in a row (1998/1999 and 1999/2000 showed this pattern). Using a 59-yr time series of January temperatures from Christchurch, we estimated the probability that the temperature would be above the critical value at Mount Hutt; the estimated probability was 0.42.

### Regression Models for Cueing and Environmental Quality

None of the estimated regression models was able to adequately describe the observed levels of synchrony (table 1). The best model, which included an interaction between a threshold temperature for flowering and degree days, gave a predicted level of synchrony of 0.22, which was significantly less than the 0.77 estimated from the field population. We, therefore, tentatively conclude that simple RM models including cues and/or measures of environmental quality are not sufficient to describe the patterns of mast flowering observed in *C. pallens*.

### Reconstruction of the Energy Budget and Predictions of the Resource Model

The fitted model for flowering against the reconstructed energy budget is shown in figure 4. The estimated value of  $A$  is 2.34 (profile likelihood 95% confidence interval: 2.20–2.60), which is in the chaotic dynamic regime. Comparison of the model with data using one-step predictions is potentially misleading because information on flowering is used to reconstruct the energy budget. We therefore further focus on the dynamic behavior of the fitted model (eq. [2]). We first generated 100 yr of data for 81 plants using  $p_{\text{good}} = 0.42$  (to initiate the population). We subsequently used the observed time series of January temperatures for the next 12 yr and calculated  $CV_p$  and synchrony,  $S$ . This procedure was repeated 1,000 times to obtain the expected distribution of  $S$  and  $CV_p$ . Using this procedure, the predicted level of synchrony was 0.79 (standard deviation 0.10) and  $CV_p$  was 1.60 (standard deviation 0.44), in good agreement with the data ( $S = 0.77$ ,  $CV_p = 1.88$ ).

We further explored the geometry of the flowering attractor by iterating the dynamic model for a population of 81 plants over a 1,000-yr period. The resulting phase-plane depiction (fig. 5) shows remarkable resemblance to the data (fig. 2b), suggesting that the fitted model gives an accurate representation of the dynamic system underlying mast flowering in *Chionochloa*. A slight discrepancy is that in the model, some plants produce a small number of flowers 2 yr running. This, however, is a relatively rare theoretical event (happening when there are two consec-

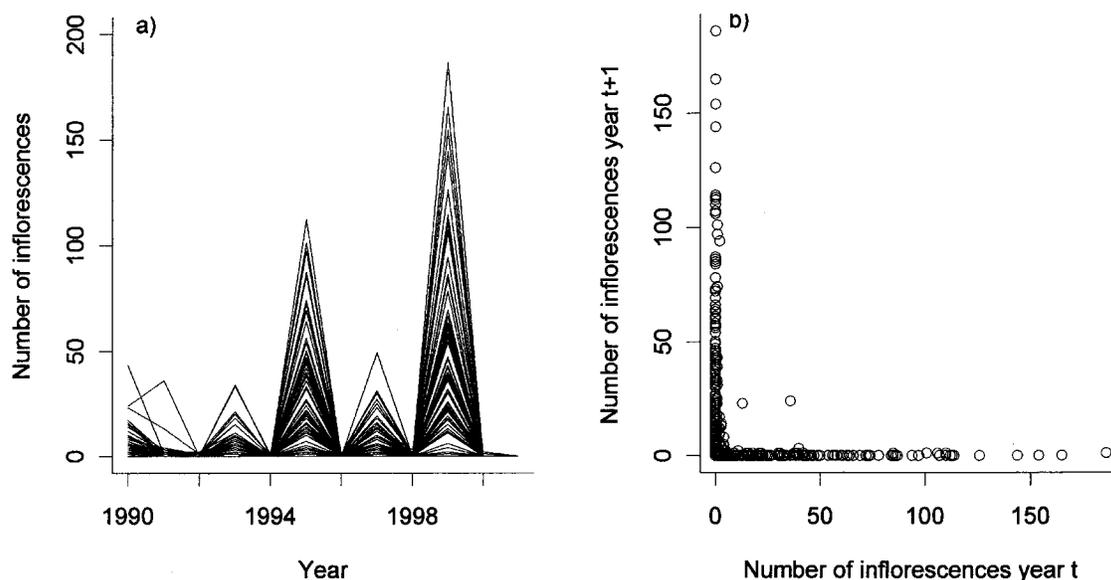


Figure 2: Long-term flowering dynamics in *Chionochloa pallens* at Mount Hutt. *a*, Flowering trajectories for individual plants over the study period, where 1990 refers to the 1989/1990 flowering season. *b*, Phase-plane plot for individual plants of flowering in year  $t + 1$  against flowering in year  $t$ .

utive years suitable for reproduction and reproductive plants have energy stores just larger than the reproductive threshold) and is observed in three of the real plants (fig. 2*b*).

#### *Evolution of Masting Behavior*

The stochastic simulation models clearly indicate that chaotic resource dynamics, as predicted by the fitted model, can be selected for under certain circumstances (fig. 6). The optimal value of  $A$  depends largely on the interplay between the advantages of predator satiation, the rates of adult mortality, and the costs of not reproducing every year (notably due to lost opportunities for establishment). When adult mortality is high, we obtain the classical life-history result that high reproductive effort is favored (Bulmer 1985; Charnov and Schaffer 1973); this leads to chaotic resource dynamics (fig. 6*d*). When adult mortality is low ( $p_a < 0.05$ ), the optimal value of  $A$  depends critically on the carryover of seeds in the seed bank (fig. 6*a–c*). If there is little carryover of seeds, selection favors stable dynamics,  $A < 2$ . This allows plants to reproduce in most years when conditions are favorable and to exploit any establishment sites that become available. When there is substantial carryover of seeds, then chaotic fluctuations in resource dynamics are favored; this reduces seed losses through predation while allowing establishment microsites to be captured even in years when no reproduction occurs. Thus, having a way of storing the gains made when mast-

ing occurs is critical to the success of the masting strategy; otherwise, density-dependent mortality during the establishment phase annuls the advantages of predator satiation.

#### *Behavior of Resource Models*

To understand in more mechanistic detail why intermediate values of  $A$  are selected, we explored the dynamic behavior of the resource model for a range of values of  $A$ , while varying the probability of a year being suitable for reproduction,  $p_{\text{good}}$ . For each of the simulations, we calculated the population-level variability,  $CV_p$ , and synchrony,  $S$ . We also studied the nature of the fluctuation using spectral analysis, with particular reference to statistical periodicity in the chaotic time series.

The simulation predicts high levels of synchrony for all values of  $p_{\text{good}}$  when the model has a stable equilibrium point,  $A < 2$ ; over this range,  $CV_p$  also increases (fig. 7). When the condition for stability is violated, the levels of synchrony decline, and the  $CV_p$  increases as the underlying dynamics become chaotic. Near the boundary for stability, and most notably for high values of  $p_{\text{good}}$ , there is a peak in synchrony and  $CV_p$ . This parameter set corresponds loosely to the estimated values of  $A$ . Detailed studies of the model dynamics reveal that this parameter interval is where the proportion of the variance “explained” by a statistical 2-yr cycle is maximized. Indeed, in the interval  $2.2 < A < 2.3$ , the period 2 cycle accounts for >80% of the variation in the power spectrum. For slightly lower values

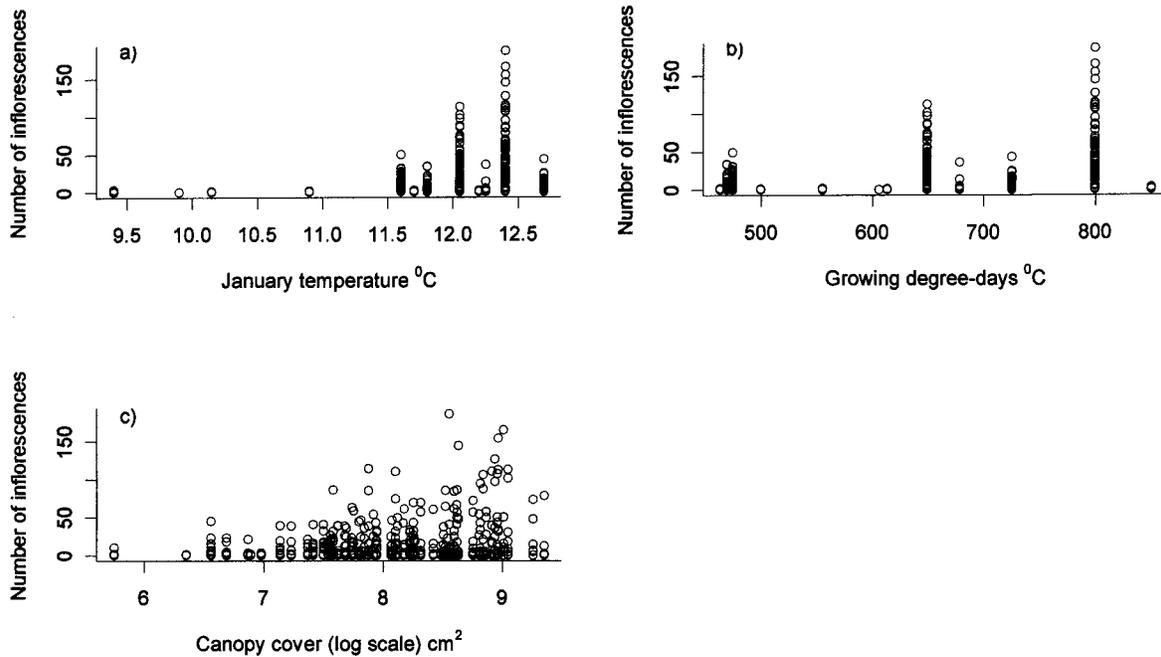


Figure 3: Relationships between the number of inflorescences produced and (a) January temperature, (b) degree days, and (c) plant canopy area (log scale).

of  $A$ , there is also an important 4-yr component to the dynamics. For greater values of  $A$ , the dynamics are increasingly chaotic and decreasingly periodic. Thus, in the weakly forced (i.e., bad years are very rare) system, synchrony is most easily induced and  $CV_p$  is most easily maximized for intermediate (but chaotic) values of  $A$  because these are the values for which the statistical spectrum of the dynamics is the simplest (i.e., a single and dominant peak in the power spectrum). This effect becomes weaker as  $p_{\text{good}}$  becomes smaller because the external cueing will increasingly dominate the flowering dynamics (fig. 7c, 7d).

### Discussion

This study leads to five key conclusions that we will consider in turn below. First, we can retrospectively reconstruct the internal energy reserves of a mast-seeding plant given a long time series of individual flowering data. Second, the masting of individual *Chionochloa pallens* plants can only be adequately modeled by including a resource storage component; simple cues or resource matching are insufficient. Third, the estimated parameters of *C. pallens* put the internal flowering dynamics significantly in the chaotic dynamic regime. Fourth, evolution selects for chaotic dynamics because such dynamics reduce losses of seed to seed predators, but only if adults are long lived and

there is some mechanism (such as a seed bank) for mast-seeding individuals to fill gaps that occur in nonmasting years. Fifth, if global climate change alters the frequency of high-temperature signals, the system may break down and seed predation may increase greatly.

### Reconstructing Energy Reserves

The method presented here to estimate retrospectively the energy balance of individual plants gets around a peculiar conundrum that the ideal data set for examining mast seeding would have information for long time series for individual plants of both flowering efforts and levels of stored reserves. Such data sets are not only nonexistent to the best of our knowledge; they are almost a logical impossibility. Reserves are normally measured destructively, whereas measuring flowering behavior requires the plants to be undisturbed. There are few situations where plant reserves can be measured nondestructively in perennials, although this is possible with some monocarpic plants (Tissue and Nobel 1980). For some species of tree, ring widths can be measured even many years later, but this is a measure of vegetative growth or general climatic favorability (e.g., Tapper 1996) not of available stored reserves. The only real limitations of the technique used in this article seem to be that at least four mast years are required

**Table 1:** Estimated synchrony,  $S$ , and  $CV_p$  for the data and model predictions not including an energy store

	$S$	$CV_p$
Data	.77 (.69, .84)	1.88 (1.13, 2.80)
Model:		
Ln (size)	-.00015 (-.008, .012)	.34 (.21, .51)
Ln (size) + Jan	.18 (.14, .23)	1.27 (1.03, 1.58)
Ln (size) + $T_j$	.13 (.12, .15)	.80 (.74, .87)
Ln (size) + $P_s$	.042 (.02, .08)	.83 (.58, 1.15)
Ln (size) + Jan + $P_s$	.20 (.16, .25)	1.38 (1.13, 1.66)
Ln (size) + Jan $\times$ $P_s$	.20 (.15, .24)	1.32 (1.10, 1.64)
Ln (size) + $T_j$ + $P_s$	.21 (.17, .26)	1.2 (1.03, 1.43)
Ln (size) + $T_j$ $\times$ $P_s$	.22 (.18, .27)	1.23 (1.05, 1.48)

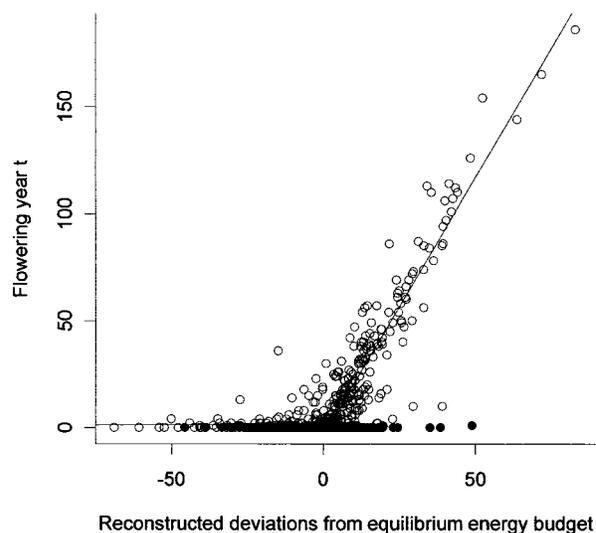
Note: Figures in brackets are 95% confidence intervals. Predictors: size, plant canopy area; Jan, previous January temperature;  $T_j$ , threshold previous January temperature for flowering;  $P_s$ , previous growing season degree days. For the data, the confidence intervals were obtained by bootstrapping (see text for details). The confidence intervals on the model predictions were obtained by generating 1,000 sets of model predictions and calculating the synchrony and  $CV_p$ . Model terms separated by a multiplication cross were fitted as interactions.

to get reasonable estimates of reserves, and that for very high depletion coefficients ( $A > 2.5$ ), the regression method that uses reconstructed reserves underestimates the depletion coefficient somewhat. In more general terms, these techniques are potentially useful in many species where an understanding of the internal energy budget is required, for whatever purpose. Finkenstädt and Grenfell (2000) used a similar technique to reconstruct the unobserved susceptible class in a time-series analysis of measles epidemics.

#### *Can Resource Matching or Cues Explain Masting?*

The statistical analysis shows that the masting flowering observed in *Chionochloa* is unlikely to be the result of resource matching alone (table 1). Of course it is difficult to refute the resource-matching hypothesis because one could always argue that some complex pattern of yet unknown environmental cues could be responsible for any observed pattern of flowering. However, the most parsimonious explanation, relying only on known aspects of the biology of *Chionochloa*, is that flowering is controlled by a simple environmental cue (Mark 1968; McKone et al. 1998; Kelly et al. 2000), and in years suitable for flowering, flowering effort is controlled by the plant's resource status as determined by previous flowering history. A simple yet critical illustration of how simple cue models fail to match real flowering pattern, even when there is an extremely sharp cue (steep log-linear relationship or on/off switch), is that resource depletion is essential to explain the absence of consecutive flowering years given consecutive warm years in a row (as seen in real data in 1998/1999 and 1999/2000).

The conclusion that masting in *C. pallens* is very unlikely to be due to resource matching is important because this has hitherto been a difficult null hypothesis to refute (Norton and Kelly 1988; Kelly and Sullivan 1997). The difficulty in refuting the hypothesis comes from the fact that if some weather variable is associated with heavy flowering, this variable could conceivably be having its effect through



**Figure 4:** Relationship between the number of inflorescences produced and the reconstructed deviations from the equilibrium energy budget. The open circles are from years when the January temperature was above the threshold (11.5°C); the filled circles are from years when the January temperature was less than the threshold (11.5°C). The fitted lines are from the threshold regression model; see text for details.

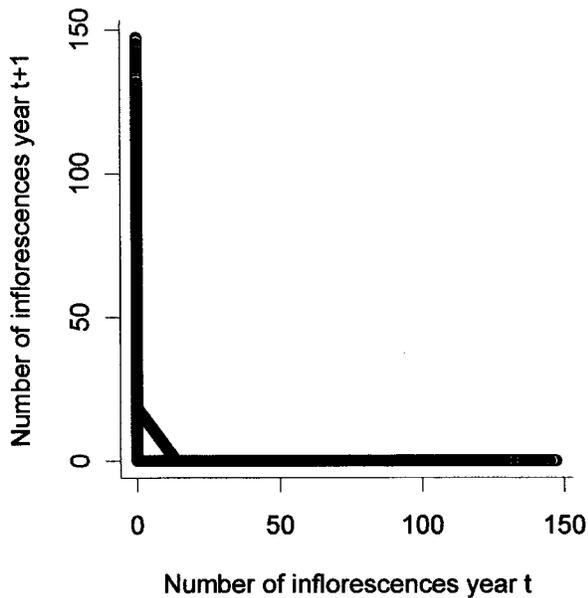


Figure 5: Geometry of the estimated dynamical attractor showing the relationship between the numbers of inflorescences produced in successive years for a population of 81 plants. Parameter values used in the simulation are as follows:  $L_T = 200$ ,  $p_{\text{good}} = 0.42$ ,  $A = 2.34$ , and  $P_s = 7.78$ .

altering the level of resource acquisition. Only by showing what variables are correlated with flowering, or alternatively with growth or resources, can the hypothesis be supported or not supported. Tapper (1996) showed that in *Fraxinus excelsior*, the weather variables associated with greater growth (wider rings in nonreproductive trees) were different from the weather variables associated with heavy flowering, so that the hypothesis was not supported in that case. We can now add a second example. For *C. pallens*, we have shown that a simple binary cue (January temperatures over a threshold value) is more important than favorable whole-season temperatures. Stored resources are vital, whereas simple accumulation in the current or previous season (resource matching) is of less importance.

What this does not determine is why the cue exists. Why is flowering in *C. pallens* apparently so sensitive to January temperatures? There could be a simple physiological explanation (perhaps some aspect of floral bud initiation or gibberellin synthesis in this genus demands warm temperatures). However, bud initiation is less obviously affected than newly opened flowers by cold or inclement weather, and the relationship is extraordinarily sensitive (whether modeled as a steep log-linear relationship or a simple binary switch). Since there is a clear predator-satiation benefit to plants of synchronized intermittent flowering (Kelly and Sullivan 1997) and since syn-

chrony requires external cueing (or forcing; Norton and Kelly 1988), the most parsimonious explanation would be that the cue has been selectively advantageous in reducing losses to seed predators.

Perhaps the most remarkable aspects of the flowering model we developed and parameterized for *C. pallens* are how readily the theoretical model of Satake and Iwasa (2000) could be adapted to the data for *Chionochloa* and how well the behavior of the real population fits the predictions from a slight elaboration of their theoretical model. All this suggests that fairly simple nonlinear mechanisms for resource allocation may be at the heart of the masting behavior of plants in the wild.

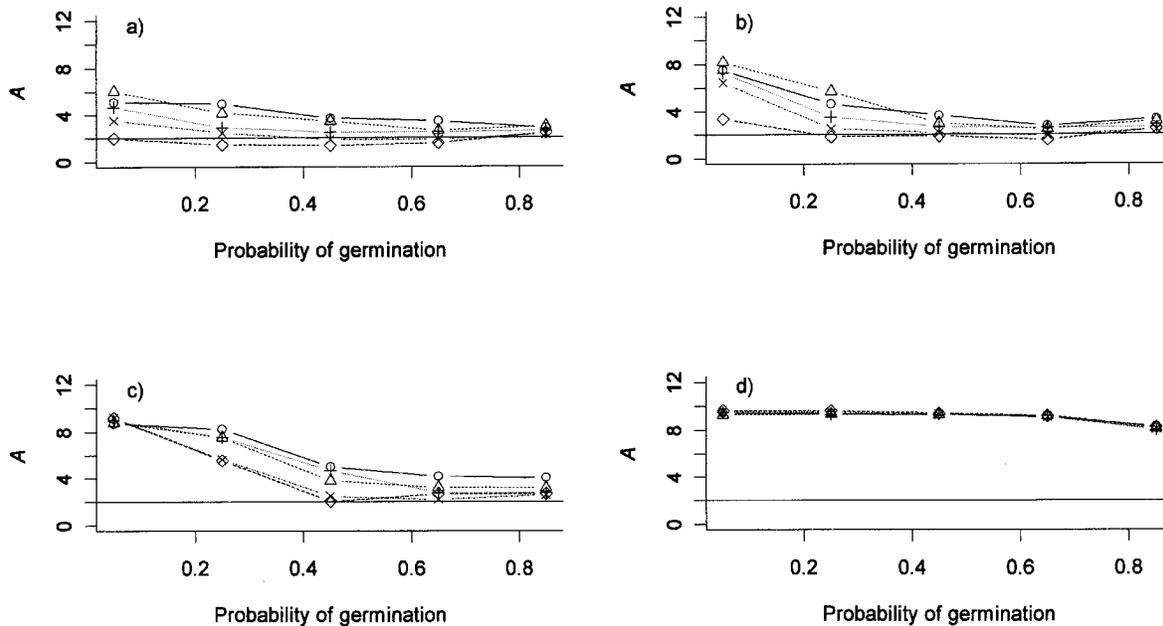
#### Why Is the Masting Behavior Chaotic?

Chaotic behavior is almost unknown in any aspect of plant population dynamics (Rees and Crawley 1989, 1991). It seems significant that *C. pallens*' flowering behavior is determined by a value of the depletion coefficient,  $A$ , which is just over the boundary into chaos. If the depletion coefficient is reduced, the variation among years for individual plants goes down (plants have smaller, more frequent flowering episodes), so population variability decreases. If the depletion coefficient is increased, the dynamics become so chaotic that synchrony declines and the population-level variability decreases. Therefore, to get the maximum benefits from satiating seed predators, individuals have to have just the right level of chaotic (but statistically periodic) dynamics built into their flowering responses.

That it apparently matters so much to achieve high  $CV_p$  is probably related to the nature of the seed predators. First, very high proportions of seed are lost to the seed predators. Second, *Chionochloa* is attacked by three different insects, and one of them (the undescribed cecidomyiid) appears to have predictive diapause, whereby the insects do not emerge from extended diapause in the following year but can wait to emerge in the next heavy flowering year for *Chionochloa* (McKone et al. 2001). This makes it extremely hard for the plant to shake off the seed predator by more moderate levels of mast seeding. The chaotic dynamics shown here would presumably be more difficult for an insect predator to track, and therefore, *Chionochloa* should minimize seed predation by having a high- $CV_p$  chaotic flowering pattern. All this is consistent with *Chionochloa* spp. having the highest reported levels of mast seeding of any plants worldwide (Kelly et al. 2000).

#### Masting, Density Dependence, and Seed Banks

It has been recognized for many years that synchronous mast seeding results in more intense density-dependent



**Figure 6:** Optimal values for the resource-depletion coefficient,  $A$ , as a function of the probability of seed germination,  $g$ , for different values of the probability of adult mortality. *a*,  $p_d = 0.001$ ; *b*,  $p_d = 0.005$ ; *c*,  $p_d = 0.01$ ; and *d*,  $p_d = 0.05$ . The solid line in each panel indicated the condition for stability,  $A < 2$ . Within each panel, the symbols indicate different values of  $p_{\text{good}}$ : circles,  $p_{\text{good}} = 0.9$ ; triangles,  $p_{\text{good}} = 0.8$ ; +,  $p_{\text{good}} = 0.6$ ;  $\times$ ,  $p_{\text{good}} = 0.4$ ; and diamonds,  $p_{\text{good}} = 0.2$ . Other parameter values are  $P_s = 940$ ,  $L_T = 20,000$ , and  $d = 0.1$ .

competition among seedlings, which is a cost of masting (Hett 1971; Kelly 1994). In our evolutionary models, there is strong selection for chaotic internal resource dynamics when there is at least some carryover of seeds in the seed bank, which allows plants to colonize gaps even in years when they do not flower. The strict form of density dependence in our models strongly penalizes plants that fail to capture establishment sites because adults cannot be displaced by seedlings, and the gaps are allocated to a winner from the pool of live seeds present in the year the gap appears. A different form of density dependence might reduce the cost of masting. Other aspects of the biology could further influence the cost of masting. For example, local dispersal would reduce the effectiveness with which individuals who are not in synchrony capture microsites (therefore favoring masting) while increasing the strength of local density dependence (which has the opposite effect). There could also be other ways that the plants could compensate for missed years of reproduction. For example, long-lived, slow-growing seedlings form a seedling bank (Mark 1969) that allows gaps to be colonized even in years with no reproduction.

Minimizing the costs of masting also depends on adult plants having long lives and correspondingly low mortality rates (Waller 1979). Over a broad range of parameter space, the simple evolutionary model predicts chaotic re-

source dynamics in agreement with the data analysis; for  $p_{\text{good}} = 0.4$ , the model predicts  $A$  in the range of 2–4, providing adult mortality is not high ( $< 0.05$ ) and the proportion of seeds germinating is  $> 0.4$ . Long-term observational data suggest that adult mortality is indeed very low in *Chionocholea* (Whitehouse 1982), and the experimental data for *Chionocholea macra* are consistent with germination in the first year being  $> 50\%$  (Spence 1990).

The general point is that mast seeding involves missing opportunities for reproduction, and this can be a strong disadvantage unless there are ways to minimize these costs. In a conceptual sense, all this was identified by Alan Mark when he wrote in 1969 “the longevity of seeds [of *Chionocholea rigida*] compensates both for the intermittent flowering in normal tussocks, and for the period of negligible flowering that follows the prolific seeding caused by burning” (Mark 1969, p. 302).

#### *Global Climate Change and Mast Seeding*

The flowering patterns shown for *C. pallens* appear to be sensitive to the sequence and level of January temperatures. This has strong implications for global warming. McKone et al. (1998) worked on *Chionocholea* spp. at a different site in New Zealand and showed similarly sharp cutoffs between warm years and high flowering efforts.

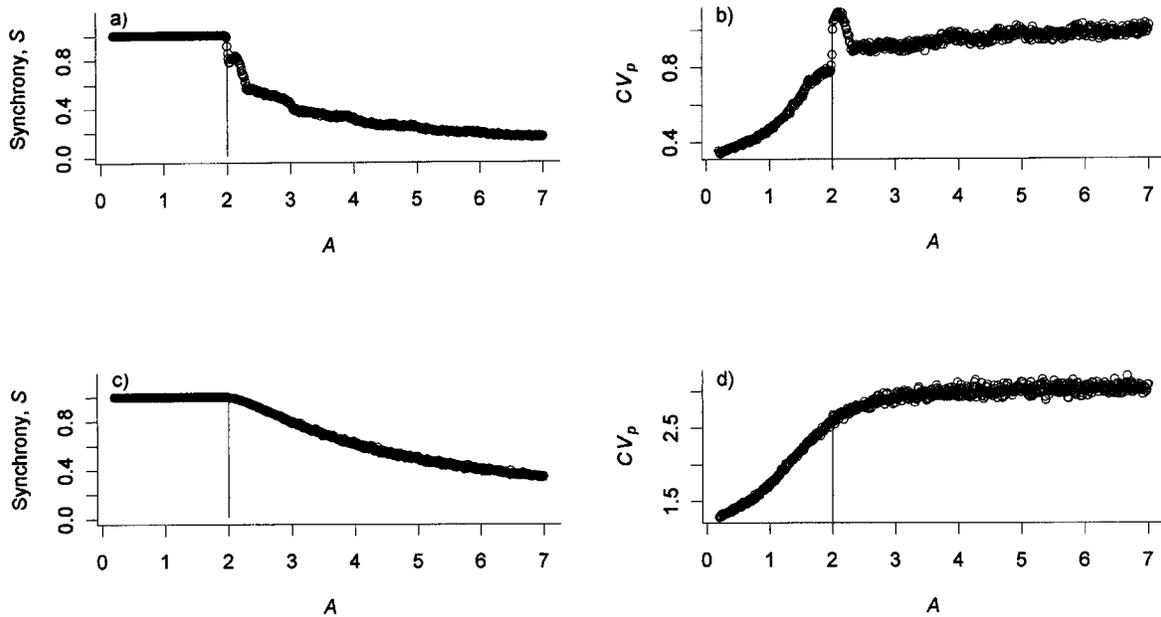


Figure 7: Relationship between  $CV_p$ , synchrony, and resource depletion,  $A$ , for various values of  $p_{\text{good}}$ .  $a, b, p_{\text{good}} = 0.9$ ;  $c, d, p_{\text{good}} = 0.4$ . Other parameter values are  $P_S = 930$  and  $L_T = 20,000$ . The results are based on 200 replicates of a 100-yr simulation with a population consisting of 100 individuals.

They considered that if mean air temperatures increased by  $1^{\circ}$ – $2^{\circ}\text{C}$ , as predicted under recent global-circulation models, the frequency of flowering would increase, and this could result in a breakdown of synchrony to decrease the  $CV_p$ . If flowering variability decreased, predator satiation would become much less effective, and the plants would have fewer surviving seeds just at the time that they need to migrate altitudinally to cope with climate shifts. The models in this article support the conclusions of McKone et al. (1998). The effect of increasing mean temperatures, at least in the short term, would be to increase the fraction of years when flowering is possible. This will decrease  $CV_p$ , since each plant will have less time between flowering efforts to accumulate reserves, and hence will decrease  $CV_p$  and increase seed predation. This problem could be relevant to a wide range of species, if the underlying resource models used here apply, because many masting species have been shown to respond to temperature cues and to suffer higher seed predation at lower  $CV_s$ .

### Conclusions

This mechanistic exploration of the mast-seeding behavior of *C. pallens* has shown that the system appears to have been driven, by evolutionary forces, into chaotic parameter space. This chaotic behavior is favored because it reduces

the impact of natural enemies, while balancing the costs of missed reproductive events. *Chionochloa* thus appears to be a rare example of chaotic dynamics that is induced by biological evolution.

### Acknowledgments

This article is a product of the Masting Dynamics Working Group supported by the National Center for Ecological Analysis and Synthesis, a center funded by the National Science Foundation (grant DEB-0072909), the University of California, and the University of California, Santa Barbara. We thank other Working Group participants (J. Buonaccorsi, R. Duncan, J. Elkinton, W. Koenig, A. Liebhold, M. Peltonen, C. Smith, V. Sork, and B. Westfall) for their comments. We thank the many developers of the open-source software package R (<http://www.cran.r-project.org>), which was used to run the models and analyses in this article, and the E. L. Hellaby Grassland Trust for funding fieldwork.

### APPENDIX A

#### Alternative Models for Energy Allocation

In the main text, the reconstruction of  $D(t)$  through the regression of cumulative flowering on cumulative energy

input was derived using the assumption that the proportion of photosynthate devoted to flowering (relative to maintenance and vegetative growth) was constant. This may not be the best assumption for all plants. If we, instead, assume that a constant amount of energy,  $k$ , is devoted to maintenance and growth (so that energy available to flowering is  $cPs(t) - k$ ), we can rewrite equation (6) as

$$S(t) = \tilde{S} + D(0) - \sum_{j=0}^t k + \sum_{j=0}^t cPs(j) - \sum_{j=0}^t F(j),$$

which on rearranging is

$$\sum_{j=0}^t F(j) = D(0) - tk + c \sum_{j=0}^t Ps(j) - D(t).$$

So under this alternative model for energy allocation,  $D(t)$  can still be reconstructed as the residuals from the multiple regression of cumulative flowering on cumulative energy and time. Using this alternative reconstruction, we

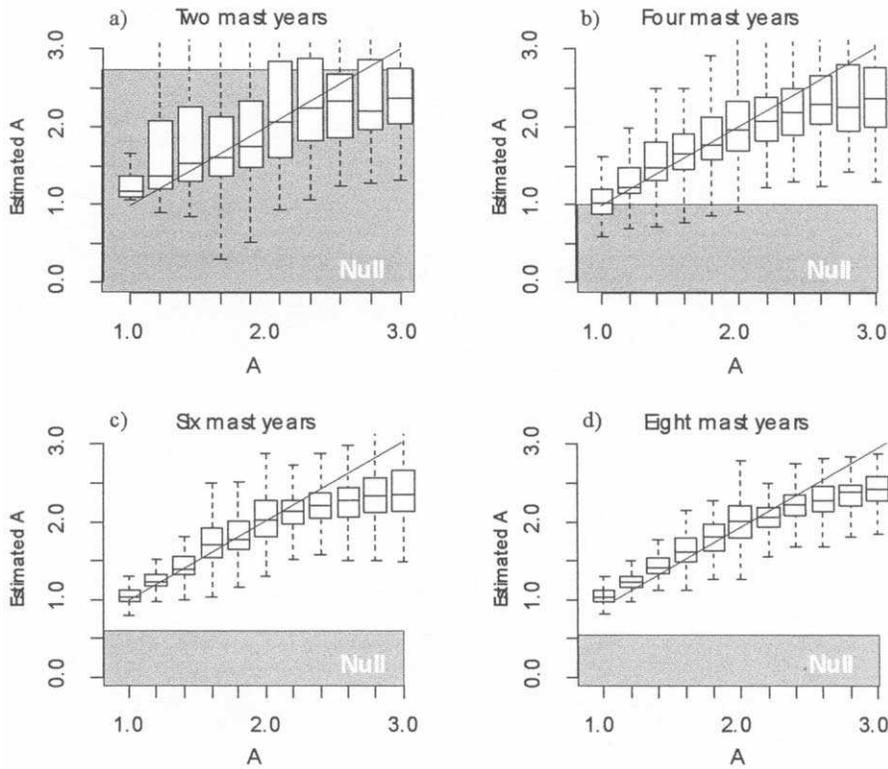
estimate  $A$  to be 2.76 (95% confidence interval using profile likelihood: 2.50–3.10), which again is significantly into the chaotic dynamic regime.

We checked that the profile likelihood produced correct coverage of the confidence interval through bootstrapping individuals. This gave a 95% confidence interval (assuming constant maintenance costs) of 2.50–3.10, in excellent agreement with the profile likelihood confidence interval (CI). The analogous bootstrap CI, assuming proportional maintenance costs, was found to be 2.20–2.60, again, in excellent agreement with the profile likelihood calculations.

## APPENDIX B

### Testing the Reconstruction Algorithm

We use energy-store reconstruction and threshold regression to distinguish between the resource-based model and the resource-matching (RM) alternatives. Three related



**Figure B1:** Box plots of the estimates of  $A$  against true values based on simulated data for which the true value is known. Twelve years of data were simulated on the basis of the model (eqq. [2], [3]). The results are broken down by number of masting years in the time series: *a*, 2 yr; *b*, 4 yr; *c*, 6 yr; *d*, 8 yr. The box plots represent the median estimate, the interquartile range, and the 95% range. The diagonal lines represent unbiased estimation. The shaded areas represent the 95% range for estimates based on the null model involving a temperature cue and degree days but no internal resource dynamics (see app. B).

concerns are, first, does the method provide correct estimates of  $A$  when the resource-based model is true? Second, does the method provide spurious estimates when the RM model is true? Third, does the method have the ability to distinguish between the two models?

To address these issues, we conducted a large simulation study applying our estimation framework to a sequence of data sets under the null hypothesis of RM and under the alternative resource-based model. For each parameter combination, we studied 500 replicate populations each consisting of 100 individuals. In both models, we assumed a “temperature” cue (a binomial variable flagging good and bad years) determining whether to flower at all, and on flowering, reproduction was either given by the resource-based model or the simpler RM model. We varied the length of the time series but will in this synoptic presentation focus on  $T = 12$  (corresponding to the data). We varied  $A$  in the RM model between 1 and 3. The energy budget was reconstructed using equation (6). Estimation of thresholds and slopes were done as discussed in the text. A likelihood-ratio test was used to select whether to use the slope from the threshold model (eq. [7]) or a simple linear regression of flowering against reconstructed energy budget. A 10% coefficient of variation was assumed in the annual number of degree days; this was also varied, but the results were robust to this.

Generally, the simulation shows that the reconstruction algorithm works well. For 12 yr of data on 100 individuals, the method provides almost unbiased and reasonably accurate estimates of  $A$  when the resource-based model is true. The coefficient is slightly biased away from 0 when RM is true; however, there is good separation between the two models (fig. B1). For, say, 30 yr of data, the reconstruction and estimation is excellent. The results further reveal that the number of masting events is a critical factor in whether one can distinguish the resource-based model from the RM. If the time series only covers one or two mast years, then the estimated slope under the RM model is biased to an unacceptable degree away from 0. This appears to result from the reconstruction algorithm requiring multiple masting events to reliably reconstruct the energy store. However, with four mast years (as seen in the *Chionochloa* data), there is good separation between the two models. We are therefore confident that the results presented are not artifacts of the reconstruction algorithm.

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Associate Editor: Mark Westoby