

Why is mast seeding in *Chionochloa rubra* (Poaceae) most extreme where seed predation is lowest?

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Abstract Mast seeding (highly variable population seed crops among years) is common in the New Zealand flora, and is especially evident in high elevation populations of *Chionochloa* (snow tussocks). However, mast seeding is less pronounced at low elevations in New Zealand plants, including *C. rubra*. Past studies of high elevation *Chionochloa* populations showed that the main benefit of mast seeding is the satiation of pre-dispersal insect seed predators. We therefore predicted that, to be able to set seed regularly, either *C. rubra* should suffer less predation than other *Chionochloa* species, or low elevation populations of *C. rubra* should experience lower seed predation than higher elevation populations. To test these predictions we surveyed seed predation in *C. rubra* and neighbouring *C. pallens* and *C. flavescens* at 22 New Zealand sites spanning over 1000 m in altitude. Total seed predation was not significantly lower in *C. rubra* (48%) than in *C. pallens* (22%) and *C. flavescens* (54%). Seed predation significantly increased with decreasing altitude, in direct contradiction to our prediction. This reveals a reproductive paradox: why do low

elevation populations of *C. rubra* not show more pronounced mast seeding? We discuss three possible answers: (1) *C. rubra* has not formed altitudinal ecotypes with different critical temperatures for heavy floral induction; (2) the seed predators at low elevation are harder to satiate; or (3) low elevation populations suffer stronger disadvantages from masting through high intraspecific competition and/or density dependent seedling mortality. We suggest that this paradox may also occur in many other masting plants with wide altitudinal ranges, that predator satiation will often break down at the lower altitudinal limit of the plant, and that seed predation may limit the lower elevational range of some masting plant species.

Keywords *Chionochloa*; Poaceae; mast seeding; seed predator satiation; effects of altitude; climate; site favourability; ecotypes

INTRODUCTION

The phenomenon of extreme, synchronous variation in seed set is known as mast seeding, and is common in plant populations worldwide (e.g., Silvertown 1980; Kelly 1994; Herrera et al. 1998), and especially in New Zealand (Brockie 1986, 1992; Webb & Kelly 1993). It is not simply a response to extrinsic annual variation in available resources, but rather a result of variation in plant resource allocation to reproduction among years (Norton & Kelly 1988; Kelly 1994; Koenig & Knops 1998; Herrera et al. 1998). Much work has explored how it could be advantageous for a plant to forgo most reproduction in one year for increased reproduction in another year, a year when all of its neighbours are also flowering (see review by Kelly 1994). The two most widely supported explanations for mast seeding are those of seed predator satiation (e.g., Salisbury 1942; Janzen 1971, 1976; Silvertown 1980; Kelly 1994) and increased wind pollination (Stearns 1976; Nilsson & Wästljung 1987; Norton & Kelly 1988; Smith et al. 1990) in years of heavy seed set.

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All studied alpine and subalpine populations of species of *Chionochloa*, the New Zealand snow tussocks, exhibit pronounced mast seeding (Connor 1963, 1966; Mark 1965a, 1968; Campbell 1981; Haase 1986; Kelly et al. 1992; Kelly & Sullivan 1997; McKone et al. 1998). For example, in a Canterbury population of *C. pallens* (nomenclature follows Connor 1991), average annual floret production per plant varies across four orders of magnitude, with a coefficient of variation (CV) of 1.8 (Kelly & Sullivan 1997). In Fiordland, reproductive CVs as high as 3.0 have been recorded for *Chionochloa* populations, which makes them the most variable plant species known (Kelly et al. 2000).

The details of mast seeding behaviour in *Chionochloa* are well illustrated by *C. rigida*, which flowered heavily in only 7 of 18 years (Connor 1966). Total plant non-structural carbohydrate reserves of *C. rigida* are depleted in high seed years (Payton & Brasch 1978), suggesting that resource allocation to reproduction is increased in heavy seeding years. Floral induction in *C. rigida* is dependent on high temperatures when the day length exceeds c. 14 hours; floral primordia over-winter and heavy flowering follows in the next summer (Mark 1965a; Connor 1966). In Takahe valley, Fiordland, floral induction in *C. rigida* and four other *Chionochloa* species occurred when average temperatures exceeded 11°C in the summer prior to flowering (McKone et al. 1998). Mark (1965b) showed that populations of *C. rigida* at different elevations are ecotypically differentiated in this temperature requirement, so that synchronous flowering occurs among populations separated by at least 1170 m of altitude. *Chionochloa rigida* mass flowering events also coincide with at least ten other *Chionochloa* species (Mark 1968; McKone et al. 1998; Kelly et al. 2000).

In *Chionochloa*, mast seeding could benefit individual plants through both predator satiation and wind pollination. *Chionochloa* populations often suffer high pre-dispersal seed predation from three insect species. Satiation of these seed predators has been clearly demonstrated for a Canterbury population of *C. pallens* (Kelly & Sullivan 1997). Seed predation in this population ranged from 9% to 94% of florets over 10 years, and 83% of this annual variation was explained by the change in flower production between years. The size of the current flowering effort did not influence seed predation, indicating a numerical response of the predators to flowering variation (i.e., predator populations are food limited). Kelly & Sullivan (1997) further dem-

onstrated that the benefits for *C. pallens* of increased wind pollination in mass flowering years are trivial relative to the benefits of seed predator satiation. The satiation of seed predators stands as the most important selective advantage known for maintaining mast seeding behaviour in *Chionochloa*.

Webb & Kelly (1993) showed that annual reproductive CVs of *Chionochloa* and other New Zealand plant species are much larger at higher altitudes. This trend has been documented within *Nothofagus solandri* var. *cliffortioides*, a strongly masting species (Allen & Platt 1990). It is also apparent in *Chionochloa rubra* (Mark 1968). High reproductive CVs have been recorded in a high elevation *C. rubra* population at Camp Creek, Westland (1100 m, CV = 1.91) and a mid-elevation population at Takahe Valley, Fiordland (600 m, CV = 1.69) (McKone et al. 1998; Kelly et al. 2000). At these sites, *C. rubra* CVs were no lower than CVs of local populations of *C. conspicua*, *C. crassiuscula*, *C. flavescens*, *C. oreophila*, *C. pallens*, and *C. spiralis*. In contrast, lowland populations of *C. rubra* from Otago and Southland have more constant flowering effort. Mark (1968, p. 58) stated that "within the genus only *C. rubra* is known to flower annually". Bycroft (1999) presented four years' flowering data for five lowland *C. rubra* sites (90–650 m elevation), and showed that the populations had relatively low CVs (mean 0.93, range 0.38–1.50).

This trend poses an intriguing question: since *Chionochloa* seed predators have been shown to respond numerically to seed set variation, and since high elevation populations greatly reduce seed predation by satiating seed predators in heavy flowering years, how could low elevation populations of *C. rubra* maintain low reproductive CVs without suffering high seed predation? Since seed predator satiation is the most important selective advantage known for maintaining mast seeding behaviour in *Chionochloa*, we predict that low elevation *C. rubra* populations should experience low seed predation (at least as low as years of predator satiation at high elevations) to be consistent with their low reproductive CVs. This is for two reasons. First, since mast seeding in *Chionochloa* can substantially reduce long-term seed predation (Kelly et al. 1992; Kelly & Sullivan 1997), any *Chionochloa* populations which are susceptible to seed predation and occur in areas where seed predators are abundant, and yet do not mast seed, are likely to experience frequent heavy seed predation. Any such populations should have been replaced long ago by mast seeding

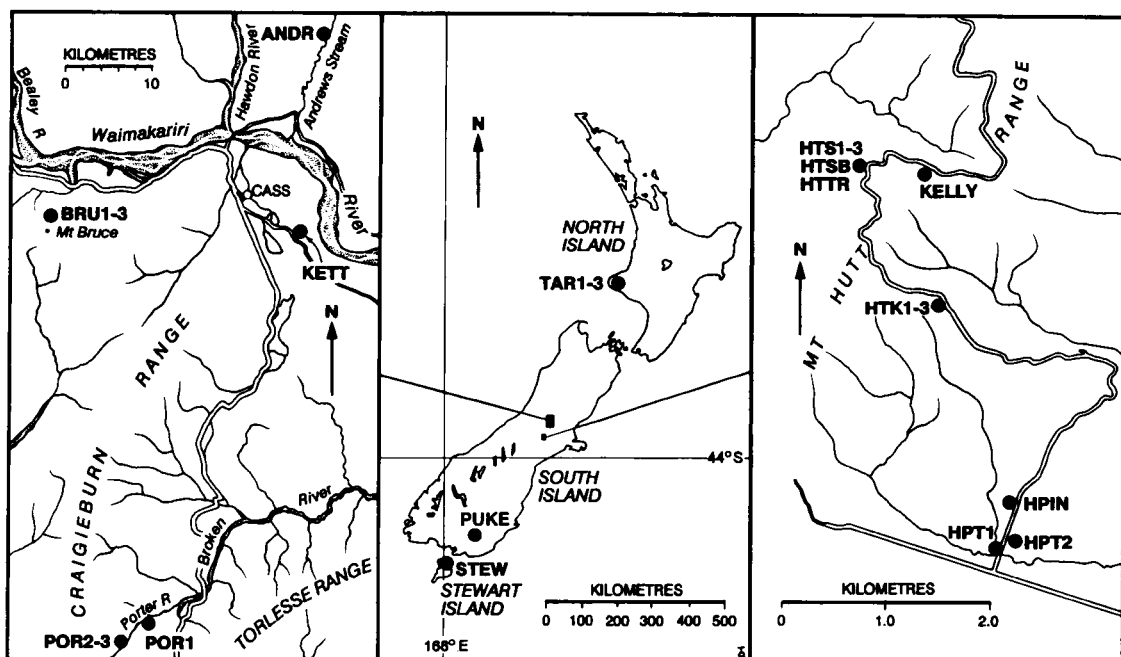


Fig. 1 Locations of the study sites. See text for site abbreviations. The "Kelly" site on Mt Hutt is the long-term *C. pallens* study site (Kelly et al. 1992; Kelly & Sullivan 1997).

populations, through migration or evolution. Second, if satiation of pre-dispersal seed predators is the main factor maintaining mast seeding in *Chionochloa*, *Chionochloa* populations that are more resistant to seed predators or exposed to extrinsically low seed predation should evolve more regular seed set, since there are many selective disadvantages to mast seeding (Hett 1971; Waller 1979; Augspurger 1981; Kelly 1994). While seed predation is generally higher at lower elevations (e.g., Kelly et al. 1992 in *Chionochloa* spp.; Lord & Kelly 1999 for *Festuca novae-zelandiae*), in some cases predation is lower at lower elevations because of interactions with parasitoids and environmental factors (e.g., Randall 1986 for *Juncus squarrosus*).

To understand why *C. rubra* flowers regularly at low elevations, we addressed four questions:

- 1 Is *C. rubra* attacked by the same three species of seed predator that have been recorded from other *Chionochloa* species?
- 2 Does *C. rubra* suffer less seed predation than other *Chionochloa* species at sites where they coexist (i.e., is the species better defended against seed predators than other *Chionochloa* species)?
- 3 Is *Chionochloa* seed predation less in wetter habitats where *C. rubra* predominates?
- 4 Do low elevation populations of *C. rubra* suffer lower pre-dispersal seed predation than higher elevation populations?

METHODS

Study plant species and study sites

Chionochloa rubra occupies a wide altitudinal and latitudinal range, occurring from the central volcanoes of the North Island to Stewart Island and from above the tree line to sea level (Connor 1991). It is one of the few *Chionochloa* species which extends to low elevations, and dominates in wet, high fertility sites (Connor 1991; Wardle 1991). Inflorescences were sampled from *C. rubra* and also from neighbouring or interdigitating populations of two other *Chionochloa* species, *C. pallens*, and *C. flavescens*. *Chionochloa pallens* occurs from central North Island to southern South Island (Connor 1991), and is restricted to low alpine habitats where it is abundant on nutrient-rich, well-drained sites (Wardle 1991). *Chionochloa flavescens* occurs from lower North Island to central South Island (Connor 1991), and is also restricted to low alpine habitats where it prefers

well-drained sites that are generally wetter than those preferred by *C. pallens* (Mark & Adams 1986).

Inflorescences were sampled from several central South Island areas, Mt Taranaki in the North Island, and Stewart Island, from late January to mid March 1993 (Fig. 1). All populations were *C. rubra* ssp. *cuprea*, except on Mt Taranaki where the subspecies is *C. r. inermis* (Connor 1991). For alpine populations of *Chionochloa*, 1993 was a year of moderate flowering effort following a year of low flowering (Kelly & Sullivan 1997). This difference in flowering strongly satiated the seed predators in the long-term *C. pallens* study population at Mt Hutt, producing in 1993 the second lowest annual seed predation in 10 years (Kelly & Sullivan 1997).

Samples in Canterbury were taken from a number of sites. Several quadrats were placed in a swampy saddle on Mt Hutt at 1060 m a.s.l., which offered a clear gradation from *C. rubra*-dominated tussock grassland in the swamp to *C. pallens*-dominated grassland on the northern slope. In February 1993, one 5 m × 5 m quadrat was randomly positioned in each of the swamp, transition, and slope zones (quadrats HTS1–3, respectively) to determine whether *C. rubra* experiences lower floret predation than *C. pallens*. One month later, the swamp quadrat was re-sampled (HTSB) and a transect (HTTR) was run between the swamp and the slope, to investigate whether new floret predators entered florets later in the season, and whether this again differed between species. Six quadrats were randomly positioned within three lower altitude Mt Hutt sites (HTK1–3 at 800 m, HPIN at 500 m, and HPT1–2 at 470 m) to estimate the effects of altitude on floret predation in the area. The tussock-covered slopes of Mt Bruce offered an altitudinal gradation from *C. rubra*-dominated tussock grassland (BRU1 at 1260 m), through a transition zone (BRU2 at 1350 m), into a *C. pallens*-dominated grassland (BRU3 at 1400 m). The Porter River area was sampled (POR1–3) for comparison with White's (1975) study in the area. Sampled were a swamp site of *C. rubra* (POR1, 820 m), and two adjacent river margin sites of *C. rubra* alongside Porter River (POR2, 860 m) and *C. flavescens* on the east-facing slope directly adjacent (POR3, 860 m). *Chionochloa rubra* populations distant from other *Chionochloa* species were sampled at Kettlehole bog, Cass (KETT, 600 m) and Andrews Stream, in Arthur's Pass National Park (ANDR, 710 m), the latter site offering a relatively unmodified, isolated population of *C. rubra* in a swampy *Nothofagus* forest clearing. *Chionochloa rubra* populations at three sites on Mt Taranaki

(North Island) and one on Stewart Island were sampled (quadrats TAR1–3 at 920, 940, 1140 m; and STEW at 550 m, respectively) to assess latitudinal changes in floret predator abundance. *Chionochloa rubra* on Mt Taranaki is further distinguished in being the only *Chionochloa* species in the region. In February 1998, *C. rubra* inflorescences were sampled from a very low altitude site at Pukerau, Otago (PUKE, 100 m), a site where A. F. Mark (pers. comm.) has routinely observed annual flowering. At Mt Hutt, 1998 was a low flowering year for *C. pallens* following the moderate effort in 1997, and predation was relatively high (49.8% of all florets).

Inflorescence sampling and environmental description

A 5 m × 5 m quadrat was positioned at each site randomly (using random number tables to generate coordinates), and one inflorescence was haphazardly sampled for dissection from each *Chionochloa* tussock and placed in a separate paper bag. The species and number of inflorescences per tussock were recorded per sample. If fewer than 15 flowering tussocks were present in a quadrat, inflorescences from the area directly surrounding the quadrat were also sampled where possible, until a sample size of at least 15 was obtained. This was not possible in some instances, due to late or scarce flowering (HPT1–2, $n = 8$; BRU3, $n = 7$; BRU1, $n = 6$; TAR1–3, HTK1–3, HPIN $n = 5$ for each). Inflorescences were placed in sealed bags and frozen as soon as possible (maximum delay 3.5 days). A further selection of inflorescences were sampled and isolated at room temperature in the laboratory to allow floret predators to develop into adults. For every quadrat, the density of tussocks, density of inflorescences, slope, aspect, and altitude were also recorded, and a soil core was placed in a sealed plastic bag and later dehydrated at 115°C for 36 hours to measure percentage soil moisture.

The same procedures were applied to the HTTR samples, taken at 2.5-m intervals along a 50-m transect from the swamp quadrat HTS1 towards the slope quadrat HTS3. Twenty-five inflorescences were haphazardly sampled from the Pukerau site, one inflorescence per tussock. Altitudes at Stewart Island and Mt Taranaki were corrected for latitude in subsequent analyses using the latitude curve for tree line altitude (Newsome 1987).

Estimating floret predation

Frozen inflorescences were thawed for dissection and the number of spikelets was recorded for each.

One *Chionochloa* inflorescence contains 30–80 spikelets, each of which contains 3–9 florets with one ovary per floret. All florets from 10 randomly selected spikelets from each inflorescence were dissected open, to give on average 58 florets sampled per inflorescence (excluding the undeveloped florets terminating most spikelets). In the rare instance where the majority of spikelets were incomplete (due presumably to loss of florets on maturity), additional spikelets were selected until at least 35 florets per inflorescence had been dissected. In total, 14 995 florets were dissected from 259 plants within 23 quadrats and one transect.

Florets were classified as eaten, healthy, or unhealthy. A measure of the average stage of floret development for each inflorescence was gained by calculating the mean stage of development of healthy florets, using the scores given under (b) below. Dehiscing anthers occurred rarely and so are given a reduced score increment of 0.5 rather than 1.0. Each floret was assigned to one of the following, mutually exclusive, categories.

(a) Eaten florets:

- (i) *Megacraspedus calamogonus* caterpillar present.
- (ii) Empty florets preyed upon by *M. calamogonus*, containing caterpillar frass (large and off-white) and/or caterpillar remains (usually a head capsule).
- (iii) Eulophid parasitoid larva/pupa present (usually associated with *M. calamogonus* remains).
- (iv) Green *Diplotoxa similis* larva/puparium present.
- (v) Orange cecidomyiid larva present.
- (vi) Empty eaten florets, with unidentified feeding signs (stained lemma or palea, chewed remains of ovary and/or anthers).
- (vi) Floret infected with ergot fungus.

(b) Healthy florets:

- (i) green anthers and small green undeveloped ovary (development score = 1).
- (ii) yellow/red anthers and small green ovary (score = 2).
- (iii) dehiscing anthers and small green ovary (score = 2.5).
- (iv) small green ovary with anthers shed (score = 3).
- (v) large green ovary, over half the length of the palea (score = 4).
- (vi) firm, brown seed (score = 5).

(c) Unhealthy florets:

- (i) very small, shriveled, translucent ovary.

- (ii) small brown/yellow ovary, often not turgid.
- (iii) large brown/yellow ovary, often not turgid, sometimes with blotches of a white mold.

Statistical analysis

Chionochloa species was tested as the sole predictor of floret predation levels using generalised linear models (GLMs) with a binomial distribution and logit link function (Dobson 1983), performed on GENSTAT (GENSTAT Committee 1987). The predictive power of the measured environmental variables in explaining variations in floret predation was estimated with multiple regression generalised linear models (with binomial distributions and logit link functions), both for biotic and abiotic variables separately and for all variables combined, with species being forced last into each model. Where necessary, skewed variables were first log transformed. The degree of interaction between environmental variables was determined by Spearman rank correlation analyses and Kruskal-Wallis (K-W) non-parametric one-way Anovas (the latter for comparisons including species) using Statistix Version 4.0 (Siegel 1992). K-W Anovas were also used to test the significance of predation differences between species at particular sites.

RESULTS

Floret predators

All three insect floret predator species previously recorded in the literature were found feeding on floral parts and seeds of florets of *C. flavescens*, *C. pallens*, and *C. rubra*. These were caterpillars of *Megacraspedus calamogonus* Meyrick (Lepidoptera: Gelechiidae) (as recorded by White (1975) and Kelly et al. (1992)); pupae and green larvae of *Diplotoxa similis* Spencer (Diptera: Chloropidae) (Spencer (1977), as recorded by White (1975)); and orange larvae of an undescribed species (Diptera: Cecidomyiidae, R. J. Gagne pers. comm.) (as recorded, under various identifications, by Burrows (1961), Mark (1965a), White (1975), and Kelly et al. (1992)). Kelly et al. (1992) incorrectly identified the orange cecidomyiid larvae as *Diplotoxa similis*. All three larvae have been reared to adults and identified, with the assistance of T. Crosby, J. Dugdale, and R. J. Gagne who confirmed that the cecidomyiid is an undescribed species. Only *M. calamogonus* is known to infest non-*Chionochloa* hosts, occurring also in the inflorescences of *Cortaderia* species (Meyrick 1885; Hudson 1928).

A hymenopteran parasitoid species of *M. calamogonus* was also found, of the Eulophidae (J. W. Early pers. comm.), represented by white larvae and black pupae associated with shrivelled caterpillar remains within florets, and by reared adult wasps. White's (1975) association of eulophid parasitoids with *D. similis* due to similar adult emergence times may be incorrect. No parasitoids were found associated with the larvae and pupae of *Diplotoxa similis* or the undescribed cecidomyiid.

Nymphal instars of a species of thrips were also commonly found associated with florets, both inside and out. Reared adults were identified as of the Terebrantia: Thripidae: Thripinae using the key of Mound & Walker (1982). The distribution of 455 thrips nymphal instars found inside 4878 florets sampled from Mt Hutt saddle sites was not independent of floret condition ($P < 0.001$, $\chi^2 = 316.0$, d.f. = 13, by a variance test for homogeneity of the binomial distribution (Snedecor & Cochran 1980)), with thrips most likely to occur in florets containing shrivelled, small, or large unhealthy ovaries (11%, 27%, and 31% of such florets, respectively, and <9% in each category of healthy florets). No causal relationship was demonstrated, although thrips damage to grass florets is well known for grain crop species (Lewis 1973). Because of the inconclusive causal link between thrips abundance and unhealthy ovaries, and the ease with which thrips were able to move between florets after sampling, potential thrips predation is not included in the results or further analyses.

An ergot fungus was found in florets in three quadrats (POR1, HTK1, and HTK2), where it affected very few florets (0.3%, 4.5%, and 0.3% of florets, respectively).

There was considerable variation in floret predation among sites and *Chionochloa* species, both in total predation (Fig. 2) and in the relative abundances of the three insect predator species (Tables 1 and 2). Total predation varied from 98.3% of *C. rubra* florets in the Kettlehole bog quadrat to 6.8% of *C. pallens* florets in one of the Mt Bruce quadrats, and only 0.6% of *C. rubra* florets at Mt Taranaki.

Variation in floret predator abundances with inflorescence development

For the three *Chionochloa* species combined, the presence of the three floret predator species was found to vary significantly with the mean stage of development of florets per inflorescence ($P < 0.0001$, $F = 56.86$, d.f. = 332, K-W Anova). *Megacraspedus calamogonus* caterpillars (as op-

Table 1 Overall *Chionochloa* species differences in mean percentage floret predation per inflorescence for each predation category, and their significances in generalised linear models (binomial error distribution and logit link function, d.f. = 227). ns, not significant; **, $P < 0.01$.

Species	Mean % floret predation				Total predation
	<i>Megacraspedus calamogonus</i>	<i>Diplotoxa similis</i>	Unidentified cecidomyiid	Empty predated florets	
<i>Chionochloa flavescens</i>	7.4	0.8	3.8	41.7	54.0
<i>Chionochloa pallens</i>	2.4	1.0	2.8	15.2	21.7
<i>Chionochloa rubra</i>	7.4	0.8	1.4	37.6	47.8
F value and significance	5.69**	(0.03, ns)	5.47**	8.06**	6.82**

Table 2 Significant partial R^2 values of generalised linear model analyses (binomial distribution and logit link function), showing the influence of biotic (plant) and abiotic environmental variables and species on *Chionochloa* floret predation and on *Megacraspedus calamogonus* parasitism. Sites TAR1–3 are excluded from all analyses, and transect HTTR from the biotic analysis, because of missing predictor values. Variables labelled “log” were ln transformed to correct for skewed distributions. –, non-significant ($P > 0.05$); *, $P < 0.05$; **, $P < 0.01$.

Environmental variable	Floret predation			Caterpillar parasitism	
	<i>Megacraspedus calamogonus</i>	<i>Diploptoxa similis</i>	Unidentified cecidomyiid	Empty predated florets	Total
Biotic:					
Inflouescence development stage	–	–	0.184**	0.203**	0.188**
Density of plants (m^{-2})	0.088**	–	0.015*	0.030**	0.052**
Log density of inflouescences (m^{-2})	–	–	–	0.055**	0.020*
Log inflouescences per plant	–	–	–	0.016*	–
Log spikelets per inflouescence	–	–	0.050**	–	–
Mean florets per spikelet	–	–	–	0.018*	–
Species (forced last)	0.076**	–	0.075**	0.071**	0.071**
plus:					
Total fit: biotic variables including species (d.f. = 198)	0.193	0.057	0.333	0.400	0.355
Abiotic:					
Altitude (latitude corrected) (m)	–	–	0.192**	0.403**	0.373**
Sine (Aspect)	0.192**	–	–	0.066**	0.090**
Cosine (Aspect)	–	–	0.029**	–	–
Slope (°)	0.164**	0.128**	0.138**	0.056**	0.062**
Soil water (% weight)	0.161**	–	–	0.034**	0.086**
Species (forced last)	–	0.088**	0.038**	–	0.011*
plus:					
Total fit: abiotic variables and species (d.f. = 217)	0.523	0.236	0.398	0.569	0.623
Species (forced last) when all variables combined	–	0.094**	0.042**	–	–
Total fit: all variables combined (d.f. = 198)	0.567	0.420	0.560	0.694	0.733
					0.338
					0.095**
					0.085**
					0.031*
					0.213
					0.056**
					0.138

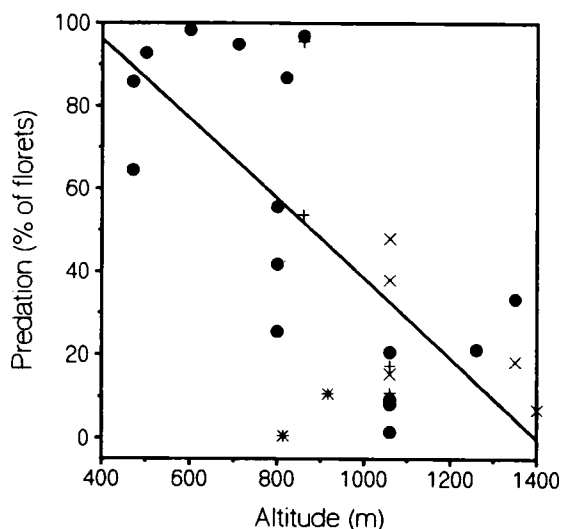


Fig. 2 *Chionochloa* total floret predation in eighteen 5 m \times 5 m quadrats throughout inland Canterbury and four outside Canterbury in 1993 for *C. rubra* (● Canterbury; * elsewhere), *C. pallens* (×) and *C. flavesceus* (+), in relation to altitude. Each point represents the percentage pre-dispersal seed predation in a random selection of florets from multiple inflorescences of one species within a single quadrat. The linear regression line shown is for the Canterbury *C. rubra* data only ($n = 16$, $y = 135 - 0.096x$, $R^2 = 0.52$, $P < 0.01$) but is also significant for all sites and species ($n = 27$, $y = 128 - 0.091x$, $R^2 = 0.45$, $P < 0.001$). Site altitude is corrected for latitude for sites outside Canterbury.

posed to vacated caterpillar-eaten florets included in the above analyses) occurred mostly in inflorescences in which healthy florets still contained mature anthers (mean \pm s.e. floret development stage of 2.6 ± 0.7 , $n = 19$). *Diplotoxa similis* larvae and puparia occurred in inflorescences with more developed florets, mostly in those with small green ovaries (mean floret development stage of 3.1 ± 0.8 , $n = 49$). The undescribed cecidomyiid larvae occurred latest, in well-developed inflorescences containing large green ovaries or hardened seed (mean floret development stage of 3.7 ± 0.6 , $n = 40$). *Chionochloa rubra* suffered significantly less predation only by the undescribed cecidomyiid (Table 1), but overall *C. rubra* also had significantly less-developed inflorescences (mean floret development stage = 2.9 ± 0.8 , $n = 123$) than *C. flavesceus* (3.7 ± 0.6 , $n = 18$) and *C. pallens* (3.6 ± 0.7 , $n = 31$) ($F = 14.03$, $P < 0.0001$, d.f. = 188). When inflorescence development stage was forced before species into a two-variable generalised linear model of cecidomyiid

predation, inflorescence development explained 21% of the variation in predation, and the species effect became nonsignificant ($F = 62.25$, $P < 0.01$, and $F = 2.34$, n.s., respectively, d.f. = 227). The reduced *C. rubra* predation by the undescribed cecidomyiid observed may therefore be attributed to the later development of *C. rubra* inflorescences. In a GLM of cecidomyiid predation using all variables, inflorescence development stage was the most powerful predictor variable (partial $R^2 = 0.184$), above altitude (partial $R^2 = 0.046$), cosine(aspect) (partial $R^2 = 0.123$), and slope (partial $R^2 = 0.109$). Inflorescence development stage is significantly negatively correlated with altitude, cosine(aspect), and soil moisture ($P < 0.05$).

This variation in floret predator phenology may have important implications for competition between the three insect species. In inflorescences containing many *Megacraspedus*-eaten florets, cecidomyiid larvae were rare, and vice versa ($\chi^2 = 20.58$, $P < 0.001$). The same pattern was evident with *Megacraspedus* and *Diplotoxa*.

Chionochloa species differences in floret predation

Over all sites, although total predation did differ significantly between *Chionochloa* species, *C. rubra* suffered intermediate levels of predation (Table 1). There were significantly more *M. calamogonus* and empty eaten florets of *C. rubra* than *C. pallens*, and *C. rubra* suffered significantly less predation only by the undescribed cecidomyiid (Table 1) although, as explained above, this last effect was nonsignificant when allowance was made for floret development.

This generalisation that *C. rubra* populations suffered comparable or higher predation frequencies than *C. pallens* and *C. flavesceus* applied to all sampled interdigitating populations. On Mt Bruce, the 1260-m *C. rubra* quadrat (BRU1) experienced significantly greater total predation than the 1400-m *C. pallens* quadrat (BRU3) ($P = 0.0124$, $F = 8.92$, d.f. = 12, K-W Anova), a trend maintained in the 1350-m mixed species quadrat (BRU2). This was despite *C. rubra* having inflorescences with less developed florets. When the Mt Hutt saddle area was first sampled in mid February, total floret predation differed significantly between quadrats, being greatest in the transition zone (HTS2) between the *C. rubra*-dominated swamp and the *C. pallens*-dominated slope, and least in the swamp (HTS1) ($P < 0.0001$, $F = 34.41$, d.f. = 39). Over the three sites, *C. pallens* suffered higher predation than *C. rubra* ($P = 0.0004$,

$F = 14.79$, d.f. = 39). However, at this time *C. rubra* had significantly less advanced inflorescences than *C. pallens*, both over all sites ($P < 0.0001$, $F = 53.01$, d.f. = 39) and for the scattered *C. rubra* growing amongst the *C. pallens* of HTS3 ($P = 0.0037$, $F = 12.95$, d.f. = 13). When HTS1 was re-sampled one month later (HTSB), and *C. rubra* inflorescences were almost as advanced as *C. pallens* had been a month earlier, there was no longer any significant difference in total predation between these species ($F = 0.92$, d.f. = 28). However, *D. similis* and the undescribed cecidomyiid were still significantly rarer in the *C. rubra* swamp ($P = 0.0101$, $F = 7.65$, and $P < 0.0001$, $F = 30.72$, respectively, d.f. = 28) (Fig. 2). At Porter River, *C. rubra* dominated the river margin quadrat (POR2), and *C. flavesceus* was the only *Chionochloa* species on the slope immediately adjacent (POR3). Total floret predation was significantly higher in POR2 than POR3 ($P < 0.0001$, $F = 34.37$, d.f. = 28), mainly due to an increased proportion of *M. calamogonus* and empty eaten florets.

Altitude and other abiotic environmental effects on floret predation

Monospecific lowland *C. rubra* populations did not suffer less predation than higher *C. rubra* populations. Rather, there was a strong significant increase in total predation with decreasing altitude (Fig. 2). For example, the six *C. rubra* sites below 800 m elevation lost $88.9 \pm 5.2\%$ of their florets (mean \pm s.e.) to seed predator insects, while the six *C. rubra* sites above 1000 m lost $15.8 \pm 4.7\%$ of florets. This altitude effect was evident for the cecidomyiid larvae and empty eaten florets, but no significant effect of altitude was found for *Megacraspedus* or *Diplotoxa* alone (Table 2). However, an altitude effect on *Megacraspedus* floret predation is still likely, as most of the empty eaten florets were probably caused by *Megacraspedus* (being both the most abundant and most mobile of the floret predators, and occurring in the youngest florets). The data from Pukerau (100 m a.s.l.) are not shown in Fig. 2 as a high percentage of empty florets (55.8%) made it impossible to give an exact estimate of predation. Both *Megacraspedus* and the undescribed cecidomyiid were present at Pukerau, and predation was between 39.7% (if empty florets had all dispersed seeds) and 95.5% (if empty florets were all cryptic predation).

When combined in a generalised linear model (GLM) for all *Chionochloa* species, the abiotic environmental variables consistently explained more

of the variation in floret predation than the plant biotic variables (Table 2). Floret predation was significantly less in wetter sites (where *C. rubra* is most abundant), but this effect was not strong, explaining only 0.9% of the variation in floret predation in the GLM (Table 2). A similar weak, significant effect was seen for temperature, with north-facing (warm) sites experiencing significantly more floret predation than south-facing (cool) sites (Table 2). Altitude is by far the best single environmental predictor of *Chionochloa* total floret predation, explaining 37% of the variation in floret predation in this study (Table 2).

When all abiotic environmental variables were included in a GLM, and *Chionochloa* species forced last, a significant residual species effect remained for all the predation categories except *Megacraspedus* and empty eaten florets (probably mostly *Megacraspedus*) (Table 2). *C. rubra* therefore experienced significantly more total floret predation than *C. pallens*, and significantly less predation by the dipterans than *C. pallens*. All abiotic and biotic environmental variables in combination (including plant species) explained 73% of the variation in total floret predation (Table 2).

Parasitism of floret predators

If parasitism frequencies increase with decreasing altitude, this could potentially offset the increased abundance of floret predators at very low altitudes. The only parasitoid species we found was a eulophid wasp that fed in *Megacraspedus* caterpillars, and at no sites was this species abundant (it was never above 2% of florets). Although no parasitoids were found in any quadrat above 880 m, overall there was no significant altitude effect on eulophid parasitoid abundance (Table 2).

DISCUSSION

Contrary to our prediction, low elevation *C. rubra* populations experienced much greater pre-dispersal seed predation than high elevation *C. rubra* populations (Fig. 2). Furthermore, it is likely that seed predators were being satiated at the high elevation but not the low elevation sites during 1993, the year of primary sampling. In *C. pallens* at 1070 m on Mt Hutt, there was a 20-fold increase in floret density between 1992 and 1993 (Kelly & Sullivan 1997). This was sufficient to strongly satiate the seed predators, producing 18.3% seed predation, the second lowest annual seed predation in 10 years

(Kelly & Sullivan 1997). Seed predation across the six *C. rubra* sites above 1000 m sampled in this study was similarly low in 1993 (mean = 15.7%), and these populations may also have been satiating their resident seed predator populations that year. In striking contrast, the six *C. rubra* sites below 800 m elevation lost 88.9% of their florets to seed predator insects (Fig. 2). These data suggest that, during 1993, seed predators were not being satiated in these low elevation populations. Furthermore, years of high *Chionochloa* seed set are closely correlated across *Chionochloa* species and altitudes (Mark 1968; Kelly et al. 1992; Kelly & Sullivan 1997; Kelly et al. 2000), and it is likely that, despite the lack of predator satiation, 1993 was also a good flowering year for these low elevation populations. The data from our lowest elevation site (Pukerau, 100 m) in 1998 also showed high levels of predation, further refuting the hypothesis that low altitude *C. rubra* populations are not heavily attacked by seed predators.

Despite this observation of high seed predation at low elevations, the annual flowering effort of *C. rubra* populations is much more variable at high elevation than low elevation sites (Mark 1968; McKone et al. 1998; Bycroft 1999; Kelly et al. 2000). These two observations are contradictory in light of the predator satiation hypothesis, as mast seeding behaviour is most likely to arise and persist in populations and species which experience the heaviest seed predation (Silvertown 1980). This presents a reproductive paradox: why does *C. rubra* not have more variable seed production (a higher CV) at lower elevations, rather than higher elevations? We cannot resolve this paradox, but list several possible explanations which could be tested in future.

(a) *Failure of C. rubra to form temperature ecotypes.*

Flowering effort in *Chionochloa* is determined by temperature the previous summer (Mark 1965a; Connor 1966; McKone et al. 1998; Kelly et al. 2000). This relationship is quantitative but for terminological simplicity it may be regarded as a threshold temperature for heavy flowering. In *C. rigida* the critical temperature for induction of high flowering varies among altitudinal ecotypes (Mark 1965b), perhaps slightly modified by environmental plasticity (Greer 1979). In the absence of such ecotypic variation or plasticity, all populations of a species would have the same critical temperature, which would be exceeded more frequently at lower elevations, resulting in more regular flowering at lower elevations (and

hence CVs proportional to altitude). In such a case, the single overall critical temperature for heavy flowering would represent a selective tradeoff. A high critical temperature would give variable flowering at low altitude, thereby reducing seed predation there, but severely limit the number of flowering years at high altitudes. On the other hand, a low critical temperature would allow more frequent reproduction at high altitudes, where seed predation is in any case less important, but result in constant flowering and associated higher seed predation at low elevations. The critical temperature is likely to be set at an intermediate level, and therefore predator satiation is likely to break down at the lower elevation limit of the plant species.

The altitudinal variation in flowering CVs for *C. rubra* suggest that it does not have pronounced altitudinal ecotypes. This leads to the question of why *C. rubra* should not form ecotypes when *C. rigida* does. All *Chionochloa* species are thought to be largely outbreeding (McKone et al. 1997; Tisch & Kelly 1998) so they should not vary in the rate at which ecotypes could evolve (Greer 1979). However, *C. rigida* is the only *Chionochloa* species where ecotypes have been demonstrated, and even there the evidence is of small effects. Mark (1965b) used reciprocal transplants of "*C. rigida*" from four sites, but the high-altitude ecotype he identified at his upper site has since been erected as a different species, *C. macra* (Greer 1979). There were large differences in temperature sensitivity between *C. macra* and the lower three sites, but "the three low-altitude populations [i.e., the *C. rigida* ones] . . . are only poorly differentiated in their temperature control of flowering" (Mark 1965b, p. 296). Greer (1979) re-transplanted surviving tussocks 15 years after Mark had first moved them and again found evidence for altitudinal ecotypes, but the pattern was somewhat unclear, with variable effects of source site, conditioning location 1960–74, transplant location post-1974, and flowering year. Greer (1979) said that the data showed some acclimation to local climates during the conditioning period, which would suggest that temperature thresholds are not totally fixed in adult plants, but the data in the paper are somewhat ambiguous. Overall the evidence suggests that altitudinal ecotypes do exist in *C. rigida*, but they are relatively poorly differentiated. In fact, we would predict that weak development of altitudinal ecotypes should be the rule rather than the excep-

tion, as altitudinal gradients often occur over such short horizontal distances that frequent gene flow should hinder the development of ecotypes. Environmental plasticity should also be uncommon as it requires the plants to alter the critical temperature for flowering based on local average temperatures over the last 5–10 years, a difficult task. In *C. rubra* the evidence is consistent with the absence of ecotypes or plasticity, but only transplant experiments with this species would provide a definitive answer.

- (b) *Satiation is ineffective at low altitudes.* Mast seeding at low elevations will be ineffective if the seed predator insects in low elevation habitats are much more difficult to satiate (McKone et al. 2000). For example, *Megacraspedus calamogonus* may be bivoltine in low elevation habitats, which would allow *M. calamogonus* populations to respond to years of high seed set through a second generation. Hudson (1928) considered *M. calamogonus* to be at least bivoltine on its less common lowland *Cortaderia* species hosts, and although White (1975) considered a multivoltine life cycle unlikely in masting populations of *Chionochloa* in Porter River (800–900 m), our study did find one *M. calamogonus* pupa in a *C. rubra* floret at 800 m at Mt Hutt as early as 26 January 1993, while seed set did not occur until March. This hypothesis cannot be discounted.
- (c) *Masting has greater disadvantages at lower altitudes.* There are many disadvantages to mast seeding, including density-dependent seedling competition, seedling predation, or pathogen attack (Hett 1971; Augspurger 1981; Kelly 1994), and lost opportunities for reproduction (Waller 1979). If one or more of these disadvantages is particularly prevalent in low elevation *Chionochloa* populations, then they could negate the satiation advantages of mast seeding and favour populations with lower reproductive CVs. For example, if early seedling survival is much higher at low elevations than high elevations, then intraspecific seedling competition and density-dependent mortality will be much more important at low elevations. This is also a plausible hypothesis for *C. rubra*.
- (d) *Recent increases in low altitude predation.* The high seed predation observed in low elevation populations could be a historically recent phenomenon as a result of human-induced alterations to the habitat and biota, which have been most severe in the lowlands. In this case there would not have been time for low elevation CVs to reach

selective equilibrium with local levels of predation. However, this seems unlikely given that many of the high elevation sites in this study, including all sites at Mt Bruce, Mt Hutt, and Porter River, are also secondary grasslands which have replaced the *Nothofagus solandri* forests that were cleared within the last few hundred years by human fires. The suggestion that high seed predation at low elevations is a historical artifact is further questioned by the observation that *C. rubra* in the most pristine site sampled, that of Andrews River (710 m) in Arthur's Pass National Park, also suffered very high seed predation (94.9%).

- (e) *Recent decreases in low altitude flowering variability.* The more constant flowering in *C. rubra* at low altitudes may be a historically recent phenomenon. If temperature ecotypes do exist in *C. rubra*, and the lowland populations of *C. rubra* were devastated by human farming activities and replaced by immigration from higher altitude ecotypes, then the populations establishing at lower elevations would flower more regularly than at their native elevation. However, this explanation requires both the presence of ecotypes, and large scale extirpation and immigration of *C. rubra* populations. We think this scenario is very unlikely.

In conclusion, the geographical disjunction in *C. rubra* between high CVs and high seed predation is a reproductive paradox. Higher reproductive CVs with increasing elevation is a general pattern among mast seeding plants (Webb & Kelly 1993), and increasing seed predation at lower elevations (as in *C. rubra*) is also often reported. If seed predation is often higher at low elevations in mast seeding species, then resolving this reproductive paradox is important not just in *Chionochloa*, but in masting species generally. Of the possible general resolutions to the paradox, there is evidence in some species for lower predation at low elevations (e.g., Randall 1986), but the other three most plausible hypotheses (failure of plants to develop altitudinal ecotypes; lowland populations of seed predators are more difficult to satiate; or greater disadvantages to masting at low elevations) are scarcely examined. We predict, firstly, that altitudinal temperature ecotypes will be rare in masting plant species. Secondly, we predict that predator satiation will be often found to break down at the lower elevation limits of mast seeding plant species. This means that the elevational range of some masting plants may be limited downwards by very high levels of seed predation, rather

than competition with other plant species or inability of the plants to grow at high temperatures. Testing of these hypotheses and predictions on any masting species would be illuminating.

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