

# Causes and consequences of frequent flowering on edges in the mast-seeding genus *Chionochloa* (Poaceae)

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**Abstract:** Recent work has shown that resource accumulation is important in allowing mast-seeding plants to display occasional intense reproductive efforts. Anecdotal reports suggest that *Chionochloa* tussocks (bunchgrasses) on patch edges flower more frequently, and it has been proposed that this is due to greater resource availability. This study aimed to quantify any edge effect in flowering effort in *Chionochloa* populations at Mt Hutt in the Southern Alps of New Zealand, and to look for correlations with available soil nutrients. It also focused on how higher flowering along edges might affect seed predation rates in these plants, since seed predation is recognised as the likely cause of masting in this genus. As predicted, in a generally low-flowering year flowering was found to be most prolific on upslope edges across a range of altitudes with at least 43% of the flowering effort in the upslope plots being concentrated in the 20% of plot area within 2 m of the upper edge. Upslope edges also exhibited higher nitrate availability than did patch interiors or downslope edges. However, other measured nutrients did not show such a clear pattern. The elevated flowering effort on upslope edges does support the importance of a resource accumulation component in flowering effort. Higher edge-flowering did not significantly affect the distribution of the insect seed predators, suggesting the scale at which these insects move in search of oviposition sites is greater than the scale of the vegetation patches studied.

**Keywords:** edge effects, masting, nitrogen, resource models, seed predation

## Introduction

The causes and implications of mast seeding (the synchronous intermittent production of large seed crops by a population of plants; Kelly 1994) are still the focus of much research and speculation. Mast seeding is a common phenomenon, being displayed in a large number of species and a variety of habitats (Silvertown 1980; Kelly 1994; Herrera et al. 1998). It is especially prevalent in the mid-latitudes of the Southern Hemisphere (Kelly & Sork 2002), and in the New Zealand flora (Webb & Kelly 1993), including members of the snow-grass genus *Chionochloa*. The prevalence of the masting strategy occurs despite several apparent evolutionary disadvantages, most obviously (1) missed opportunities to reproduce (Waller 1979), and (2) high density-dependent seedling mortality in years of high seed production (Hett 1971; Kelly & Sork 2002). The fact that masting remains a relatively common evolutionary strategy despite these apparent evolutionary disadvantages implies that these factors must be offset by significant adaptive advantages, most notably benefits through predator satiation (Kelly 1994; Kelly & Sork 2002) and/or increased pollination efficiency during mast years (Burd 1994; Kelly & Sork 2002).

The genus *Chionochloa* is represented in New Zealand by 23 endemic species of tussock-forming snow grasses (Connor 1991; Connor & Lloyd 2004 for a synopsis of the biology and masting behaviour of *Chionochloa* see Rees et al. (2002)). All *Chionochloa* species for which data are available exhibit mast seeding behaviour, and in general *Chionochloa* exhibit perhaps the highest average coefficient of variation ( $CV = \text{standard deviation}/\text{mean}$ ) in flower production of any masting genus worldwide (Kelly et al. 2000). *Chionochloa* species also exhibit a high degree of intraspecific and interspecific synchronisation (Kelly et al. 2000; Schaubert et al. 2002), which appears to be achieved through a temperature cue consisting of warmer-than-average summer temperatures the year before flowering (McKone et al. 1998; Rees et al. 2002). This has led to predictions that masting in *Chionochloa* could be disrupted by global climate change (McKone et al. 1998).

Seed predator satiation appears to be the main evolutionary driver for masting in *Chionochloa* (Kelly & Sullivan 1997; Kelly et al. 2000). Three insect species have been reported as *Chionochloa* seed predators: a moth (*Megacraspedus calamogonus*: Gelechiidae) and two flies (*Diptotoxa similis*: Chloropidae and *Eucalyptodiplosis*

*chionochloae*: Cecidomyiidae; McKone et al. 2001; Kolesik et al. 2007). These insects can inflict significant seed losses, with usually >50% and sometimes up to 94% of florets showing damage in different years (White 1975; Kelly et al. 1992). All three insects are widespread and appear to attack all species in the genus (McKone et al. 2001; McCall et al. 2004). Mast flowering has been shown to confer significant benefits on *Chionochloa* through predator satiation, through both the maintenance of lower predator numbers due to the low-flowering years and the swamping of predators during mast years, making this the favoured hypothesis to explain masting in the genus (Kelly & Sullivan 1997; Kelly et al. 2001). Conversely, *Chionochloa* species appear to receive very little benefit from increased wind pollination in mast years, since they only experience pollen limitation in extremely low flowering years (Kelly & Sullivan 1997) and through experimental manipulation (Tisch & Kelly 1998). There may be some masting pollination benefits through increasing outcrossing and reducing inbreeding depression (Tisch & Kelly 1998) but these have not yet been properly explored.

Recent modelling work, focused on the mechanisms of masting in *Chionochloa pallens* Zotov, showed a need for a resource storage component in individual plants, pulsed by a weather cue to accurately predict observed flowering patterns (Rees et al. 2002). This modelling suggests rate of accumulation of resources affects when a plant will next be able to flower. In their general discussion of mast seeding, Kelly and Sork (2002) also predict more frequent flowering in sites with higher resource availability. Resource accumulation rates should vary among plants in a population depending on their access to water, light and nutrients, and the levels of competition in their immediate neighbourhood.

Plants growing on edges are exposed to significantly different conditions to those experienced in the interior of vegetation patches. Edges are subjected to different microclimatic conditions than the interior of vegetation patches, including higher light, greater temperature variability, and lower moisture availability (Jose et al. 1996; Redding et al. 2003; York et al. 2003). Soil nutrient levels are also likely to vary between the edge and the interior (Murcia 1995). Competition for these resources is also reduced, since individual plants are not surrounded by competitors on all sides. These conditions can lead to enhanced growth of edge plants (York et al. 2003). If plants on edges are exposed to higher levels of a limiting resource, this can be expected to translate to increased ability to invest in reproduction (Montgomery et al. 2003). Therefore, plants on patch edges might be expected to be able to flower more frequently than plants in less favourable sites. In masting species, this is predicted to cause increases mainly in low-flowering years rather than high-flowering years (Kelly & Sork 2002; Richardson et al. 2005).

Burrows (1968, pp. 153–154) noted that for *Chionochloa* the ‘occasional plants which flowered in the field in “off” years were a) on eminences b) on scree edges or edges of erosion patches c) round deer carcasses’. Further to this he suggested (p. 154) ‘the factor...common to all these sites, is that they are probably places of higher fertility, at least in respect to some nutrients, than the surrounding areas...scree edges and similar sites are probably flushed by nutrients from weathered minerals and there is less root competition at such sites’. However, these factors raised by Burrows have not been formally tested.

### Aims of study

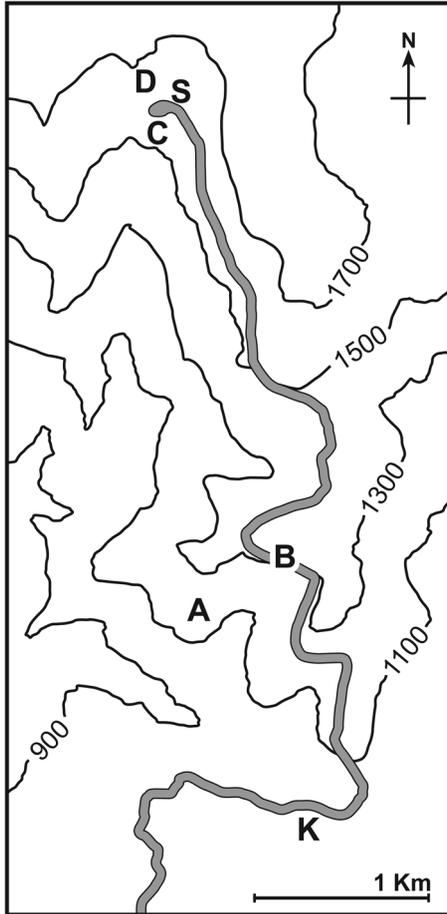
This study investigated four interrelated predictions of resource-based masting models for the distribution of flowering effort in *Chionochloa* during a low-flowering year.

- (1) That *Chionochloa* tussocks located on patch edges would be more likely to flower in a low-flowering year than plants in the interior of patches.
- (2) That any observed increase in flowering effort on patch edges should be associated with higher resource availability, since resource accumulation is crucial for flowering (Rees et al. 2002), and that this effect should be most pronounced on upslope edges where any nutrient flushing effect would be strongest, whereas it should be small or absent from downslope edges.
- (3) That this edge effect should be more pronounced at higher altitudes where resources are more strongly limiting due to the shorter growing season (Kelly & Sork 2002).
- (4) If flowering was more common on edges then seed predation rates should be higher among edge plants because insects would be able to be reared in the local vicinity in a larger proportion of years (Kelly et al. 2000).

## Materials and methods

### Study site and year

This study was carried out on the southern side of Mount Hutt, on the eastern edge of the Southern Alps, near the skifield access road. Study sites were located at each of four altitudes (1150 m, 1300 m, 1550 m and 1620 m above mean sea level; Fig. 1) spanning the range of dense snow-tussock vegetation on the mountain. All these sites had a similar southerly aspect (ranging between 150° and 230°), and similar slope (approximately 25°). This area is characterised by large patches of vegetation, interspersed with areas of bare soil and shingle scree. In the vegetated patches *Chionochloa* tussock grasses are the dominant vegetation type, with *C. macra* Zotov and *C. pallens* and their hybrids (McKone 1990) in various mixtures at different altitudes, but usually with *C. macra* being the more abundant.



**Figure 1.** Map of Mt Hutt skifield access road, showing the four study sites at (A) 1150 m, (B) 1300 m, (C) 1550 m and (D) 1620 m with contours at 200-m intervals, the skifield base station (S), and the site of previous long-term work (e.g. Rees et al. 2002) (K) at 1070 m.

At Mt Hutt 2003 was a low-flowering year for *Chionochloa*, with *C. pallens* at 1070 m (Site K, Fig. 1) averaging 0.55 inflorescences per tussock, the eighth-lowest year in the 21 years 1986–2006 (Kelly et al. 2000 and unpublished data).

### Flowering distribution

At each altitude eight plots ( $10 \times 4$  m) were mapped to investigate the spatial distribution of flowering effort. This took place between 29 January and 19 February 2003. Plots were located randomly along edges of tussock patches, with the longer axis of the plot extending into the patch

interior, at right angles to the edge of the patch. In all cases the interior end of the plot was located at least 10 m from any other edge. Four plots at each altitude were located on edges with bare ground upslope (upslope edges), while four had bare ground downslope (downslope edges). The upslope edges generally had bare shingle scree right up to the patch edge, while the downslope edges had a mixture of shingle and soil, which appeared to be strongly affected by freeze–thaw erosional processes (Gradwell 1960). Within each of these plots the distribution of tussocks was mapped, with note being taken of the basal diameter and number of inflorescences on each tussock. Tussock area and number of flowering shoots have been shown to accurately estimate pollen production (accounting for c. 90% of variation in pollen production; McKone 1990), while number of spikelets, florets per spikelet, and average anther length account for very little of the variation in pollen output. For the purposes of analysis, distance from the patch edge was aggregated into bands 1 m wide.

*Chionochloa pallens* and *C. macra* readily hybridise, producing hybrids whose morphological characteristics grade between the two parent species (McKone 1990; Kelly et al. 1992). Such hybridisation can cause trouble with identification (Connor 1991), meaning that unambiguous classification of these plants to species level in the field is not always possible. A preliminary analysis based on the lowest-altitude sites (where hybridisation is least prevalent; McKone 1990) showed no significant effect of species on flowering effort, after variation in basal area had been accounted for. Also, *C. pallens* and *C. macra* are known to flower in almost perfect interspecific synchrony at Mt Hutt (Kelly & Sullivan 1997; Kelly et al. 2000). On the basis of this information species identity was disregarded as a predictor of flowering distribution for the remaining altitudes.

### Nutrient availability

The question of nutrient availability in the different habitats was addressed using cation–anion exchange resin. Twenty soil resin bags ( $50 \times 50$  mm), resembling tea bags, were constructed using plastic mesh ( $365 \mu\text{m}$ ) screen. Into each of these bags 2.5 g of Dowex HCR-S (Sigma-Aldrich) and 2.5 g of Dowex SBR anion exchange resin were measured.

The resin bags were placed in the field site at 1300 m on 3 May 2003. They were buried approximately 80 mm beneath the soil surface. Six were buried at randomly located positions along an upslope edge, six along a downslope edge, and eight in the patch interior. They were located in the same patches used for the vegetation plots at that altitude, but were placed independently of the plot locations. Bags placed in edge habitat were buried on the very edge of the patch–bare-ground interface, but within the extent of overhanging foliage of the edge-most tussocks in the patch. The soil along the upslope edge had a considerably larger fraction of coarse gravel particles

than was the case in either of the other habitats. Overall the resin bags were spread over an area of approximately  $80 \times 80$  m. The resin bags were retrieved on 18 June 2003 (6.5 weeks after placement). All resin bags were placed into their own individual plastic zip-lock bags upon retrieval and were kept frozen until assayed.

The resin was removed from resin bags into individual plastic containers and eluted with 20 ml of  $1 \text{ mol L}^{-1}$  KCl, five times over a period of 2–3 hours. The eluted liquids were subsequently assayed for nitrate, ammonium, and phosphorous concentrations. Nitrate levels were assayed using the cadmium nitrate method (Sloan & Sublett 1966), ammonium was assayed using the method described in McCullough (1967), and the phosphorus assay is described in Hay (unpublished thesis, 2003; summarised in Appendix 1).

### Seed predation

To address the question of seed predation, inflorescences were collected from *Chionochloa* along upslope edges (where flowering was more abundant, see Results) and within patch interiors (at least 5 m from an edge) at each of the four altitudes, on 19 February 2003. Ten plants were sampled in each habitat at each altitude (except the interior habitat at 1620 m, where only eight flowering plants could be found). Every endeavour was made to ensure the 10 samples from each habitat were independent, by sampling tussocks over as broad a spatial range as possible, within the constraints of the altitude classes. In each case only one inflorescence was collected per tussock. These were cut from the plant, placed in individual paper bags, and frozen the same afternoon to reduce the chances of insect movement between florets. The inflorescences were then kept frozen until dissected. Note was also taken of the number of inflorescences within a radius of 1 m of the sampled inflorescence (including those on the same plant), and the species of tussock from which the inflorescence was collected.

Ten spikelets were selected at random from each inflorescence and all florets on these spikelets were opened under a dissecting microscope. One inflorescence from the edge at 1150 m had already shed the majority of its florets and was consequently excluded from further analyses. On average, 49 florets were dissected from each inflorescence. Each floret was classified according to the fate of the ovary (unpollinated, expanded, ripe, aborted) and according to any evidence of seed predator activity (see Cone 1995; McKone et al. 2001; Kolesik et al. 2007).

### Analysis

All analyses were performed using S-Plus (Insightful Corporation © 1988, 2001). Altitude was treated as a factor in all analyses involving measurements at multiple altitudes. The soil nutrient data were analysed using simple one-way ANOVAS, with the response (ion concentration),

in each case,  $\log(e)$  transformed to fulfil the assumptions of normality and homoscedasticity. Tukey tests were employed to investigate differences between groups, with an  $\alpha$  level of 0.05.

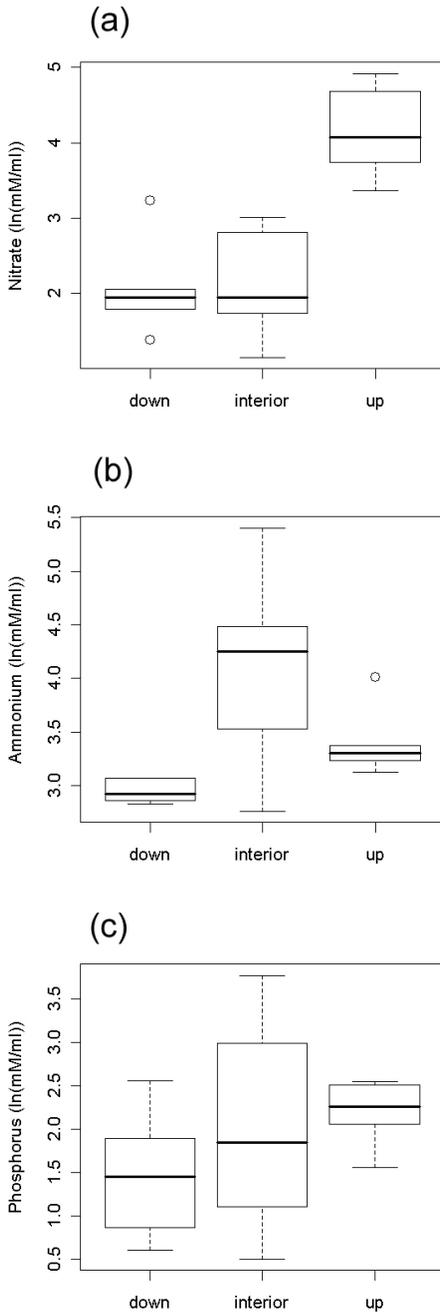
The flowering distribution data were analysed using a Poisson generalised linear model (GLM). Because the assumption of independence necessary for the use of the chi-squared distribution appeared to be breached, the fit of this model was tested using  $F$  ratios. This necessitated the use of a split-split-plot design in order to test the effect of each predictor against their appropriate error terms. Both altitude (which was treated as a factor) and habitat (upslope vs downslope) were replicated at the plot level. The appropriate error term for these was the altitude  $\times$  habitat  $\times$  plot interaction. The true level of replication of distance from the patch edge (and its interactions) was the total number of bands 1 m wide of distance from the edges of plots, calculated as the four-way interaction altitude  $\times$  habitat  $\times$  plot  $\times$  distance from edge (as a factor). Although distance was treated as a variate predictor in the model it had to be employed as a factor in the error term, in order to calculate the appropriate number of error degrees of freedom at this level. Basal area of plants was replicated by individual plant measurements, so basal area and all its interaction terms were tested against the residual error. The predictor, tussock basal area, was square-root transformed to improve its normality.

The seed predation data were analysed using binomial GLMs. In both cases significance was tested using the  $F$  distribution, since these data did not conform to the assumption of independence of the chi-squared distribution. The predictor, number of flowers within a radius of 1 m, was  $\log$  transformed to improve normality. Because the data collected with respect to *Chionochloa* species were not well balanced between the different habitats and altitudes, both species and the species  $\times$  habitat interaction were always entered into models after all other main effects and their interactions, to see if species could explain any residual variation.

## Results

### Nutrient availability

Levels of both the nitrogen compounds tested for varied significantly between habitat types (ANOVAS of nitrate concentration  $F_{2,17} = 22.24$ ,  $P < 0.001$  and ammonium concentration  $F_{2,17} = 7.66$ ,  $P = 0.004$ ). Nitrate levels were significantly higher (Tukey test  $\alpha = 0.05$ ) in the upslope edge habitat than in either of the other habitat types (Fig. 2a). Ammonium levels were lower along the downslope edge than in the interior habitat (Tukey test  $\alpha = 0.05$ ; Fig. 2b). However, levels at the upslope edge did not differ significantly from the other two habitats. Although the pattern for phosphorous levels (Fig. 2c) appeared to be similar to that seen in nitrate, no significant difference



**Figure 2.** Differences in nutrient levels, measured using soil resin bags. Measurements were taken on downslope edges (down), upslope edges (up), and patch interior (interior), for (a) nitrate, (b) ammonium and (c) phosphorus. All concentrations were log(e) transformed. The boxplot shows the 5, 25, 50, 75, and 95th percentiles with outliers as circles.

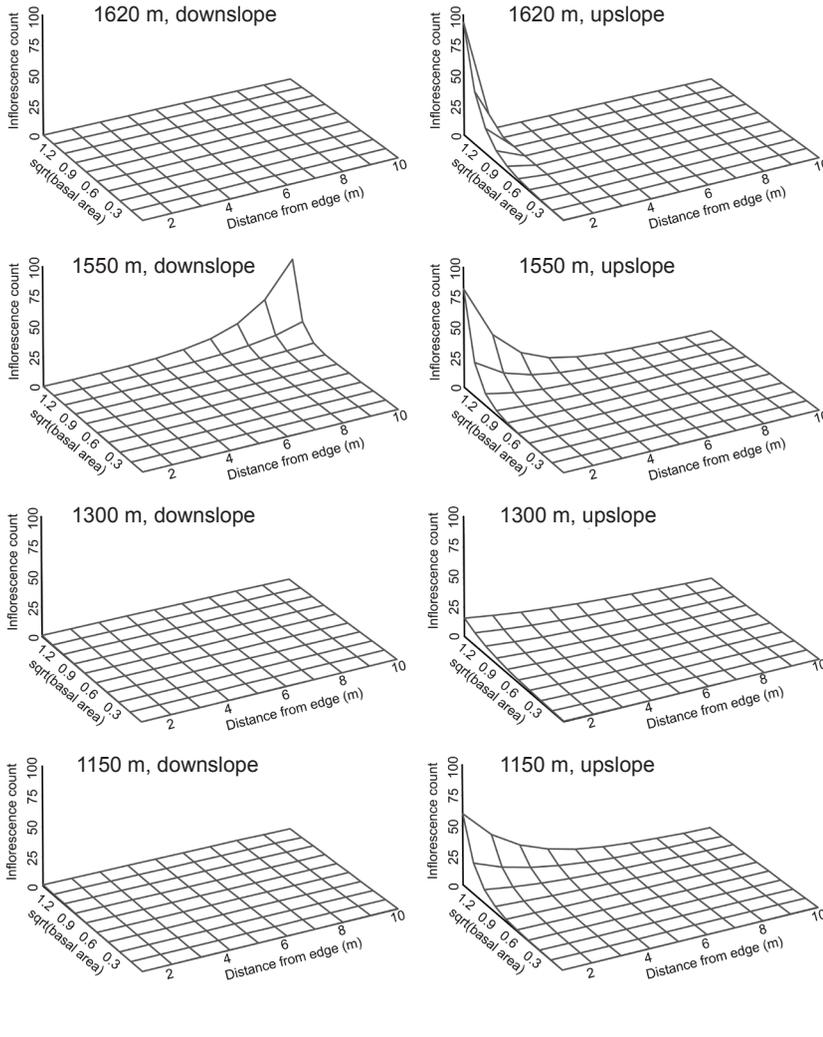
was detected between habitats (ANOVA of phosphorous concentration,  $F_{2,17} = 1.10$ ,  $P = 0.355$ ). However, a post-hoc power analysis indicated that the statistical power in this test was low ( $1 - \beta < 0.20$ ).

Unfortunately, when the resin bags were retrieved in June from the upslope habitat, the soil was frozen and had to be chipped away to retrieve the bags. This was not the case in the other two habitats, where only a thin layer of soil on the surface was frozen. Therefore, nutrient uptake in the ion exchange resin from the upslope sites may have been retarded to some extent by the cold conditions, with the result that the ambient nutrient concentrations may have been underestimated in the upslope habitat. Despite this limitation, however, nutrient concentrations appeared to be highest on upslope edges for nitrate and phosphorus, and lowest on the downslope edge for all nutrients measured.

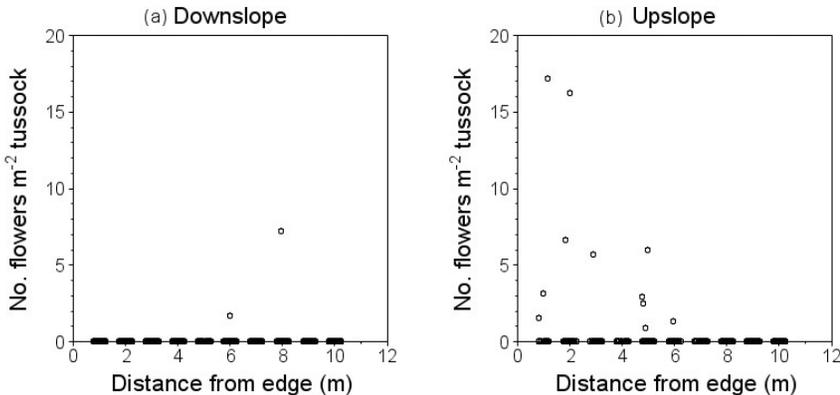
### Flowering distribution

Flowering varied significantly between altitudes and between upslope and downslope habitats (Table 1), being generally higher overall in the upslope plots. It also varied significantly with distance from the edge (Table 1). This relationship differed significantly between habitat types (distance  $\times$  habitat interaction; Table 1), typified by low and reasonably uniform levels of flowering in downslope plots, while flowering decreased with distance from the upslope patch edges. At least 43% of the flowering effort in the upslope plots was concentrated in the 20% of plot area within 2 m of the edge, at all altitudes. However, the strength of the overall distance versus flowering relationship did vary between altitudes (distance  $\times$  altitude interaction; Table 1), with a stronger decline in flowering with increasing distance from the edge in the higher altitude plots (Fig. 3).

Perhaps more interestingly though, the significant relationship between flower counts and basal area (essentially flowering effort per square metre of plant) also differed between altitudes (Table 1), but was independent of habitat type or distance from the edge overall. However, flowering effort per square metre of plant did respond differently to increasing distance from the edge in each of the two habitats, as evidenced by the last two interaction terms in Table 1 (i.e. basal area  $\times$  habitat  $\times$  distance and basal area  $\times$  altitude  $\times$  habitat  $\times$  distance interactions). This difference was expressed as an increase in flowering effort per square metre on upslope edges, which is well illustrated by the predicted flower count surfaces derived from the fitted model (Fig. 3). In these fitted surfaces the predicted flower count per square metre of plant is generally close to zero over the majority of the surfaces at all altitudes and habitats. However, there is a notable increase in the predicted flowering effort per square metre close to the patch edge in upslope habitats at all altitudes, seen as an upward curve in the predicted



**Figure 3.** Predicted surfaces of inflorescence counts, based on distance from edge and the square-root of basal area, for each altitude  $\times$  habitat combination. Downslope edges are on the left, upslope on the right, and rows are ordered by altitude. Surfaces are based on back-transformed predictions of the Poisson GLM fitted to the tussock-flowering dataset.



**Figure 4.** Relationship of flowering effort per square metre of tussock basal area with distance from patch edge at 1550 m (note: jitter has been added in the horizontal axis to make coincident data points more visible): (a) downslope (2 of 525 plants flowering), (b) upslope (11 of 333 plants flowering).

**Table 1.** ANOVA table of the Poisson GLM on inflorescence counts, predicted by altitude, habitat (upslope vs downslope), distance from the patch edge, and the square-root of tussock basal area. Analysed as a split-split-plot design (see methods for explanation of experimental design and appropriate error terms). Significant effects are in bold.

|  | d.f. | SS       | MS       | F      | P                |
|--|------|----------|----------|--------|------------------|
| Altitude   | 3    | 249.3715 | 83.12383 | 6.07   | <b>0.003</b>     |
| Habitat  | 1    | 320.3642 | 320.3642 | 23.38  | <b>&lt;0.001</b> |
| Altitude × habitat                                     | 3    | 55.6132  | 18.53773 | 1.35   | 0.281            |
| Error(altitude × habitat × plot)                       | 24   | 328.791  | 13.6996  |        |                  |
| Distance   | 1    | 344.2319 | 344.2319 | 131.50 | <b>&lt;0.001</b> |
| Distance × altitude                                    | 3    | 513.0164 | 171.0055 | 65.33  | <b>&lt;0.001</b> |
| Distance × habitat                                     | 1    | 63.49975 | 63.49975 | 24.26  | <b>&lt;0.001</b> |
| Distance × altitude × habitat                          | 3    | 17.63703 | 5.87901  | 2.25   | 0.083            |
| Error(altitude × habitat × plot × as.factor(distance)) | 280  | 732.948  | 2.61767  |        |                  |
| Basal area   | 1    | 304.5346 | 304.5346 | 636.40 | <b>&lt;0.001</b> |
| Basal area × altitude                                  | 3    | 28.76947 | 9.589823 | 20.04  | <b>&lt;0.001</b> |
| Basal area × habitat                                   | 1    | 1.551024 | 1.551024 | 3.24   | 0.072            |
| Basal area × distance                                  | 1    | 0.03995  | 0.03995  | 0.08   | 0.773            |
| Basal area × altitude × habitat                        | 3    | 12.22256 | 4.074187 | 8.51   | <b>&lt;0.001</b> |
| Basal area × altitude × distance                       | 3    | 9.501536 | 3.167179 | 6.62   | <b>&lt;0.001</b> |
| Basal area × habitat × distance                        | 1    | 1.901936 | 1.901936 | 3.97   | <b>0.046</b>     |
| Basal area × altitude × habitat × distance             | 3    | 5.056345 | 1.685448 | 3.52   | <b>0.014</b>     |
| Residual error   | 2689 | 1286.76  | 0.47853  |        |                  |
| Total  | 3024 | 4276.298 |          |        |                  |

flowering surfaces. This edge effect is most prominent at the highest altitude site.

The upward curve in the downslope surface at 1550 m was driven by the only two flowering plants found in these plots being in the interior of one plot (Fig. 4a), while the upward trend in flowering effort on upslope edges was based on larger numbers of flowering individuals (Fig. 4b). Despite the visual impact of the downslope surface at 1550 m in the graphs, it did not show up as a significant difference in the model, as evidenced by the non-significant distance × altitude × habitat interaction term (Table 1). Removal of the two anomalous data points resulted in a flat, near-zero predicted surface for downslope habitat at 1550 m, similar to those predicted at other altitudes.

### Seed fates

Of the three insects known to prey upon *Chionochloa* seeds, only *Diplotoxa similis* and *Eucalyptodiplosis chionochloae* were found in appreciable numbers in this study. A single suspected *Megacraspedus calamogonus* pupa was found, in an inflorescence at 1550 m. This predator was excluded from the subsequent analyses, since little can be said from a single sighting beyond that *M. calamogonus* activity was low in this sample.

There did not appear to be any significant difference in the predation rates of florets between the upslope edge and interior habitats (Table 2). However, the impact of both of the common seed predators in this study declined sharply with altitude. *D. similis* were found almost exclusively in the lowest altitude (1150 m) population, and were not

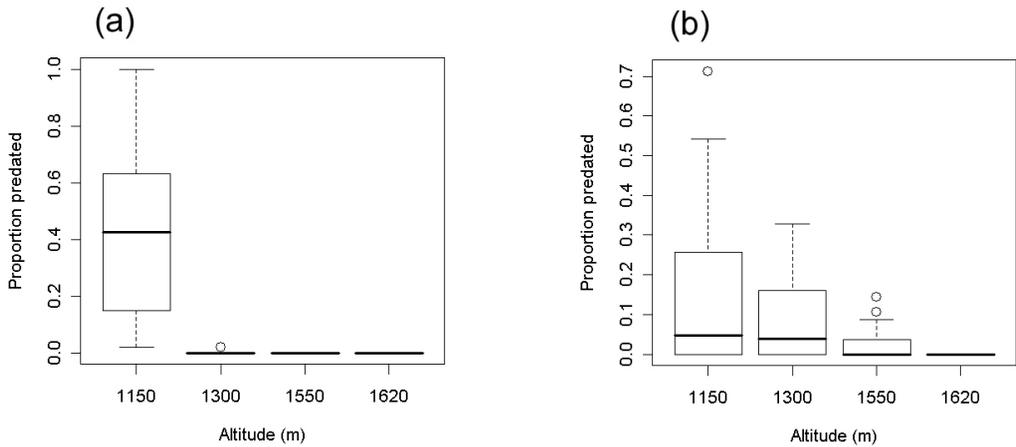
found above 1300 m (Fig. 5a). *E. chionochloae* was also more common at lower altitudes than higher up (Fig. 5b), although it was active at higher altitude than *D. similis*.

Both *D. similis* and *E. chionochloae* seed predation showed a significant relationship with the number of flowers in the immediate neighbourhood (Table 2). However, these relationships were very weak, explaining only about 3% of the variation in their respective models. The effect of flowers close by was also dependent on habitat type for *D. similis* (Table 2), with a stronger positive response in the interior habitat.

Both of the seed predators also showed a significant preference for different species of *Chionochloa* (Table 2). However, the direction of the relationship was reversed between seed predators, with *D. similis* preferring *C. pallens* and *E. chionochloae* being more common in *C. macra*. The strength of the preference exhibited by *D. similis* toward *C. pallens* was dependent on habitat type. A stronger preference was shown in interior habitat than on edges.

## Discussion

The results of this study lend quantitative support to previous anecdotal suggestions that flowering effort in *Chionochloa*, during low-flowering years, is concentrated along patch edges. Flowering effort was consistently higher along the upslope edges of tussock patches than would be predicted if flowering was distributed randomly. However,



**Figure 5.** Floret fates against altitude (m a.s.l.): (a) proportion predated by *Diplotoxa similis*; (b) proportion predated by *Eucalyptodiplosis chionochloae*.

**Table 2.** ANOVA of binomial GLM on the proportion of *Chionochloa* florets suffering seed predation. Significant effects are in bold.

(a) by *Diplotoxa similis*

|                                    | d.f. | SS       | MS       | F      | P                |
|------------------------------------|------|----------|----------|--------|------------------|
| Altitude                           | 3    | 1058.012 | 352.6707 | 113.39 | <b>&lt;0.001</b> |
| Habitat                            | 1    | 1.634    | 1.634    | 0.53   | 0.471            |
| Flowers close                      | 1    | 33.561   | 33.561   | 10.79  | <b>0.002</b>     |
| Altitude × habitat                 | 3    | 2.507    | 0.835667 | 0.27   | 0.848            |
| Altitude × flowers close           | 3    | 0.117    | 0.039    | 0.01   | 0.998            |
| Habitat × flowers close            | 1    | 31.909   | 31.909   | 10.26  | <b>0.002</b>     |
| Altitude × habitat × flowers close | 3    | 0.01     | 0.003333 | 0.00   | 1.000            |
| Species                            | 1    | 63.55651 | 63.55651 | 20.44  | <b>&lt;0.001</b> |
| Species × habitat                  | 1    | 38.47158 | 38.47158 | 12.37  | <b>0.001</b>     |
| Residual                           | 59   | 183.4984 | 3.110142 |        |                  |
| Total                              | 76   | 1413.257 |          |        |                  |

(b) by *Eucalyptodiplosis chionochloae*

|                                    | d.f. | SS       | MS       | F     | P                |
|------------------------------------|------|----------|----------|-------|------------------|
| Altitude                           | 3    | 298.9477 | 99.64923 | 16.93 | <b>&lt;0.001</b> |
| Habitat                            | 1    | 9.879    | 9.879    | 1.68  | 0.200            |
| Flowers close                      | 1    | 28.8226  | 28.8226  | 4.90  | <b>0.031</b>     |
| Altitude × habitat                 | 3    | 4.5591   | 1.5197   | 0.26  | 0.855            |
| Altitude × flowers close           | 3    | 5.5755   | 1.8585   | 0.32  | 0.814            |
| Habitat × flowers close            | 1    | 17.5811  | 17.5811  | 2.99  | 0.089            |
| Altitude × habitat × flowers close | 3    | 9.06     | 3.02     | 0.51  | <b>0.675</b>     |
| Species                            | 1    | 31.31334 | 31.31334 | 5.32  | <b>0.025</b>     |
| Species × habitat                  | 1    | 15.09042 | 15.09042 | 2.56  | 0.115            |
| Residual                           | 59   | 347.2954 | 5.886363 |       |                  |
| Total                              | 76   | 768.1242 |          |       |                  |

the same was not true of downslope edges, which did not generally exhibit more abundant flowering than plants in interior habitat. This pattern in flowering distribution was even more pronounced when the size of tussocks was taken into account. There was a prominent increase in flowering effort per square metre of tussock, close to the edge of upslope plots. This shows that the more prolific flowering on upslope edges is not simply the result of larger plants being concentrated on this edge. Downslope edges did not show this type of increase. Therefore, the observed increase in flowering effort on upslope edges cannot be explained solely by reduced competition along the edge or simply by elevated temperatures adjacent to shingle scree, invoked as a possible explanation of extra flowering efforts by Mark (1965). If reduced neighbourhood competition and/or elevated temperatures were responsible for the increase in flowering observed, then it should apply equally to upslope and downslope edge plants. This leads to the conclusion that the disparity between upslope and downslope edges (as well as with plants in interior habitat) is likely to stem from a difference in resource supply between these habitats.

The notion that resource supply varies between habitats within a vegetation patch is supported by the soil nutrient data collected in this study. The upslope edge had substantially higher nitrate concentrations than the other two habitat types, and although there was not sufficient power to establish a difference in phosphorous concentrations, they appeared to conform to a similar pattern. The highest levels of these two resources, then, occurred in association with elevated flowering effort, along the upslope edge. In contrast, the downslope edge consistently exhibited the lowest concentrations of all nutrients measured. Although the levels of ammonium were significantly higher in the interior habitat than in the downslope edge, concentrations along the upslope edge did not differ significantly from either of the other habitats. However, it is possible that the upslope edge concentrations were underestimated to some extent, due to the soil freezing. The freezing of soil observed along this edge may have retarded diffusion of ions into the soil resin bags, potentially leading to underestimates of all nutrient concentrations along the upslope edge. Despite the limitations of the present study, a significant difference in resource availability was observed that appears able, at least in part, to explain the preponderance of flowering effort toward upslope edges, corroborating Burrows's (1968) assertion that most flowering in low-flowering years was associated with more-resource-rich sites.

Since resource supply, particularly in low-productivity environments, is often pulsed (Goldberg & Novoplansky 1997), it is possible that the nutrient availability measured by the soil resin bags in autumn does not offer a complete picture of nutrient availability over longer time periods. In the alpine environment considered here, spring snowmelt is likely to bring a large pulse of mineral nutrients from

further up the slope to plants on upslope edges (Jackson & Caldwell 1992). As well as mineral nutrients from rock weathering, snow has been shown to capture appreciable levels of atmospheric nitrogen as ammonium (McSweeney 1983), which would be released during snowmelt. McSweeney also showed through experimental addition of nitrogen as urea that *Chionochloa* plants are capable of rapidly absorbing the quantities of nitrogen made available during these periodic surges in nutrient levels. This type of nutrient supplement early in the growing season might be at least as important as average ambient nutrient levels over the growing season, as an influence on the internal resource dynamics of these plants.

Plants exposed to higher levels of resource availability should accumulate sufficient resources for flowering more rapidly than those plants in more-resource-poor situations. This expectation is supported by our findings that *Chionochloa* along the more-nutrient-rich upslope edges exhibited more prolific flowering during a low-flowering year than those located elsewhere in the patch. It is also consistent with the findings of other studies that show local resource availability influences reproductive output. For instance, Gysel and Lemmien (1964) found that reproductive output was higher in shrubs grown in more fertile soils in Michigan. The present finding also adds weight to existing evidence for the importance of resource accumulation to mast seeding provided by negative autocorrelations in seed production time series data (Norton & Kelly 1988; Sork et al. 1993; Rees et al. 2002; Monks & Kelly 2006). Such negative autocorrelations in reproductive output between years imply that resource reserves must be rebuilt before subsequent reproductive efforts, and have been shown in a large number of cases (Kelly & Sork 2002). For example, Sork et al. (1993) showed negative autocorrelations, with different lag times, for three *Quercus* species in East Missouri. Overall, these observations, along with our findings, provide support for the assumed need for a resource storage component in mast seeding, which has formed the basis of recent modelling work in this area (e.g. Satake & Iwasa 2000; Rees et al. 2002).

The implication of the dependence of flowering on resource accumulation is that plants growing in very favourable situations will be able to flower more often, or even annually. This is seen in transplant experiments, where *Chionochloa* plants moved to lower altitudes often adopt an annual flowering pattern (Mark 1968; Burrows 1968; Greer 1979). Although our study only spans a single year, if there is more flowering in low-flowering years, the overall population-level variability of flower crops (CV) will be reduced and masting will be less pronounced, as shown for shrubs on more fertile soils by Gysel and Lemmien (1964).

A reduced intensity of masting has likely flow-on effects for the seed predators and the effectiveness of the predator satiation strategy. The observed proliferation

of flowering effort on upslope edges did not have any discernible impact on the spatial distribution of seed predation in this study. The inflorescences of plants located on the edge were no more likely to be attacked by insect seed predators than those in the interior habitat. This suggests the mobility of these seed predators is such that, even if edge habitat does provide more reliable food resources, the insects do not restrict their activity to these areas. This is consistent with the fact that both *D. similis* and *E. chionochloae* have a winged adult phase, which presumably means they can search for oviposition sites at scales at least as large as our individual vegetation patches.

Seed predation rates did, however, decline significantly with increasing altitude. This trend is in accordance with findings of previous studies (White 1975; Kelly et al. 1992; Sullivan & Kelly 2000). This again raises the question, posed with regard to *C. rubra* by Sullivan & Kelly (2000), of why mast seeding appears to be most extreme where seed predation is lowest. Our findings, along with other studies (Sullivan & Kelly 2000; Rees et al. 2002), suggest the shorter growing season and inherently slower resource accumulation rates at higher altitudes would produce increasingly small and intermittent flowering efforts. At very low flowering intensities pollination success has been seen to suffer in *Chionochloa* (Kelly & Sullivan 1997), which would help select for masting at high altitudes, particularly if self-pollination results in inbreeding depression (Tisch & Kelly 1998). Previous work showing that increased pollination efficiency through masting provides little benefit to *Chionochloa* has mainly been based on observations of populations below 1100 m (Kelly & Sullivan 1997; Kelly et al. 2001), whereas this present study looked at populations ranging from 1150 m to 1620 m in altitude. A shift toward increased importance of resource accumulation and wind pollination efficiency with increasing altitude might help explain part of the seeming paradox of strong masting at high altitudes.

Although edge plants do not appear to be selectively targeted by predators as a result of their more prolific flowering, higher flowering effort along upslope edges is still likely to provide an increased food supply for *Chionochloa*'s seed predators during low-flowering years. Therefore, any increase in the amount of upslope edge habitat is likely to result in increased local resource availability for *Chionochloa*'s seed predators, by increasing the number of plants likely to flower during a low-flowering year. Increased local flowering resulting from the fragmentation of tussock grasslands (e.g. through the development of roads) may therefore reduce the magnitude of the numerical benefits of predator satiation for local *Chionochloa* populations and hence have a negative impact on the effectiveness of masting with regard to predator satiation, especially at a local scale. This may act to exacerbate the predicted breakdown of predator satiation resulting from climate change (McKone et al.

1998). At high altitudes in the Takahe Valley in Fiordland, which is free of disturbances such as roads, years of zero flowering are relatively common (Kelly et al. 2000). It is possible that the relative rarity of human-disturbed edge habitat in Takahe Valley provides a partial explanation for the rarity of asynchronous flowering efforts among plants within its *Chionochloa* populations.

## Conclusions

The observed pattern of increased flowering effort by *Chionochloa* on the upslope edge of vegetation patches confirms previous anecdotal evidence for such a trend, and the nutrient data are consistent with the hypothesis that this pattern in flowering intensity is caused by greater resource availability along upslope edges. This result adds to the growing body of evidence supporting the importance of resource assimilation and storage in mast flowering in *Chionochloa*, and in masting species generally. This provides additional support for the use of a resource storage component as a basis for the modelling of masting dynamics. Although the observed trend toward more prolific flowering on upslope edges does not appear to directly influence the distribution of seed predation in *Chionochloa* on scales of less than 10 m, increases in flowering through fragmentation might reduce the ability of *Chionochloa* populations to satiate their seed predators at a scale determined by the search radius of the insects (perhaps a few hundred metres).

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#### Appendix 1. Method for determination of phosphorus in resin extracts

The principle behind this method is that phosphorus, reduced from phosphate in the presence of hydrogen ions, forms a coloured complex with molybdate tartrate, which can be measured photometrically at 880 nm. The reagents are sulphuric acid [50%], [25%]; ascorbic acid [10%/wt]; 0.026 M ammonium molybdate in 37.5% sulphuric acid; antimony potassium (+) tartrate 0.5 hydrate; combined molybdate tartrate solution (4 volumes ammonium molybdate solution and 1 volume antimony potassium

oxide (+) tartrate solution); potassium dihydrogen phosphate (phosphorous stock solution, used to construct a calibration curve).

Method: Pipette 10 ml of sample into a test tube, 10 ml of water into a 'blank' test tube, and 10 ml of standard solution into an appropriate 'standard' test tube. Adjust pH to 3–4 with 50% sulphuric acid solution. Add 250 µl 10% ascorbic acid to all tubes. Mix. Add 500 µl combined molybdate tartrate solution to all tubes. Mix well. Stand 20 min. Read absorbance at 880 nm.