Mast seeding of *Chionochloa* (Poaceae) and pre-dispersal seed predation by a specialist fly (*Diplotoxa*, Diptera: Chloropidae)

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Abstract  Levels of seed predation were recorded between 1986 and 1992 in *Chionochloa pallens*, *C. oreophila*, *C. flavescens*, *C. macra*, and *C. crassiuscula* populations at various altitudes at three sites in Canterbury. There were consistently high levels of attack by a chloropid fly, *Diplotoxa similis*: between 22 and 94% of florets showed evidence of fly damage, except at higher altitudes (decreasing to 2% in *C. pallens* at 1620 m) and in *C. oreophila* (6 – 10%). Since *D. similis* emerges rapidly from the pupa and since larvae possibly move between florets, the number of insects found underestimated the number of florets predated by up to 90%. Seed set varied from 2% to 59% and was negatively correlated with seed predation.

Two other *Chionochloa* seed predators have been reported previously: a moth, *Megacrampedus calamogonus*, and an unidentified cecidomyiid (gall midge) larva. In this study, larvae similar to *Megacrampedus* were very rare, and we suggest that the unidentified cecidomyiid is actually a misidentification of *Diplotoxa*.

The pattern of seed predation and flowering intensity at Mt Hutt in *C. pallens*, 1986–1992, suggests that masting may be effective at reducing seed predation in this species. Since the same species of *Diplotoxa* seems to attack all the studied species of *Chionochloa*, the observed synchrony of masting between these species may be adaptive.

Keywords  pre-dispersal seed predation; variable reproduction; mast seeding; predator satiation; search range: *Chionochloa pallens*: *C. oreophila*: *C. flavescens*: *C. macra*: *C. crassiuscula*; Poaceae: *Diplotoxa similis*: Diptera: Chloropidae: Cecidomyiidae: New Zealand alpine grassland

INTRODUCTION

Variable seed production between years in perennial plants, termed mast seeding, is common worldwide (Silvertown 1980), but particularly so in New Zealand (Norton & Kelly 1988; see also Mark 1970; Beveridge 1973; Campbell 1981; Wardle 1984; Brockie 1986; West 1986; Haase 1986; Allen & Plat 1990). Various hypotheses have been advanced as selective advantages for mast seeding (for reviews, see Norton & Kelly 1988; Smith et al. 1990). Resource limitation was the earliest suggestion (Busgen & Munch 1929) but has recently fallen from favour since masting is concerned with the packaging of reproduction between years, rather than the absolute amount of reproduction (Norton & Kelly 1988). A frequently invoked explanation is predator satiation, where masting reduces the levels of loss to seed predators (Smith 1970; Silvertown 1980). Reproductive efficiency has been suggested as an advantage to masting in wind pollinated species (Steers 1976; Nilsson & Wastljung 1987; Norton & Kelly 1988; Smith et al. 1990). Certainly, many well known masting species are wind pollinated, though animal pollinated plants may also mast, such as *Celmisia* spp. (Campbell 1981), *Aciphylla* spp. (Mark 1970), and *Phormium* spp. (Brockie 1986). There may be other causes for masting, such as high accessory costs of reproduction (Norton & Kelly 1988).
One widespread New Zealand genus that shows masting is *Chionochoa*, which includes about a dozen alpine species of snow-tussocks that dominate extensive areas, especially in the South Island (Connor & Edgar 1986; Connor 1991). Information is available on the flowering regularity of ten species of *Chionochoa*, and all mast except for *C. rubra* (Connor 1966; Mark 1968). Moreover, there are often high levels of seed loss to invertebrate seed predators (White 1975), and it has been suggested that masting may serve to reduce these losses (Mark 1968). Although White (1975) published extensive data on seed losses in five species of *Chionochoa*, he gave no data on flowering intensity which could be used to test the predator satiation hypothesis.

In this study, we examined the relationship between mast seeding and seed predation in *Chionochoa*. Our aims were to (1) quantify the levels of seed predation in different species and years; (2) identify the various predators involved; and (3) evaluate the effectiveness of masting in reducing seed losses in *Chionochoa*.

### MATERIALS AND METHODS

#### Study sites

The main study site (43° 32′ S, 171° 33′ E) was by the Mt Hutt skiff field road, Canterbury, at 1070 m altitude on a south-east facing slope. The area was covered in dense *Chionochoa pallens* Zotov. While there were occasional *C. macra* Zotov present and the two species may hybridise, the sampled plants were believed to be non-hybrid *C. pallens* (McKone 1990). This site was studied from 1986 to 1992. A higher *C. pallens* site at 1620 m facing south-east on Mt Hutt (43° 30′ S, 171° 32′ E) was sampled only in 1986. In 1989 a wider survey was conducted, and seed samples were collected at Craigeburn (43° 07′ S, 171° 42′ E), 39 km north-east of Mt Hutt, from *C. pallens* (1400 and 1450 m), *C. oreophila* (Petrie) Zotov (1500 m), *C. macra* (1250 and 1450 m), and *C. crassiuscula* (Kirk) Zotov (1450 m). Samples were also taken in 1989 from Temple Basin (42° 55′ S, 171° 35′ E), 61 km north of Mt Hutt, from both *C. crassiuscula* and *C. flavescens* Zotov at 1500 m.

#### Table 1: Fates of florets (% of all florets) and flowering intensity in *Chionochoa pallens* at Mt Hutt, 1070 m altitude, 1986–92. The Kruskal-Wallis test statistic *H* for comparisons among years (excluding 1987), and mean air temperatures at the Craigeburn Forest climate station (914 m altitude), are also given. Categories included in the minimum and maximum damage estimates are marked *†* and ††, respectively.

<table>
<thead>
<tr>
<th>Year</th>
<th>1986</th>
<th>1987</th>
<th>1989</th>
<th>1990</th>
<th>1991</th>
<th>1992</th>
<th><em>H</em></th>
<th><em>P</em> &lt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Filled seed</td>
<td>26.5†</td>
<td>–</td>
<td>9.7</td>
<td>7.5</td>
<td>32.4</td>
<td>2.2</td>
<td>11.7</td>
<td>39.2</td>
</tr>
<tr>
<td>Shriveled seed</td>
<td>4.1</td>
<td>–</td>
<td>2.4</td>
<td>6.3</td>
<td>4.8</td>
<td>0.8</td>
<td>3.5</td>
<td>15.9</td>
</tr>
<tr>
<td>Unexpanded ovary</td>
<td>8.4</td>
<td>–</td>
<td>4.4</td>
<td>3.2</td>
<td>15.4</td>
<td>3.1</td>
<td>11.2</td>
<td>27.6</td>
</tr>
<tr>
<td><em>Diplotoa</em> (larva or pupa)††</td>
<td>43.5</td>
<td>–</td>
<td>14.3</td>
<td>14.9</td>
<td>10.5</td>
<td>9.8</td>
<td>8.4</td>
<td>45.6</td>
</tr>
<tr>
<td>Feeding sign, no ovary†</td>
<td>1.8</td>
<td>–</td>
<td>3.2</td>
<td>44.5</td>
<td>24.0</td>
<td>75.5</td>
<td>62.2</td>
<td>63.1</td>
</tr>
<tr>
<td>No feeding sign, no ovary††</td>
<td>11.9</td>
<td>–</td>
<td>36.2</td>
<td>23.6</td>
<td>9.2</td>
<td>8.6</td>
<td>2.8</td>
<td>41.3</td>
</tr>
<tr>
<td>Ergot attacked</td>
<td>3.8</td>
<td>–</td>
<td>1.7</td>
<td>0</td>
<td>3.8</td>
<td>0</td>
<td>0.1</td>
<td>30.4</td>
</tr>
<tr>
<td>Min. insect damage (*)</td>
<td>45.3</td>
<td>–</td>
<td>45.5</td>
<td>59.4</td>
<td>34.5</td>
<td>85.2</td>
<td>70.6</td>
<td>38.6</td>
</tr>
<tr>
<td>(standard deviation)</td>
<td>(13.5)</td>
<td>(20.1)</td>
<td>(14.8)</td>
<td>(21.3)</td>
<td>(11.1)</td>
<td>(35.2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. insect damage (††)</td>
<td>57.2</td>
<td>–</td>
<td>81.7</td>
<td>83.0</td>
<td>43.6</td>
<td>93.8</td>
<td>73.4</td>
<td>40.5</td>
</tr>
<tr>
<td>(standard deviation)</td>
<td>(11.8)</td>
<td>(22.3)</td>
<td>(15.1)</td>
<td>(23.3)</td>
<td>(7.47)</td>
<td>(35.8)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percent of tussocks flowering</td>
<td>100</td>
<td>90</td>
<td>20</td>
<td>53</td>
<td>71</td>
<td>37</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>Florets per spikelet</td>
<td>5.29</td>
<td>(5.19)</td>
<td>5.71</td>
<td>3.32</td>
<td>5.87</td>
<td>5.54</td>
<td>5.38</td>
<td>41.6</td>
</tr>
<tr>
<td>Spikellets per inflorescence</td>
<td>41.6</td>
<td>(40.5)</td>
<td>43.7</td>
<td>42.5</td>
<td>45.8</td>
<td>39.7</td>
<td>29.9</td>
<td>19.7</td>
</tr>
<tr>
<td>Inflorescences per tussock</td>
<td>46.8</td>
<td>3.9</td>
<td>0.27</td>
<td>2.46</td>
<td>4.38</td>
<td>1.24</td>
<td>0.28</td>
<td>151.1</td>
</tr>
<tr>
<td>No. of florets sampled</td>
<td>1299</td>
<td>–</td>
<td>857</td>
<td>498</td>
<td>880</td>
<td>831</td>
<td>807</td>
<td></td>
</tr>
<tr>
<td>No. of plants sampled</td>
<td>20</td>
<td>–</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Date sampled</td>
<td>19 Feb</td>
<td>26 Jan</td>
<td>5 Feb</td>
<td>31 Jan</td>
<td>2 Feb</td>
<td>5 Feb</td>
<td>13 Feb</td>
<td></td>
</tr>
<tr>
<td>Mean temp. Oct-Jan (°C)</td>
<td>10.99</td>
<td>11.56</td>
<td>11.35</td>
<td>12.33</td>
<td>11.36</td>
<td>11.08</td>
<td>10.41</td>
<td></td>
</tr>
<tr>
<td>% <em>Diplotoa</em> seen as pupae</td>
<td>0 †</td>
<td>–</td>
<td>67.1</td>
<td>18.9</td>
<td>100</td>
<td>83.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* 21.5% of all filled seeds were soft, possibly affected by an unknown mould; † includes florets with insect frass and lemma damage, which was not searched for in 1988; †† not recorded, so mean from other 6 years used; †† average including non-flowering tussocks.
Mean temperatures for each season were calculated from mean daily maximum and minimum air temperatures recorded at the Craigieburn Forest climate station (914 m), for the months of October, November, December, and January, for comparison with the phenology of the predator.

Sampling methods
At the main Mt Hutt site, both predation of seeds (technically carpylopses) and flowering intensity (florists per tussock) were measured. Sampling was carried out in late January or early February each year, as recommended by White (1975). In 1986 20 plants were selected for sampling by taking the nearest tussock to points at 5 m spacing on two transects 50 m long and 10 m apart. For each selected plant, the number of inflorescences was recorded, and inflorescences were collected for determination of seed fates. In 1987 only the number of inflorescences per tussock was recorded; mean number of florists per tussock was estimated using the means from other years for spikelets per inflorescence and florists per spikelet, since neither varied much between years (Table 1). From 1988 onwards, the number of inflorescences per tussock was determined on three 10 m transects. The transects were put in the same places each year; from 1990 onwards, the ends of the transects were marked with steel pegs and the individual tussocks mapped. Inflorescence number was recorded for all Chionochloa tussocks touching each line. To record seed predation, inflorescences were collected from plants in the study area (in 1986, from the 20 plants on the transects; in later years, from 15 plants haphazardly selected away from the transects, since removal of inflorescences may affect subsequent local density of Diploptera).

At the Craigieburn and Temple Basin sites, only

<table>
<thead>
<tr>
<th>Species</th>
<th>pallens orephila flavescens macra</th>
<th>pallens pallens crassiuscula crassiuscula macra</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>MTH</td>
<td>CRA</td>
</tr>
<tr>
<td>Altitude (m)</td>
<td>1620</td>
<td>1500</td>
</tr>
<tr>
<td>No. florists</td>
<td>732</td>
<td>969</td>
</tr>
<tr>
<td>Maximum % insect damaged</td>
<td>2.4</td>
<td>10.2</td>
</tr>
<tr>
<td>SD</td>
<td>2.1</td>
<td>9.2</td>
</tr>
<tr>
<td>Infl. min.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Infl. max.</td>
<td>6.6</td>
<td>37.5</td>
</tr>
<tr>
<td>Minimum % insect damaged</td>
<td>2.2</td>
<td>6.1</td>
</tr>
<tr>
<td>SD</td>
<td>2.0</td>
<td>6.7</td>
</tr>
<tr>
<td>Infl. min.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Infl. max.</td>
<td>6.6</td>
<td>29.4</td>
</tr>
<tr>
<td>Filled seed %</td>
<td>mean</td>
<td>29.1</td>
</tr>
<tr>
<td>SD</td>
<td>22.1</td>
<td>21.7</td>
</tr>
<tr>
<td>Infl. min.</td>
<td>6.8</td>
<td>15.4</td>
</tr>
<tr>
<td>Infl. max.</td>
<td>79.6</td>
<td>96.0</td>
</tr>
<tr>
<td>Shrivelled %</td>
<td>mean</td>
<td>27.4</td>
</tr>
<tr>
<td>SD</td>
<td>14.9</td>
<td>13.2</td>
</tr>
<tr>
<td>Infl. min.</td>
<td>6.8</td>
<td>0</td>
</tr>
<tr>
<td>Infl. max.</td>
<td>44.4</td>
<td>46.2</td>
</tr>
</tbody>
</table>

* all florets were examined on 10 spikelets per inflorescence, except at Craigieburn 1450 m where all florets on all spikelets on the inflorescence were examined.
seed predation was recorded. At least 20 inflorescences were collected for each species (Table 2) and these were examined for seed set.

**Damage categories**

For each inflorescence, the total number of spikelets was recorded, and on 10 spikelets all florets were examined under a dissecting microscope and assigned to one of the following categories:

(a) Full seed: ovary filled (in 1986, defined as > 0.8 mm long; in later years as more than half the length of the lemma).

(b) Shrivelled seed: contained long ovary, as above, but seed not well filled, often collapsed or wrinkled; unlikely to be viable, and not known to be caused by insect attack.

(c) Undeveloped ovary: ovary present, but too small to be considered a seed. Usually the shrivelled stigma was present. These seem unlikely to be related to insect attack.

(d) *Diplotoxa* present: floret contained larva, pupa, or pupal case of *Diplotoxa*.

(e) Empty floret with feeding sign: ovary absent, and positive signs of insect damage (frass, chewing on inside walls of lemma and palea, or ovary and base of anthers eaten preventing anthesis).

(f) Empty floret without feeding sign: ovary absent, but no direct evidence of insect damage. May represent cryptic insect damage (White 1975).

(g) Ergot: seed attacked by ergot fungus, producing enlarged, misshapen, black seed.

The minimum level of insect damage to florets was taken as (d) plus (e); the maximum level of damage was taken as the minimum plus (f).

**Analysis**

Since many of the variables were not normally distributed, differences among years (excluding 1987) at the main Mt Hutt site were tested for significance using the non-parametric Kruskal-Wallis test. Correlations between maximum levels of predation and other variables were done using both parametric and rank correlations; both gave the same results.

**RESULTS**

**Identity of the predators**

By far the most common insect recorded in the florets of *Chionochloa* was a chloropid fly, *Diplotoxa similis* Spencer. In some years, large numbers of green to black pupae (depending on stage of maturity) were seen, which readily hatched into adult flies (Fig. 1). In other years, most or all of the insects seen in florets were orange larvae (Table 1, Fig. 1), which were identified as Chloropidae (P. M. Johns, pers. comm.). Florets were occasionally found containing two insects, or an insect and a filled seed, suggesting that the larvae may be able to move between florets in a spikelet.

The *Diplotoxa* larvae seen at Craigieburn and Temple Basin appeared to be the same species as at Mt Hutt, but this is yet to be confirmed.

A second type of insect larva, similar to the moth *Megacraspedus calamogonus* (Lepidoptera: Gelechiidae) described by White (1975), was seen in only 4 of 2937 florets examined in 1986 from the main Mt Hutt site. A few were seen in casual observations of florets collected in 1987 from the
same site. No sign of the moth was found at any site between 1988 and 1992.

Variation between years at Mt Hutt, 1070 m

There was wide variation between years in the fate of florets at the main Mt Hutt site (Table 1), but the number of filled seeds was always low (2–32%), while the estimates of predation were always high (35–94%). The percentage of florets actually containing Diplotoxa varied; there was no clear relationship between Diplotoxa seen and overall minimum or maximum losses, possibly because of the differences in timing of the insect life cycle between years. In some years most or all of the Diplotoxa were seen as larvae, and in other years most were pupae (Table 1). The years with high percentages of pupae were not always those with later sampling dates or warmer mean temperatures. For example, 1986 had 0 pupae (despite a late sampling date) and the lowest mean temperatures, and 1989 had 67% pupae and the highest mean temperatures, but 1991 had 100% pupae despite being the second coldest season. However, in years when the insect life cycle was more advanced (high % of insects as pupae) a much higher fraction of florets were recorded as having feeding sign and neither ovary nor Diplotoxa present (n = 5, parametric R = 0.987, P < 0.01), suggesting that the insects had already departed. Ergot-infested seeds were rare in all years. The incidence of all the various floret fates varied significantly between years.

There was also a wide variation in flowering intensity over the study period (Table 1, Fig. 2). This resulted mostly from changes in the number of inflorescences per tussock, which varied 173-fold. The number of florets per spikelet and spikelets per inflorescence were both much more constant, with lower values in 1989 and 1992, respectively.

There was large variation among individual tussocks in the level of insect attack (see standard deviations for insect damage in Table 1). The standard deviation was particularly high in the year of lowest flowering intensity (1992). In that year, inflorescences were very widely separated across the study site, and the inflorescences examined tended to be either very heavily attacked (9 of the 15 inflorescences had >90% maximum damage) or very lightly attacked (3 inflorescences had <30% maximum damage, and 92% of the filled seeds seen were set by 4 inflorescences). It may be that when flowering tussocks are widely spaced, and numbers of Diplotoxa surviving from the previous year are low, Diplotoxa may not be able to disperse to all
inflorescences and isolated plants may suffer little damage. In the laboratory, *D. similis* walk actively but fly only infrequently and for short distances (1–2 cm), so their powers of dispersal may be limited.

Other sites and other *Chionochloa* species

There was a wide range in the fates of florets at other sites (Table 2). Predation was lowest at the highest altitude (1620 m) and in *C. oreophila*, a high-altitude species. The fraction of florets ripening seed was about 30% except in *C. oreophila* (59%) and *C. macra* (5–9%). The data for the number of shrivelled seed are presented in case it is later found that these are caused by a seed predator (White 1975). There was much variation from one inflorescence to another in the levels of seed predation.

Taking all data from the various sites together, despite the year-to-year variation at the main Mt Hutt site, there was a clear decrease in seed predation with altitude (Fig. 3; n = 15, parametric R = -0.854, P < 0.001). There was also a negative correlation between levels of seed predation and percentage of florets with a ripe seed (n = 15, parametric R = -0.680, P < 0.001).

**DISCUSSION**

**Insect seed predators**

*Diptera*

In our samples, we assumed the orange chloropid larvae were *Diptoxa similis*, since we found no other types of dipteran larvae or pupae. Other workers from Canterbury have reached similar conclusions. Janice Lord (pers. comm.) studied seed predation in *Festuca novae-zelandiae* at Cass (near Craigieburn). She found orange chloropid larvae, and black pupae that hatched into adult *Diptoxa moorei* (Salmon) Spencer, a wingless species.

However, White (1975, p. 167), working on five *Chionochloa* species (*C. pallens, C. flavescens, C. macra, C. rigida*, and *C. rubra*) in the South Island high country described *Diptoxa similis* (see Spencer, 1977, for identification of the fly) as having greenish-white larvae, which "distinguishes them from the orange larvae of the Cecidomyiidae midge of *Mark* (1965a, b, c) and Burrows (1961)*. This unidentified Cecidomyiidae has an interesting history in the literature. Burrows (1961, p. 51) reported an insect larva in flowers of *Chionochloa* (as *Dantonia*) *australis, C. crassiuscula, C. flavescens, C. rigida*, and mid-ribbed snowgrass (= *C. pallens*; C.J. Burrows, pers. comm.). The larvae “answer the description of the larvae of the orange wheat blossom midge . . . none of those collected pupated and there is no indication of the nature of the adult”. Later, Burrows (1968, p. 155) reported that *Chionochloa* “is attacked by a small orange grub, believed to be the larva of a Cecidomyiidae fly”. Mark (1965, p. 189) reported that in *C. rigida* and *C. macra* “gall midge larvae, probably a native species of Cecidomyiidae (Diptera) occupied some fertile florets at several sites, feeding on the ripening grain (Dumbleton, pers. comm.)”. White (1975) cited Mark’s (1965) "unidentified cecidomyiid . . . which appears from the larval size and colouration descriptions to be the same species as recorded by Burrows (1961)" (p. 163). White found the cecidomyiid in only three adjacent samples at one site in one of the five years of study. He noted that “almost nothing is known of the feeding habits and damage caused by the unidentified cecidomyiid midge of *Mark . . . and Burrows*” (p. 177).

White, Lord, and ourselves have all found *Diptoxa* species to be common seed predators in *Chionochloa* and *Festuca*. We, like Lord, frequently found orange chloropid larvae with the *Diptoxa* adults. The putative cecidomyiid has never been seen as an adult. Although cecidomyiids and chloropid larvae are distinguishable, the presence of a cecidomyiid seed predator in *Chionochloa* remains unconfirmed. We suggest that published reports of it actually refer to orange larvae of *Diptoxa* spp. However, this does not explain why White (1975) described larvae of *Diptoxa similis* as greenish-white in colour, while we have seen only orange larvae.

Host specificity of *Diptoxa*

Apparently similar *Diptoxa* were seen in all five species of *Chionochloa* that we studied, though we have not yet been able to confirm that they are all *D. similis*. Burrows (1961) also commented on the apparent non-specificity of his unidentified insect.

A single species of *Diptoxa* could attack all these species of *Chionochloa* (K. A. Spencer, pers. comm.). The plants have similar reproductive biology, and all five have ripe seeds of similar size (0.76–1.09 mm; Lee & Fenner 1989) except for *C. oreophila*, which has both much smaller seeds (0.44 mm) and very low levels of seed predation (Table 2). It may be that the smaller seeds of *C. oreophila* make this a less favoured host for *Diptoxa*. Burrows (1968) also found lower frequencies of larvae in *C. oreophila* (0–0.3% of florets at two sites) than in *C. crassiuscula, C. pallens*, and *C. australis* (range 3.1–9.6%). The coincidence with our data
strenghens the suspicion that his "cecidomyiid" is actually Diplotoxa similis.

Lepidoptera
The other seed predator seen by White was the moth Megacarpopus calamonogus. In our samples it was tentatively identified only at the lower Mt Hutt site and only in the first two years. Interestingly, in White's (1975) comment the moth was common in the first two years but by the end of his study Diplotoxa was much more common than M. calamonogus. Clearly the populations of this moth may vary substantially from year to year, which would affect seed set in Chionochloa. White (1991) has documented a general decline since 1961 in density of many native moths in the Cass area, apparently due to the replacement of native dicotyledons by the adventive grass Agrostis capillaris L.

Levels of seed loss

We found little relationship between the number of Diplotoxa actually seen, and the overall estimates of seed losses to the insect. This is because, firstly, Diplotoxa seems to pass rapidly through the pupal stage to emerge as an adult (see also White 1975), so that a delay of a week in the sampling date may mean that a large number of Diplotoxa have already flown the floret. The timing of pupation does not seem to be at all predictable by calendar date, and only poorly by seasonal mean temperatures. Secondly, it may be that larvae move between florets and feed on more than one, as suggested both by our data and those of White (1975). (However, this has not been directly verified, and the tightly appressed lemma and palea might make such movement difficult.) Therefore, many eaten florets are empty of insects, but usually these contain signs such as frass or damage to the lemma. For these reasons, a low incidence of larvae or pupae cannot be taken as evidence of low seed losses (cf. Mark 1965; Burrows 1968). In our samples, the number of insects seen was sometimes as low as 10% of total estimated losses. There is clearly a need to search empty florets carefully for evidence of departed insects.

At the main Mt Hutt site there were consistently high losses of Chionochloa pennis seed to Diplotoxa similis. Over six years, between 35% and 94% of florets showed damage. Many florets were also damaged in 1989 in C. macra (c. 55%), C. crassiuscula (c. 45%), and C. flavescent (c. 22%). Only C. oreophila had less than 10% losses, possibly because of its small seeds (see above). Although C. oreophila is a high-altitude species, it showed lower levels of loss than the other sampled species at the same altitude. C. oreophila was also the species with the highest seed set. The negative correlation between levels of floret damage and seed ripening reinforces the conclusions of White (1975) that insects are capable of severely reducing seed production in Chionochloa, and that Chionochloa may not have inherently low levels of seed set, as was sometimes assumed.

Effect of altitude

In C. pennis the levels of seed predation decreased with increasing altitude, shown most clearly by the two Mt Hutt sites; the other Chionochloa species also fitted the same relationship (Fig. 3). Though most Chionochloa species grow in the alpine zone, some species occur down to sea level (Connor & Edgar 1986). Among our study species, C. macra is found down to 500 m, C. crassiuscula to 600 m and C. flavescent to 750 m, while C. oreophila is found above 1000 m (Connor 1991). The colder climate at higher altitude may be less suitable to Diplotoxa; for example late snow cover may inhibit egg laying. White (1975) noted an apparent altitude effect in his data, but ascribed this to habitat differences (nearness to forest). Spence (1990) suggested that Trypaeon longipennis (Diptera: Tephritidae), a seed predator of Celmsia spp. (Asteraceae), was less common at higher altitudes in Craigieburn.

Relation between seed predation and masting

Chionochloa pennis varied widely in reproductive output between 1986 and 1992 (Fig. 2). If masting was effective at predator satiation, as hypothesised for Chionochloa by Mark (1968), there should be lower levels of seed predation in high flowering years. At this stage we cannot conclusively test this prediction, for three reasons. Firstly, there are no data for 1987, when predation would be expected to be very high. Secondly, the mast year of 1986, which would normally be expected to have low predation, unusually followed what was probably a moderate flowering year in 1985 (based on observation of Chionochloa flowering generally in the South Island in 1984–85: McKone, pers. obs.; A. F. Mark, pers. comm.; R. H. Taylor & P. R. Wilson, pers. comm.). Thirdly, the lowest flowering year (1992) had only moderate levels of seed loss, possibly because the very low inflorescence density, combined with low numbers of Diplotoxa emerging from the low flowering in 1991, apparently meant that predation levels were limited by the search range of the insect.

However, the available data are at least consistent
with predator satiation. The overall levels of seed loss are certainly high enough to provide a selective advantage to reducing predation. Despite following another mast year, 1986 had the second lowest levels of seed loss. Between 1988 and 1992, the lowest predation was seen in the highest flowering year (1990) and the highest predation in the year following (1991) when fewer inflorescences may have coincided with more insects raised in the previous year. Therefore, masting may be serving to reduce the levels of seed predation in C. pallens at Mt Hutt. While the basic pattern is evident in the Porter River data of White (1975), the presence of a second predator, M. calamogonus, clouds the issue (the second insect may be affected by different climatic factors or have different lag periods, so total seed losses may not be so clearly related to flowering intensity).

Normally, it is very difficult to separate the possible effects of environmental variation and predator satiation as causes of variable seed output. However, if Diplotropa densities are reduced at high altitudes, the two could possibly be separated in Chionochloa. In the absence of selective pressures from seed predators, the higher altitude sites would probably be more variable in seed production due to harsher environmental conditions near the climatic limits for the species (Harper 1977, p. 699). For example, Allen & Platt (1990) reported that periodic seedling was more distinct at higher altitudes in Nothofagus solandri (Fagaceae) in the Craigieburn Range, and Harper (1977, p. 699) showed that Pinus silvestris had greater variability of seed output in northern Sweden than in the south.

In contrast, the predator satiation hypothesis predicts that if seed predation decreased with altitude, then masting could be less marked in higher altitude Chionochloa ecotypes and higher altitude species (especially C. oreophila with its small seeds and low levels of predation). Therefore, more variable reproduction in low-altitude Chionochloa ecotypes or species would suggest that predator-satiation effects were more important than the effect of an increasingly favourable environment at lower altitudes. However, less variable reproduction at low altitudes would not necessarily disprove the predator satiation hypothesis, because of the confounding effects of environmental variability. Unfortunately, the relevant data for other Chionochloa species are not yet available, and it is not known whether there is any ecotypic variation in reproductive variability within any of these species over different altitudes.

Of course, masting may have arisen originally in response to other selective forces like wind pollination, and only secondarily be effective at reducing seed predation (Norton & Kelly 1988). Many masting species are wind pollinated; Mark (1968) considered masting uncommon in perennial grasses, but some North American prairie grasses have high year-to-year variation in flowering intensity (Cornelius 1950; Rabinowitz et al. 1989). Although resource constraints were suggested as accounting for the frequency of masting in Chionochloa (Mark 1965, 1968), this was not confirmed (Payton & Brasch 1978). Moreover, resources alone are unable to account for occasional large rather than regular small bouts of reproduction (Norton & Kelly 1988).

It may be significant that all the species of Chionochloa examined here seem to share a single species of seed predator. At least nine species of Chionochloa are known to mast seed. C. rubra is the only known exception, although C. macra has relatively few years of low flowering intensity (Campbell 1981). The different species often mast in the same years (Mark 1968). Norton & Kelly (1988) argued that such synchrony may arise simply because different species are all using the same cue to trigger masting, often warm summers as in Chionochloa (Mark 1965). However, where several species share a common seed predator, synchrony between species would be required for masting to be most effective. This is exactly what is seen in Chionochloa.

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REFERENCES

Kelly et al.—Mast seeding and predation of Chionochloa


