

# Soil nutrient supply modulates temperature-induction cues in mast-seeding grasses

ANDREW J. TANENTZAP,<sup>1,2,4</sup> WILLIAM G. LEE,<sup>2,3</sup> AND DAVID A. COOMES<sup>1</sup>

<sup>1</sup>Department of Plant Sciences, University of Cambridge, Cambridge CB2 3EA United Kingdom

<sup>2</sup>Landcare Research, Dunedin 9054 New Zealand

<sup>3</sup>School of Biological Sciences, University of Auckland, Auckland 1142 New Zealand

**Abstract.** Synchronous and intermittent reproduction in long-lived plants, known as mast seeding, is induced by climatic cues, but the mechanism explaining variation in masting among neighboring but edaphically segregated species is unknown. Soil nutrients can enhance flowering, and thus, populations on nutrient-rich soils may require less-favorable growing temperatures to flower. We tested this hypothesis by predicting the probability of flowering in response to air temperature for five species of alpine *Chionochloa* grasses in South Island, New Zealand, over 37 years and relating our predictions to soil N supply ( $\text{NH}_4^+ + \text{NO}_3^-$ ). Summer air temperatures better predicted flowering than spring air temperatures, which were correlated with soil N mineralization. Species on N-rich soils required lower mean temperatures to induce flowering and/or responded more consistently across a gradient of air temperatures, contributing to the higher probability of their tillers and tussocks flowering at low summer temperatures. Our results suggest that flowering primarily occurs in response to warm summer temperatures, but species on N-rich soils require less favorable growing conditions because they invest relatively less N in seeds. Thus, predicting masting requires a consideration of the interactions among climate, the internal resources of plants, and mineral nutrient uptake.

**Key words:** alpine grasslands; Bayesian; *Chionochloa* spp.; environmental change; mast flowering; Murchison Mountains, New Zealand; snow tussock grass; soil fertility.

## INTRODUCTION

Mast seeding, defined by large, synchronous, and intermittent reproductive events in long-lived plants (i.e., life span >100 years), can increase the fitness of plants by increasing their pollination success (if wind pollinated) and/or reducing seed predation (Kelly and Sork 2002). Mechanistic models have replicated large interannual variation in reproduction by identifying three processes that capture how the internal resource dynamics of plants interact with their external environment (Rees et al. 2002). First, individual plants will only reproduce when their internal resources (i.e., carbohydrate and mineral nutrient reserves) exceed a minimum threshold, re-accumulating resources that are subsequently depleted during flowering while reproduction is depressed (Isagi et al. 1997, Satake and Iwasa 2000). Internal resource dynamics alone cannot, however, account for the levels of synchrony observed in natural populations (Rees et al. 2002). Plants secondly require tightly evolved extrinsic cues to flower synchronously, often weather related (Schauber et al. 2002). Third, the intensity of flowering will be proportional to an

individual's level of internal resources and the costs of flower production (Isagi et al. 1997, Satake and Iwasa 2000). Despite the success of resource-based models in forecasting mast seeding, they do not include an explicit role for soil fertility in mediating levels of carbohydrates and mineral nutrients within plants.

The frequency and intensity of reproductive events that characterize masting are proximally determined by within-plant resource allocation (Rees et al. 2002, Crone et al. 2009), which in turn, is strongly influenced by soil nutrient availability (Marschner 1995). For example, competition for nitrogen (N) and carbohydrates between floral and leaf buds may drive variation in flowering in some species (Han et al. 2008), and these competitive interactions may be relaxed through increasing soil nutrients (e.g., Neilsen et al. 1990). High-fertility soils are thus predicted to increase reproductive output (i.e., seeds per  $\text{m}^2$ ) and lower interannual variation, increasing the number of years with medium- or low-intensity flowering at the expense of those with negligible flowering (Kelly and Sork 2002). Evidence from New Zealand beech (*Nothofagus* spp.) forests support these predictions (Smaill et al. 2011), as warm summer temperatures are hypothesized to increase soil N mineralization, leading to greater accumulation of carbon-based resources within plants and more frequent and intense masting (Richardson et

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<sup>4</sup> E-mail: ajt65@cantab.net

al. 2005). By contrast, plants on soils with fewer mineral nutrients should take longer to accumulate the internal resources required for flowering, and hence, mast less frequently and intensely (Kelly and Sork 2002). Recent evidence from a single-year study suggests that spatial variability in flowering intensity of a masting species varies with soil nutrients (Hay et al. 2008), but no study has explicitly examined the role of soil fertility in the expression of long-term masting strategies across species.

Our objectives were to identify the temperature cues that induce flowering over 37 years in five *C<sub>3</sub> Chionochloa* grass species distributed along a soil fertility gradient, and to relate these to variation in soil nutrients. Rees et al. (2002) identified interactions between summer temperatures and internal energy dynamics as a proximal mechanism explaining synchronous masting in *C. pallens*, postulating that this behavior ultimately confers an evolutionary advantage through predator satiation, which is optimized against the costs of missed opportunities for reproduction. Although there is some synchronicity in masting among different *Chionochloa* spp., not all species flower in the same year or with the same intensity, despite exposure to similar climatic variation across years (McKone et al. 1998). Genetic differences among populations have relatively little influence on flowering, as demonstrated using reciprocal transplant experiments in which plants only flower when lowered in elevation to sites with warmer temperatures (Mark 1965, 1968, Greer 1979). We expected that differences in masting among species are proximally influenced by soil nutrients because the distributions of *Chionochloa* species are strongly delimited by soils (Williams et al. 1976, Lee and Fenner 1989) and soil nutrients influence flowering (Hay et al. 2008).

Our approach was to fit empirical relationships between long-term flowering patterns, air temperatures, and soil nutrient availability. We predicted that within the same bioclimatic zone (i.e., the alpine): (1) warm spring temperatures increase nutrient mineralization; (2) species located on sites with greater mineral nutrient supply have more nutrients available to allocate toward reproduction than species on less fertile sites, and hence, flower more frequently, as measured by a lower coefficient of variation for the annual proportion of flowering tussocks; but (3) species' ability to exploit temperature-dependent N pulses depends on summer growing conditions rather than simply the extent of N mineralization; whereby (4) species on nutrient-rich soils express a greater probability of flowering tussocks (equal to higher frequency) due to a lower summer growing temperature required to induce flowering and/or a more evenly spread probability of flowering across the range of potential temperatures than species on less fertile sites; presumably because they maintain resource gains over less favorable growing temperatures (e.g., Jonasson et al. 1999).

## METHODS

### *Study species*

We studied five *Chionochloa* snow tussock species: *C. crassiuscula*, *C. pallens*, *C. rigida*, *C. rubra*, and *C. teretifolia* (tribe Danthonieae). The five species occupy different communities because their relatively recent radiation (9.5 Ma to present) is driven by strong edaphic segregation (Pirie et al. 2010). Plants grow as discrete tussocks 0.1–1.5 m tall and up to 50 cm in basal diameter, and comprise individual tillers that die after producing a single inflorescence or culm (Appendix A: Table A1). Flowers are wind pollinated and seeds are gravity dispersed (Mark 1969). Adults may live for several hundred years with little juvenile recruitment and delayed sexual maturity (Mark 1969). Differences among species in plant traits and biomass allocation are primarily explained by variation in soil fertility (Lee and Fenner 1989).

*Chionochloa* flowers in response to long day lengths (ca. >14 hours) and warm January and February temperatures the preceding year, because floral buds are initiated towards the end of the growing season and overwinter prior to opening (Mark 1965, 1968). A shortage of mature tillers does not limit reproduction (Rees et al. 2002); only a small proportion of tillers flower during masting (mean of 10% across all species at our site; Appendix A). Floral induction invariably results in seeding, because abortion of floral primordia is negligible, particularly during mild winters (Mark 1968). However, the elongation of pre-formed floral buds, and consequently seed production, can be inhibited by low spring temperatures in the year of flowering, but weakly compared with the positive effects of warm air temperatures on floral induction (Kelly et al. 2008).

### *Study site*

Our study site was Takahe Valley (TV), situated in South Island, New Zealand (45°14' S, 167°33' E). Grasslands of *C. rubra* occur where temperature inversions restrict forest growth on the valley floor, while the four other species occupy valley head basin cirques above 1050 m above sea level (a.s.l.), with distinct communities dominated by individual species delineated by edaphic variation created by topographic position and soil age (Williams et al. 1976). Mean annual precipitation is 2500 mm and is evenly distributed among months (monthly mean  $\pm$  SE = 211  $\pm$  7 mm), leading to few periods with limited soil moisture. Air temperatures have been monitored at TV with a meteorological station on the valley floor (891 m a.s.l.) since October 1972. The mean of minimum and maximum daily temperatures, hereafter "daily temperature," ranges from monthly averages of 10.4°C in February to −1.1°C in July. We used three surrounding weather stations (14–72 km from TV) to calculate missing values, which represented 5.8% of daily temper-

atures between 1 January 1973 and 31 October 2008 (see Appendix B for further details).

#### *Monitoring of flowering and soil nutrients*

Tussocks were monitored annually to measure flowering frequency along a single, permanently marked 1–2 km line transect within each of the five *Chionochloa* communities, separated by a maximum distance of 3.5 km. The number of flowering tussocks intercepting each line was recorded from 1973 to 1992 for each species ( $n = 93$ –1375 tussocks per species). From 1993 to 2009, the number of measured tussocks was standardized, such that line transects intersected between 100 and 130 tussocks per species (ranging 42–102 m in length).

We focused on how N supply affects flowering, because mean foliar, shoot, and soil N:P ratios for each species of <10 (Williams et al. 1976, Lee and Fenner 1989; Appendix C) indicate that sites are N-limited (Güsewell 2004). We monitored  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N from 2003 to 2009 with 5-g anion-cation exchange resin bags buried at a depth of 5 cm at three locations 2 m apart and 3 m from the flowering transects. Resin bags were replaced annually, and removed bags were dried at 35°C for  $\geq 5$  d. Samples were measured at Landcare Research Environmental Chemistry Laboratory (Palmerston North, New Zealand) following standard procedures (Blakemore et al. 1987). We averaged the three resin bag samples along each transect and over years, and only relate induction cues to total N supply ( $\text{NH}_4^+ + \text{NO}_3^-$ ) due to our small sample size ( $n = 5$  species). Since resin bags may poorly reflect absolute soil N supply in some soil types (Giblin et al. 1994), we used the rank-order of total N supply in analyses, and these values were perfectly correlated with the sum of the individual rank orders for  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N supply. Among-transect variation in soil nutrients was several orders of magnitude greater than within-transect variation, further demonstrating the strong edaphic segregation of species (Appendix C).

#### *Temperature dependence of N mineralization*

We tested whether soil N supply increased with mean daily November and December air temperature at each site from 2003 to 2009. We chose the spring period because freeze–thaw cycles stimulate N mineralization and release of N from snowmelt, providing an important plant-available resource pulse that is enhanced by warmer temperatures (Bilbrough et al. 2000). We predicted log-transformed soil N supply in each year at each species-transect by fitting a linear model to temperatures, after applying an adiabatic correction to each site (see Appendix B). The model intercept varied among species to capture residual differences among soils and we used a Student's  $t$  test to determine whether the slope of the temperature effect was greater than zero.

#### *Modeling individual and population level flowering*

We predicted the probability of a tussock flowering using a binomial density function. This approach views flowering as a series of trials and successes, respectively defined by the total number of tussocks in a population in a given year ( $N$ ) and the number of these tussocks that flower ( $K$ ):

$$\Pr(K) = \binom{N}{K} p^K (1-p)^{(N-K)} \quad (1)$$

where  $p$  is the probability of flowering irrespective of flowering intensity (i.e., producing at least one flowering tiller). A limitation of this approach is that  $p$  may poorly predict the probability of a flowering tussock where flowering intensity is high, since tussocks with many flowering tillers will have a different probability of flowering from tussocks with a few tillers flowering (i.e., the probability of a tussock flowering is positively and nonlinearly correlated with flowering intensity; Appendix: Fig. A1). In contrast,  $p$  should be a more robust estimator where flowering intensity is low and differences among years are in whether plants produce any flowers.

Summer (hereafter defined as January and February) temperatures in the year preceding flowering are the principal determinant of floral induction (Mark 1965, 1968, Kelly et al. 2000, 2008). Therefore, the probability of an individual tussock flowering in a given year was determined by the extent to which mean daily temperature between 1 January and 28 February of the year preceding flowering ( $T$ , °C) exceeded the mean temperature required to induce flowering ( $T_{\text{crit}}$ , °C). This relationship was modeled with a logistic function:

$$\Pr(T > T_{\text{crit}}) = \frac{1}{1 + e^{-s(T-T_{\text{crit}})}} \quad (2)$$

where  $T_{\text{crit}}$  is the inflection point of the logistic curve (i.e., the mean temperature at which the probability of flowering is 0.5),  $e$  is the exponential function, and  $s$  controls the spread of the curve (see Appendix D for details). Mean daily summer temperature was by far the most strongly supported flowering cue when we tested alternative models based on degree-days (Appendix D).

We tested whether the summer growing period better predicted flowering within and among species than solely the effects of N supply, as approximated by warm spring air temperatures. Although it would have been desirable to directly include annual variation in soil N supply when estimating flowering, there were only six years of data for which N was measured the year preceding monitoring, and only one occurrence of intense flowering (i.e., >50% tussocks flowering). Models including soil N supply consequently failed to converge. Instead, we assumed that mean daily spring temperatures between November and December reflected annual variation in temperature-dependent N mineralization, and applied the model defined by Eqs. 1 and 2

with temperatures from this period to capture the effects of N supply on flowering. All models were fit to temperatures recorded at the TV station to allow comparison of species occurring at different elevations, rather than using adiabatic corrections to estimate transect-specific temperatures and then standardizing parameter estimates to a common elevation for comparisons.

#### Parameter estimation and model comparison

We used Bayesian methods based on an adaptive Metropolis-Hastings Markov chain Monte Carlo (MCMC) algorithm to estimate the posterior probability distribution of model parameters,  $\theta$ , for each species individually, using the log-likelihood function ( $\ell$ ) of observed population-level flowering ( $\mathbf{K} = K_1, K_2 \dots K_{37}$ ; see Appendix D for details):

$$\ell(\mathbf{K} | \theta) = \sum_{i=1}^{37} K_i \log[p_i(\theta)] + (N_i - K_i) \log[1 - p_i(\theta)] \quad (3)$$

where  $p$  is the probability of a tussock flowering in year  $i$  given  $\theta$  (which equals  $s$  and  $T_{\text{crit}}$ ). Our estimates should be similar to those using maximum likelihood since we set non-informative uniform priors for  $\theta$  (Appendix D). Models were run for at least 100 000 iterations and a 100 000-iteration burn-in period. We extracted the Bayesian mean and 95% credible intervals (CIs) from a subset of the MCMC, comprised of every 100th sample of  $\theta$  post-burnin, to reduce autocorrelation in estimates. We compared models using summer and spring temperatures with the small-sample corrected Akaike information criterion ( $\text{AIC}_c$ ) and Bayesian information criterion (BIC), approximated with the maximum likelihood estimates for each species from the MCMC subset (Ntzoufras 2009).

#### Relating flowering to soil fertility

We used Spearman's rank correlations to test whether variation in observed masting patterns decreased (as measured by CV), and the mean probability of a tussock flowering over the study period increased, with increasing soil N supply. By using rank correlation tests, we compared relative differences among species independent of absolute levels of N supply. For each species, we calculated interannual variability in flowering frequency ( $\text{CV}_f$ ) by dividing the standard deviation (SD) of the yearly proportion of flowering tussocks by the mean. Since species could vary in either  $T_{\text{crit}}$  or  $s$ , we calculated the mean probability of a tussock of each species flowering by substituting  $T$  in Eq. 2 with the mean daily summer air temperature averaged over 37 years. Observed air temperatures were normally distributed from 1973 to 2009 (Shapiro-Wilk test:  $W = 0.98$ ,  $P = 0.649$ ). All analyses were performed using R v.2.9 (R Development Core Team 2009).

## RESULTS

### *Soil N mineralization increases with spring temperatures, promoting flowering*

Total N supply increased with late-spring air temperatures (effect =  $0.15 \pm 0.08$  [mean  $\pm$  SE],  $t_{29} = 2.04$ ,  $P = 0.025$ ; Fig. 1a), and was associated with more consistent flowering frequency (correlation between total N and  $\text{CV}_f$ ,  $\rho = -0.90$ ,  $P = 0.042$ ; Appendix A: Figs. A2, A3). Summer temperatures were unrelated to N (effect  $-0.01 \pm 0.15$ ,  $t_{29} = -0.06$ ,  $P = 0.476$ ). The lower  $\text{CV}_f$  of species on sites with high N supply was due to both greater flowering frequency and less variation among tussocks (i.e., greater synchrony), because neither the mean nor SD of the annual proportion of flowering tussocks systematically varied with soil N (Appendix A: Table A1). Flowering was synchronized among tussocks within species, with no indication of systematic temporal dependence or spatial aggregation (Appendix E).

### *Differences in floral induction cues among species*

Summer growing temperatures were by far the better predictor of flowering frequency within and among species than N mineralization, as approximated by spring air temperatures (>99% supported based on  $\text{AIC}_c$  and BIC weights; Table 1). Both the critical temperature for flowering ( $T_{\text{crit}}$ ) and the slope of the probability function ( $s$ ) for the summer temperature model differed among species (Appendix F), leading to cross-species variation in floral responses to air temperatures that reflected the soils upon which species were distributed (Fig. 2). The probability of a tussock flowering increased along the gradient of total N supply (Fig. 1b), including in perfect rank order from  $\sim 9.6^\circ$  to  $10.4^\circ\text{C}$ , but flowering followed a different hierarchy above the 37-year mean of  $10.4^\circ\text{C}$ . Species on sites with low total N supply, i.e., *C. crassiuscula* and *C. teretifolia*, were relatively more likely to flower in years with high air temperatures (i.e., greater than the long-term means) compared with the other species, which also flowered at low temperatures (Fig. 1).

Species with a lower mean probability of tussocks flowering (*C. crassiuscula* and *C. teretifolia*) were located on sites with low total N supply while species that were more likely to flower, *C. pallens*, *C. rigida*, and *C. rubra*, were located on sites with greater total N ( $\rho = -0.90$ ,  $P = 0.042$ ; Fig. 2c). Neither  $T_{\text{crit}}$  nor  $s$  varied with soil N supply in a systematic direction (Appendix F: Fig. F1), suggesting that both a higher summer temperature to induce flowering ( $T_{\text{crit}}$ ) and lower responsiveness ( $s$ ) of plants at low temperatures (i.e., shallower probability curve) contributed to the lower probability of flowering on N-poor soils.

Analyses of flowering intensity with a 17-year subset of permanently marked tussocks produced identical results to those derived from the 37-year data set of flowering frequency (Appendices A and F), because tiller



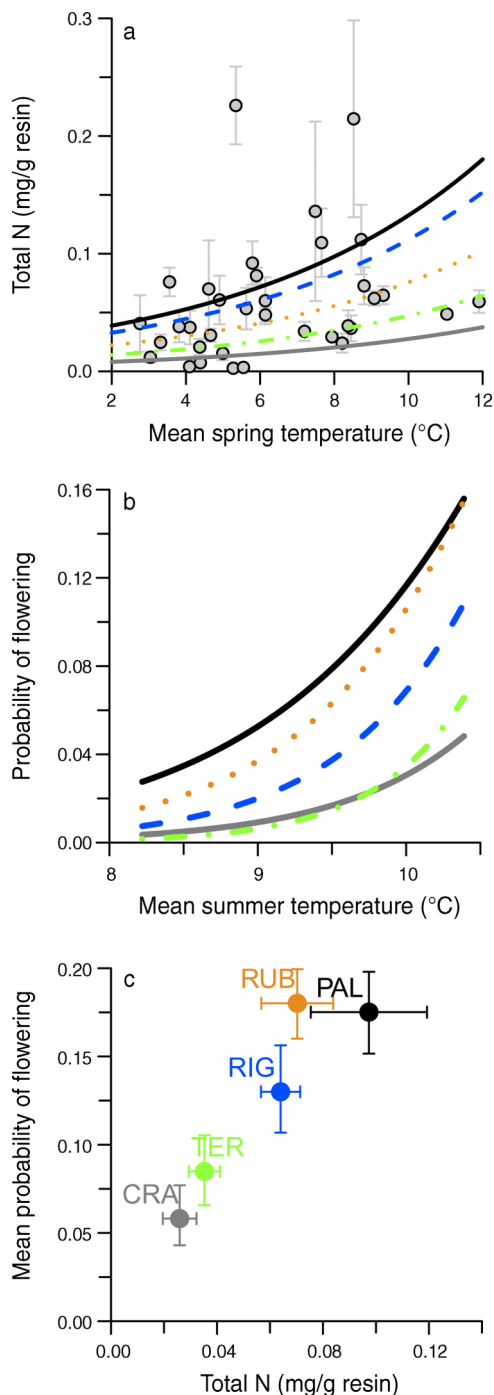


FIG. 1. Temperatures, soil N, and probability of *Chionochoa* flowering. (a) Soil N (mean  $\pm$  SE) increases with mean daily spring, but not summer, air temperatures (data are from the period 2003–2009) (see Results: Soil N mineralization increases with spring temperatures, promoting flowering). (b, c) Probability of a tussock flowering along a soil fertility gradient, estimated with Eq. 2 and using mean parameter values (Appendix F: Fig. F1) (b) at a range of summer air temperatures below the 37-year mean of 10.6°C and (c) at the 37-year mean summer temperature. For panel (c), vertical bars are 95% CIs, and we plotted mean  $\pm$  SE for total N observed along each species transect (2003–2009). In all panels, *C.*

and tussock flowering was strongly correlated (Appendix A: Fig. A1).

#### DISCUSSION

We found that less frequent and intense flowering of species on N-poor soils than congenics on N-rich soils results from a lower probability of flowering, which is explained by summer air temperatures rather than temperature-dependent N mineralization. Importantly, plants require favorable growing conditions to utilize increased soil N supply. Where species experience relatively similar climatic variation, flowering patterns (e.g., CV) should vary with N supply because plants can maintain growth and presumably reproductive investment at lower summer temperatures when soil N supply increases (Jonasson et al. 1999). Thus, our results suggest that masting is a hierarchical process, whereby warm, long-day temperatures initiate floral buds (Mark 1965, 1968, Kelly et al. 2008), but N supply modulates the magnitude of these temperature cues. Predicting masting patterns will require not only an understanding of climate, which can provide most of the information required for accurate predictions (e.g., Kelly et al. 2008), but also of the resource economy of plants (i.e., the accumulation and depletion of internal resources; Satake and Iwasa 2000), and how these processes interact with the uptake of soil nutrients.

#### Role of soil nutrients in modulating floral induction

Reproductive costs for species on N-poor soils may explain why these plants flower less frequently and intensely than congenics on N-rich soils despite species sharing climatic variation and strong evolutionary pressures for predator satiation (Kelly and Sullivan 1997, Kelly et al. 2008). N investments in seed relative to vegetative biomass decline with increasing soil fertility across *Chionochoa* (Lee and Fenner 1989; Appendix A: Table A2), and so seed production is costliest on N-poor soils. Species on N-poor soils may thus require more favorable growing conditions to accumulate sufficient N to invest in seeds. Increased soil N mineralization at higher spring temperatures may exceed a species-specific threshold required to initiate flowering (Richardson et al. 2005, Smaill et al. 2011), but will foremost depend on growing conditions; e.g., species on N-poor soils may be as likely to flower as those on N-rich soils at high summer temperatures. While we have identified an important link between flowering, temperature, and soil nutrient availability, other factors may be mutually correlated with flowering and species' abilities to exploit soils with different N supply, including genetic variation

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crassiuscula is represented by CRA (solid gray lines), *C. pallens* by PAL (solid black lines), *C. rigida* by RIG (dashed blue lines), *C. rubra* by RUB (dotted orange lines), and *C. teretifolia* by TER (dotted-dashed green lines).

TABLE 1. Support for models of flowering probability in five *Chionochloa* species, Murchison Mountains, New Zealand (1973–2009), as a function of summer and spring temperatures corresponding, respectively, with growing conditions and N mineralization.

Species	Growing conditions (mean daily summer air temperatures)		Soil N mineralization (mean daily spring air temperatures)	
	AIC <sub>c</sub>	BIC	AIC <sub>c</sub>	BIC
<i>C. crassiuscula</i>	<b>4941</b>	<b>4944</b>	5979	5982
<i>C. pallens</i>	<b>11 824</b>	<b>11 826</b>	13 278	13 281
<i>C. rigida</i>	<b>5195</b>	<b>5198</b>	6832	6835
<i>C. rubra</i>	<b>11 720</b>	<b>11 723</b>	13 957	13 960
<i>C. teretifolia</i>	<b>3229</b>	<b>3232</b>	5055	5058
Sum	<b>36 909</b>	<b>36 923</b>	45 102	45 116

Notes: The sum of the corrected Akaike information criterion (AIC<sub>c</sub>) and Bayesian information criterion (BIC) values is used to test whether difference in growing conditions or N mineralization better explains flowering among species. Models shown in boldface are more strongly supported, i.e., lower AIC<sub>c</sub> and BIC by >2.

(Mark 1965, Pirie et al. 2010), seed predation (Kelly et al. 2000), mycorrhizal associations (Crush 1973), and the sizes of flowering crops (McKone et al. 1998), and their influences on masting patterns cannot be discounted.

Levels of carbon-based resources can alter masting in some species (Crone et al. 2009), but carbohydrates tend to be unrelated to the carbon costs of reproduction (Körner 2003, Ichie et al. 2005). In *Chionochloa*, the supply of photosynthates, which would increase with soil nutrients, cannot alone explain observed flowering patterns (Rees et al. 2002). Biomass growth and flowering rates in montane *Chionochloa* populations following prescribed burns are more tightly linked to the replacement of mineral nutrients in roots and stems than carbohydrate levels (Payton et al. 1986). Rather, carbohydrates can play important roles in signaling plant development, including floral induction (Smeekens 2000). Experimental manipulations of soil fertility, while measuring levels of carbohydrates and mineral nutrients, would provide a critical test of the correlations we have identified between flowering and soil N supply, but will ultimately lack long-term data, which are needed when flowering is relatively rare (i.e., intervals of  $\geq 2$  years).

The finding that the probability of floral induction increases with soil N supply may be explained at a physiological level by the positive relationship between soil N and the production of plant hormones that promote flower primordia (reviewed in Marschner 1995). For example, gibberellin application promotes floral induction in *Chionochloa* (Martin et al. 1993), including in the field (M. H. Turnbull and D. Kelly, unpublished data). Greater soil N levels increase gibberellins by favoring the expansion of leaf and shoot meristems, which are the primary sites of gibberellin synthesis (Marschner 1995, Jang et al. 2008). Plants growing on more fertile soils may thus require a lower  $T_{crit}$  in order to attain the levels of gibberellins required for floral development, and our predicted flowering probabilities are broadly consistent with the productivity of the soils associated with our study species (Lee and Fenner 1989). Therefore, our results provide a new hypothesis to test how nutrient uptake alters signaling of hormone production in masting plants.

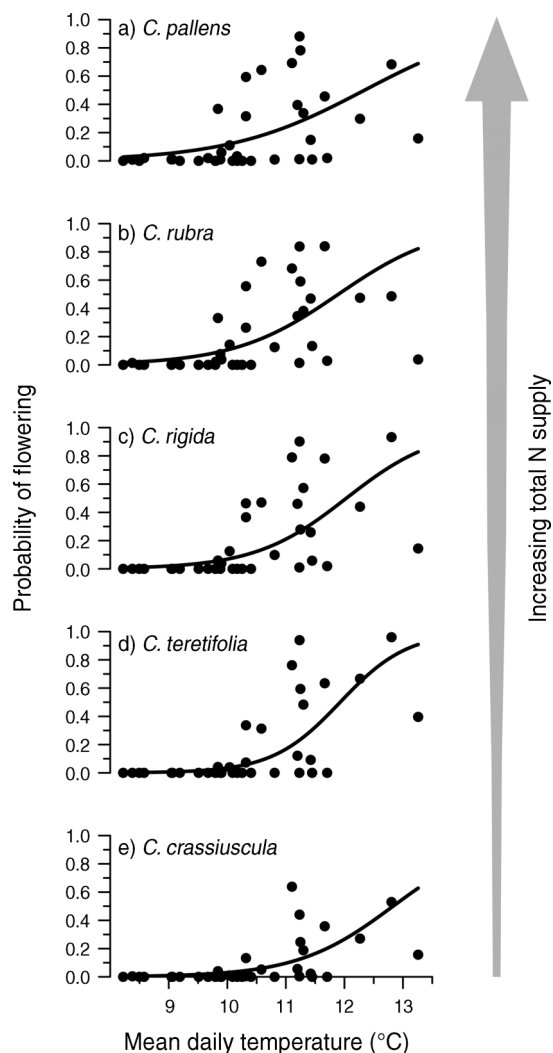


FIG. 2. Probability of tussocks flowering in five *Chionochloa* species, Murchison Mountains, New Zealand, as a function of mean daily summer temperature in the preceding year. Curves represent predicted probabilities of flowering in response to mean daily summer air temperature in the year preceding flowering (Eq. 2), while points are observed proportion of flowering tussocks in each year. The arrow is positively scaled relative to mean total N supply (2003–2009).

### Implications of soil fertility as a factor affecting masting

Long-term sustained changes in soil fertility or air temperature can relax reproductive costs. More frequent flowering or decreased interannual variation in flowering, arising from higher levels of mineral nutrients and/or air temperatures, may consequently dampen the evolutionary benefits of masting by increasing populations of food-limited seed predators (Kelly and Sullivan 1997). Populations of seed predators may further benefit from constant seed production by forgoing costly adaptations used to anticipate masting events (e.g., Boutin et al. 2006). Changes in masting patterns can also affect community and trophic cascades (Kelly et al. 2008). For *Chionochloa*, these changes will directly affect the population dynamics of non-native mammals, i.e., mice and their stoat predators, and may have large cascading impacts for the conservation of endangered bird species, e.g., takahe (*Porphyrio hochstetteri*; Wilson and Lee 2010).

Evolutionary pressures explain the development of masting strategies, but the functional expression of reproductive traits may equally be determined by environmental or physical “constraints” (sensu Gould 1989). Our finding that suggests the energetic costs of reproduction for species on nutrient-poor soils may limit their ability to flower as frequently as species on more fertile sites demonstrates the potential for edaphic conditions to constrain key life-history traits that evolved under strong selection pressures, i.e., seed predation. Several studies have similarly found that the temperatures required to induce flowering within *Chionochloa* species are lower at higher altitudes, where air temperatures are colder, emphasizing that selectively favored traits interact with the local, external environments of plants in fine-tuned ways (Mark 1965, Greer 1979, Kelly et al. 2008). While our results do not compare the relative importance of environment vs. evolutionary pressures in influencing masting (i.e., proximal vs. distal mechanisms), they do provide new evidence for the role of ecological processes in determining why and how plants control the adaptive allocation of resources towards immediate vs. future reproduction.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Flowering statistics for five *Chionochloa* species in the Murchison Mountains, New Zealand (*Ecological Archives* E093-043-A1).

### Appendix B

Accuracy of temperature data from the Takahe Valley meteorological station (*Ecological Archives* E093-043-A2).

### Appendix C

Concentrations of soil nutrients in soil for five *Chionochloa* species in the Murchison Mountains, New Zealand (*Ecological Archives* E093-043-A3).

### Appendix D

Additional details for models of population-level flowering (*Ecological Archives* E093-043-A4).

### Appendix E

Tests of temporal and spatial correlation for proportion of flowering tillers and tussocks of five *Chionochloa* species in the Murchison Mountains, New Zealand (*Ecological Archives* E093-043-A5).

### Appendix F

Additional results for flowering tillers and tussocks of five *Chionochloa* species in the Murchison Mountains, New Zealand (*Ecological Archives* E093-043-A6).