

## Effect of climate change on mast-seeding species: frequency of mass flowering and escape from specialist insect seed predators

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### Abstract

Global surface temperatures are expected to increase by several degrees in the next century, with potentially large but poorly understood impacts on ecological interactions. Here we propose potential effects of increased temperatures on ecologically dominant New Zealand grasses (*Chionochloa* spp.) that mass flower and mast seed. Twenty-two years' data from five masting *Chionochloa* species in New Zealand showed that the cue for heavy flowering was unusually high temperature in the summer of the year before flowering. Attack by predispersal insect seed predators was much reduced in mast years, apparently because predator populations were satiated. Increased temperatures would greatly decrease interannual variation in *Chionochloa* flowering, allowing seed predator populations to increase and potentially to devastate the seed crop annually. Similar responses are likely in masting species worldwide. This previously unrecognized effect of global warming could have widespread impacts on temperate ecosystems.

**Keywords:** *Chionochloa* (Poaceae), global warming, masting plants, New Zealand alpine grassland, plant–insect interactions

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### Introduction

Greater atmospheric concentrations of greenhouse gases are expected to increase global temperatures in the next century (Kattenberg *et al.* 1996; Mitchell *et al.* 1995). The impact of warming on ecosystems in general is poorly understood, and in particular little is known about effects on ecological interactions among species (Kareiva *et al.* 1993; Harrington & Stork 1995).

The effect of climate change on the interactions between plants and their seed predators are especially important to understand, since seed predators can determine the net reproductive capacity of a plant population. Because climate warming will cause the potential ranges of many plant species to shift in latitude and altitude, it may be necessary for new populations to be established if a species is to survive (Peters & Darling 1985; Davis & Zabinski 1992). As a result, any effect of warming on the rate of seed predation may be critical to a plant population's ability to respond to a warmer climate.

Snow-tussock grasses (*Chionochloa* spp.) are the eco-

logical dominants in most indigenous alpine and sub-alpine grasslands of New Zealand (Wardle 1991), and are attacked by a number of flower-feeding insects (White 1975; Kelly *et al.* 1992). We used long-term records of climate, flowering behaviour, and seed predation to predict the outcome of increased temperatures on the rate of seed predation in *Chionochloa*.

### Materials and methods

There are 22 species of *Chionochloa* endemic to New Zealand, and most species have mass flowering and mast seeding (Connor 1966; Mark 1968; Kelly *et al.* 1992). The plants grow as long-lived tussocks (Connor 1991), with only occasional regeneration from seed (Rose & Platt 1990; Lee *et al.* 1993).

#### Takahe Valley

The flowering intensity of five species (*C. crassiuscula*, *C. pallens*, *C. rigida*, *C. rubra*, *C. teretifolia*) has been measured annually since 1973 in Takahe Valley, Fiordland

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National Park, New Zealand. This site contains a remnant population of takahe (*Porphyrio mantelli*; but see Trewick 1997 for recent taxonomic treatment) an endangered flightless bird (Bunin & Jamieson 1995). To protect the takahe, the valley is a restricted-access area and so is almost completely unmodified by direct human activity.

Flowering was recorded as number of flowering shoots per tussock on annual visits to permanent transects in the alpine grassland. Initially (1972–91) between 150 and 200 tussocks per species were sampled. In 1992 the transect lines were adjusted to sample 100 tussocks per species.

*Chionochloa* inflorescences are induced in the summer prior to the flowering season (Mark 1965a), and it has been suggested that the proximate cue for flowering is unusually high temperatures during the induction season (Connor 1966; Mark 1968, 1965b). To test this hypothesis, we used daily temperature data from a permanent weather station located in the valley.

#### Mt. Hutt

Annual measurements of *Chionochloa* flowering intensity and insect seed predation have been made from 1988 to 1997 at a study site at 1070 m on Mt. Hutt, Canterbury, New Zealand. The site is described more fully in Kelly *et al.* (1992). Three permanent 20 m transects were laid through the centre of a dense population of *C. pallens* and the number of inflorescences on each of 76 plants touching the transects was counted annually. Number of florets per tussock was calculated as the product of number of inflorescences per tussock, spikelets per inflorescence, and florets per spikelet.

To determine the extent of insect damage, inflorescences were collected from 15 plants near the transects, usually in February when the seed (technically a fruit, the caryopsis) was maturing but not yet dispersed. There are at least three specialist insects whose larvae attack *Chionochloa* inflorescences: *Diplotoxa similis* (Diptera: Chloropidae), an undescribed (R) Gagne, personal communication) cecidomyiid (Diptera: Cecidomyiidae), and *Megacraspedus calamogonus* (Lepidoptera: Gelechiidae). These insects can cause severe losses of seed (White 1975; Kelly & Sullivan 1997) and other floral structures (unpubl. data).

Individual florets were examined under a dissecting microscope. Any florets that contained larvae of one of the insects or any signs of insect feeding damage were counted as insect damaged; such florets very rarely produce intact seed. Complete methods for assessing insect damage are described in detail in Kelly *et al.* (1992) and Kelly & Sullivan (1997); in contrast to these earlier papers, we have *not* counted empty florets (no pistil or seed present, but no insect feeding sign) as insect damaged. We have concluded that, in the absence of signs of

insect attack (such as frass, stained lemmas, or egg remains), such empty florets are probably the result of early seed dispersal. Thus the estimates of insect damage in this analysis are slightly lower than those published in Kelly & Sullivan (1997).

Non-parametric statistical tests (Spearman rank correlation, Mann–Whitney test) were used throughout because of deviations from normality in the data. We used the sequential Bonferroni procedure (Rice 1989) to maintain experiment-wise  $\alpha$  at the appropriate level when multiple statistical tests were performed.

#### Results

For each of the five study species in Takahe Valley, a majority of years had no or very low flowering; these were interspersed with occasional years of medium to very heavy flowering (Fig. 1a, b). The coefficient of variation (CV) for flowering rate among years in the five species ranged from 1.7 to 2.8, which makes them among the most variable plant species known (Kelly 1994). Flowering rate was highly correlated among the five *Chionochloa* species: Spearman rank correlations ( $r_s$  with 22 d.f.) ranged from 0.85 to 0.94 ( $P$  for each of the 10 pair-wise correlations  $< 0.0001$ ); these are highly significant even after use of the sequential Bonferroni procedure to adjust for multiple tests (Rice 1989).

Weather data from Takahe Valley strongly support the hypothesis that high temperatures induce flowering (Fig. 1c, 2a). Flowering intensity and temperature data were available for 22 years from 1973 to 1996; daily temperature data were missing for part of 1987 so this year was not used. During this period flowering intensity was strongly correlated with temperature in the previous summer for each of the five *Chionochloa* species: rank correlation ( $r_s$  with 20 d.f.) between average temperature in the previous January and February and flowering intensity (number of inflorescences per tussock) was 0.76 for *C. crassiuscula*, 0.70 for *C. pallens*, 0.82 for *C. rigida*, 0.77 for *C. rubra*, and 0.77 for *C. teretifolia*. All of these correlations are individually highly significant ( $P < 0.0002$ ), and remain so with the sequential Bonferroni adjustment (Rice 1989). When the previous January–February temperature was below 10 °C, there was no appreciable flowering of any *Chionochloa* species; heavy flowering was common only when the previous summer's temperature was above 11 °C (Fig. 2a).

At Mt. Hutt, the annual variation in flowering intensity of *Chionochloa pallens* was qualitatively similar to the Takahe Valley population. We defined a mast year as one in which the flowering intensity was greater than 10 times that of the previous year. There was an average of six times as much insect damage in the seven nonmast

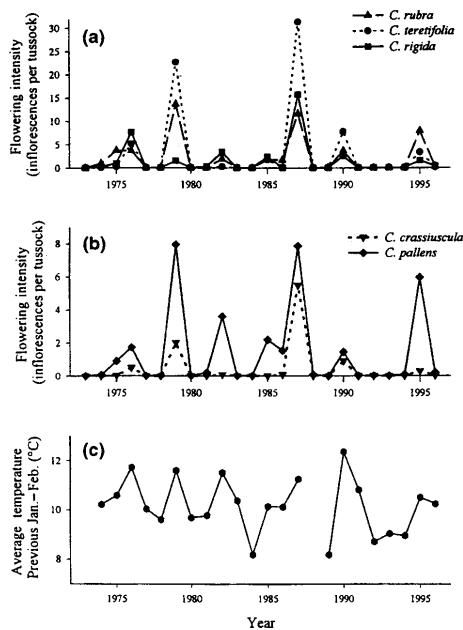


Fig. 1 Flowering rate for five species of *Chionochloa* (a, b) and average temperature (c) between 1973 and 1996 at Takahe Valley, Fiordland National Park, New Zealand. Year of flowering is designated by the year at the end of summer, e.g. the 1979–80 summer is labelled 1980. Temperature shown is the average daily temperature (mean of maximum and minimum for the day) for January and February. Average temperature is shown for the previous year (when flowering is induced) so that flowering intensity is aligned with temperature during the season of flowering induction, e.g. the temperature labelled 1980 shows the average temperature in January and February of 1979. Daily temperature data were missing for part of 1987 so 1988 is not shown.

years as compared to the three mast years (Fig. 3; Mann-Whitney test,  $U_{s[3,7]} = 21$ ,  $P < 0.05$ ).

### Discussion

The data from Takahe Valley show that mass flowering in *Chionochloa* is a response to high temperatures in the previous season, when flowering is induced. During mast years at Mt. Hutt, insect predation in *C. pallens* is greatly reduced compared to nonmast years. Based on this information, we predict that an increase in average temperatures will change the flowering behaviour of *Chionochloa* species and that this is likely to cause an increase in the rate of seed predation.

Current global circulation models predict an increase

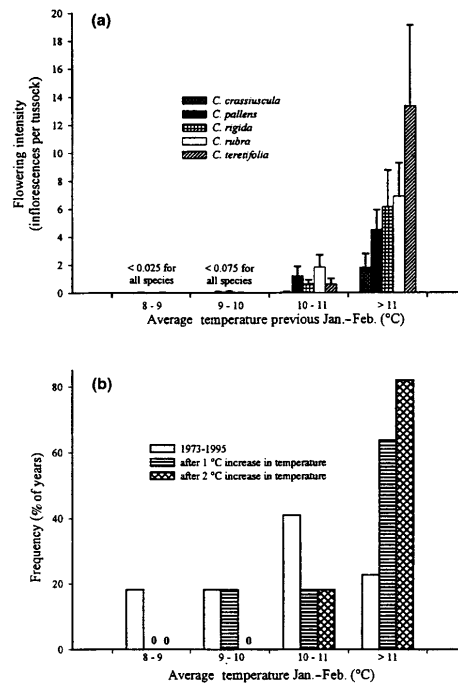
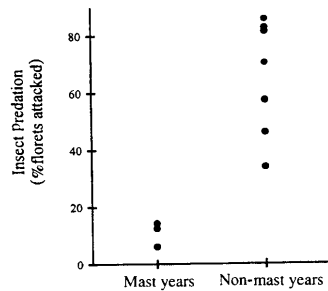


Fig. 2 (a) The effect of temperature on *Chionochloa* flowering at Takahe Valley from 1973 to 1995. Temperature is the average daily temperature (mean of maximum and minimum for the day) for January and February of the year before flowering was measured, since floral induction occurs in the season before flowering. Error bars show one SE above the mean flowering intensity. (b) Frequency of different summer temperatures from 1973 to 1995 and if temperatures increased by either 1 or 2 °C, as predicted by many models of global warming. Summers with average temperatures below 10 °C are the proximal cause of nonflowering years, and would be rare or absent after the predicted climate change.

in average global temperature in the next century between 1 and 3 °C (Mitchell *et al.* 1995; Kattenberg *et al.* 1996), though without great certainty (Trenberth 1997). Estimates for New Zealand are mostly between 1 and 2 °C (Salinger & Hicks 1990; Kattenberg *et al.* 1996). If the summer temperature at Takahe Valley during the study period were increased by 1 °C, the number of years with a January–February average > 11 °C would have increased from 5 (23%) to 14 (64%) (Fig. 2b). With a 2 °C increase in temperature, 18 years (82%) would have had a January–February average > 11 °C (Fig. 2b). Thus increases in temperature predicted by current climate models would almost eliminate cool years (< 10 °C) that



**Fig. 3** Insect predation in florets of *Chionochloa pallens* in mast ( $N = 3$ ) and nonmast ( $N = 7$ ) years from 1988 to 1997 at Mt. Hutt, Canterbury, New Zealand. A mast year is defined as a year with greater than 10 times as many florets produced per tussock than in the previous year. There is a significant difference in insect damage between mast and nonmast years, which supports the hypothesis that the function of masting is to satiate seed predators.

have negligible flowering; most years would be warm enough ( $> 11\text{ }^{\circ}\text{C}$ ) to be mass-flowering years (Fig. 2b).

Transplant experiments verify that an increase in temperatures experienced by individual *Chionochloa* plants produces annual flowering. When *C. rigida* tussocks were transplanted from  $> 850$  m altitude to 10 m at Dunedin, where temperatures are consistently higher, they flowered every year for at least seven years (Mark 1965b; personal communication). Tussocks of our five *Chionochloa* study species were transplanted in 1989 from 1100 m in Fiordland to near sea level at Palmerston North (850 km north-east), and have flowered there annually for seven years (B. Campbell, pers. comm.). Since resources for flowering are limited (Payton *et al.* 1986), it might seem that annually flowering *Chionochloa* plants would have substantially lower reproductive effort per year than plants in current mast years. However, the higher concentration of atmospheric carbon dioxide could increase resources available to individual *Chionochloa* plants by means of greater photosynthetic rate or water use efficiency (Sellers *et al.* 1996; Fields *et al.* 1997; Owensby *et al.* 1997). Such effects have not been demonstrated specifically for *Chionochloa*. But, if they did occur, such physiological responses to increased carbon dioxide would increase the resources available for reproduction in *Chionochloa* plants that flowered annually in a future warmer climate.

The fact that *Chionochloa* species may escape from their specialist predators only in occasional years of very heavy flowering (Fig. 3) is consistent with the hypothesis that masting evolved as a predator satiation strategy (Janzen 1971; Silvertown 1980; Kelly & Sullivan 1997). If seed-predator populations are food-limited, as Kelly & Sullivan (1997) contend, and if global warming produces annual

flowering of *Chionochloa*, the insect populations would increase to match the consistently available resources. Predator satiation would no longer function. The reproductive capacity of *Chionochloa* species could fall significantly as a result of increased predispersal flower and seed predation. If the CV of seed production in *C. pallens* fell from 2.0 to 1.0 (still a moderately high value), the long-term mean predation could increase from 18% of all florets to 69% (Kelly & Sullivan 1997), equivalent to a 62% reduction in seed output.

Loss of reproductive capacity could hamper both the recruitment of new individuals into existing *Chionochloa* populations and the establishment of populations at new sites. Climate warming will cause the potential ranges of many species to shift in latitude and altitude (Peters & Darling 1985). There is little information about the long-distance dispersal ability of *Chionochloa* species, but their long-term survival may soon require establishment of new populations at higher altitude as warming raises the treeline into their current range. Temperature change has been a common feature of Earth's climate for millions of years; given centuries to respond to a change in climate, *Chionochloa* species probably would be able to disperse to newly available habitats even if seed production were relatively low. But the rate of warming predicted for the near future is faster than at any time since the deglaciation at the beginning of the Holocene (Overpeck *et al.* 1991). Based on maximum rates of migration of North American trees from glacial refugia, some trees may not have the capacity to disperse to new potential ranges after the climate change predicted for the next century (Davis & Zabinski 1992). The same could be true of *Chionochloa* spp., especially if seed production is reduced by insect attack.

A shift to annual flowering in a taxon as common as *Chionochloa* would be expected to have a large impact on diverse members of the alpine grassland community. At least two of *Chionochloa*'s insect seed predators have specialist parasitoids (White 1975; pers. obs.), which may be expected to become more common if their hosts' populations are consistently large. It is unknown if the parasitoids can regulate seed-predator populations under current or future conditions. In Fiordland, *Chionochloa* inflorescences are an important food for the endangered takahe (Mills *et al.* 1991). The availability of this food every year could improve habitat quality for takahe, yet this could be offset by loss of grassland habitat if *Chionochloa* species are unable to shift their range quickly enough in response to warming.

Most temperate habitats are dominated by species that mast seed. In New Zealand, masting occurs in many common taxa such as *Nothofagus* spp., *Dacrydium cupressinum*, and *Phormium tenax* (Wardle 1991; Webb & Kelly 1993). In northern temperate and boreal forests, ecologically important tree genera such as *Quercus*, *Fagus*,

*Pinus*, *Picea*, and *Abies* typically mast (Silvertown 1980). Many masting species use high temperature as the proximal cue for heavy flowering (Matthews 1955; Maguire 1956; Connor 1966; Brockie 1986; Norton & Kelly 1988; Allen & Platt 1990; Sork *et al.* 1993; Tapper 1996) and could experience dramatic changes in reproductive behaviour as global temperatures increase (Fenner 1991). Mast-feeding birds and mammals show strong population responses to variation in mast production among years (Smith & Scarlett 1987; Matthysen 1989; Pucek *et al.* 1993) and will undoubtedly be affected by a changed pattern of masting. There could be unexpected but far-reaching repercussions of these changes in vertebrate populations (Murphy & Dowding 1995; Ostfeld *et al.* 1996; Elkinton *et al.* 1996). Also, as in *Chionochloa*, many masting trees are attacked by specialist flower- and seed-feeding insects that are satiated in mast years (Silvertown 1980). If increasing temperatures reduce interannual variation in flowering, the potential increases in seed predator populations and consequent loss of reproductive capacity raise further doubts about the ability of plant species to migrate rapidly in response to global climate change.

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