Can wind pollination provide a selective benefit to mast seeding in *Chionochloa macra* (Poaceae) at Mt Hutt, New Zealand?

PHILLIP A. TISCH

DAVE KELLY*

Plant and Microbial Sciences
University of Canterbury
Private Bag 4800
Christchurch 1, New Zealand

Abstract Mast seeding, which is very pronounced in *Chionochloa* (Poaceae) in New Zealand, could provide selective advantages through reduced seed predation or through more efficient wind pollination. The importance of wind pollination in favouring masting was tested experimentally by measuring the pollination success of *Chionochloa macra* individuals in 10 m x 10 m plots subject to a range of experimentally altered flowering densities within a single season. Very low local flowering densities produced a moderate but non-significant increase in the proportion of unfilled seeds (assumed to represent unsuccessful pollination). This result is consistent with the conclusions from between-year observational studies on *Chionochloa pallens* that wind pollination makes only a small contribution to any present selective benefit of masting in *Chionochloa*. However, masting may provide larger benefits from higher seed quality (reduced inbreeding depression) than from seed quantity.

Keywords Mast seeding; mass flowering; wind pollination; inbreeding depression; predator satiation; economies of scale; *Chionochloa*; Poaceae

INTRODUCTION Mast seeding is a striking phenomenon whereby perennial plants reproduce heavily in some years, and very lightly or not at all in others (Kelly 1994). This is seen in a wide range of taxa, including Northern Hemisphere trees (Silvertown 1980; Nilsson & Wästljung 1987; Smith et al. 1990; Sork et al. 1993; Koenig et al. 1994; Tapper 1996) and Southern Hemisphere trees, herbs, and grasses (Webb & Kelly 1993). The reason that mast seeding is so striking is that there are clear selective disadvantages to not reproducing heavily every year. These disadvantages include lost opportunities for reproduction, lower population growth rates, higher costs of storage, and greater losses to density-dependent self-thinning (Hett 1971; Waller 1979; Ims 1990a, 1990b; Kelly 1994).

The most likely explanation for this strategy of irregular reproduction is the theory of *economies of scale* introduced by Norton & Kelly (1988), where large episodes of reproduction are more efficient than smaller ones. Plants which concentrate their reproductive effort in large sporadic bursts, rather than small regular events, are hypothesised to leave more surviving offspring (Norton & Kelly 1988). These gains must be sufficiently high to outweigh the disadvantages associated with skipping reproduction during the intervening years. The two most popular types of economy of scale advanced to date are the predator satiation hypothesis and the wind pollination hypothesis (reviewed by Kelly 1994). The predator satiation hypothesis says that individuals flowering and fruiting in heavy-seed years lose a relatively small proportion of their seed crop to predators; the wind pollination hypothesis says that individuals flowering in heavy-flowering years experience relatively high pollination success. Although the predator satiation hypothesis is quite well tested, much less experimental evidence has been gathered for the wind pollination hypothesis (Kelly & Sullivan 1997).

The genus *Chionochloa* Zotov (Poaceae) consists of 22 species collectively known as snowgrasses.
They occupy extensive areas of the montane, subalpine, and alpine zones in New Zealand (Conner 1991) and in many places are the dominant plant species. All studied species (except perhaps C. rubra) show very pronounced mast seeding (Mark 1968; Kelly et al. 1992; Webb & Kelly 1993) and Chionochloa species have some of the highest CV's (coefficients of variation) of seed production of any species worldwide (McKone et al. 1998). Chionochloa species are wind-pollinated, like all grasses. They also suffer very high levels of pre-dispersal seed and flower predation from at least three native insects (Kelly et al. 1992; Kelly & Sullivan 1997). Therefore, any possible benefits from mast seeding could come from wind pollination, or from predator satiation, or both.

Kelly & Sullivan (1997) used ten years of observational data on seed predation and pollination success for Chionochloa pallens, to quantify the benefits of mast for this species. Their results suggested that predator satiation gave c. 95% of the present benefits from masting, and wind pollination, though significant, played a much smaller role. That study was based on estimating pollination success between years which varied in flowering intensity. However, other factors which vary between years (such as rain or fog during the time of pollination) also strongly affect pollination success, potentially confounding observational studies.

This study used an experimental approach to manipulate local flowering density during one season and determine the effect on pollination success and predation rates. The within-season approach has been used successfully before. Nilsson & Wästljung (1987) selected beech (Fagus) stands of different sizes as a spatial analogue of mast and non-mast years, and compared the pollination success of individuals within them. They were able to show that individuals flowering in large stands produced a relatively high percentage of viable seed, presumably because of high pollen densities, lending support to the wind pollination hypothesis. The present study differs from Nilsson & Wästljung’s (1987) in one important respect. Instead of using existing stands of different sizes, natural flowering densities in continuous tussock grassland were artificially manipulated by thinning inflorescences pre-anthesis to create local flowering densities similar to those in high and low-flowering years. The overall aim was to determine whether wind-pollination could be providing a current selective benefit to masting in Chionochloa.

METHODS
This study was carried out on Chionochloa macra Zotov, which grows with C. pallens over wide areas of the eastern Southern Alps in the South Island of New Zealand. The experiment was implemented at two sites on upper slopes of Mt Hutt, Canterbury, during February and March 1995. The sites were close to those used for previous work on mast seeding in Chionochloa (Kelly et al. 1992; Kelly & Sullivan 1997). The mid-altitude site (1350 m, grid reference NZMS 260 K35/533434) was situated on the east face adjacent to Rakaia Saddle, and the high altitude site (1620 m, NZMS 260 K35/518446) was just below the Mt Hutt Skifield car park and only about 20 m from the high altitude site of Kelly et al. (1992). Vegetative cover at both sites was fairly continuous C. macra tussocks with interstitial herbs and some small areas of bare rock and bare soil.

The flowering manipulations were feasible because the 1995 season was a prolific flowering year (mast year), second over the last decade only to that of 1986 (Kelly & Sullivan 1997). Three flowering densities within plots were chosen: unthinned (controls), thinned, and super-thinned. Flowering density in the control plots was about 15 inflorescences m⁻². Thinned plots had developing inflorescences clipped off pre-anthesis to leave approximately one inflorescence m⁻², and in super-thinned plots about 0.2 inflorescences m⁻² were left. These thinned values are within the range of flowering intensities recorded during low years. For example, at Kelly & Sullivan’s (1997) site at 1060 m on Mt Hutt where the flowering effort of C. pallens was usually higher (66.2 m⁻² in 1995), the lowest recorded flowering intensity over 10 years was 0.09 inflorescences m⁻² and the median year had a flowering intensity of 7.0 inflorescences m⁻². Hence, the three flowering density treatments were similar to good, low, and very low flowering years at Mt Hutt (Kelly & Sullivan 1997).

At the high altitude site, two thinned and two super-thinned plots, each 10 m x 10 m with a 10 m buffer zone, were randomly located and each had a paired 5 m x 5 m control plot. Since control plots were untreated, their size had no effect on pollination success and so smaller plot dimensions were used. Control plots were c. 10 m beyond the buffer zone of the treatment plot (effectively giving them a 10 m buffer of high inflorescence density), and treatment/control pairs were separated by 30–80 m from other pairs. At the mid-altitude site, two control plots and two thinned plots were set up using identical sizes and similar spacings. Because of time
constraints, no super-thinned plots were established at the mid-altitude site. Flowering densities were reduced by cutting off developing inflorescences 10 cm above the base of each tussock. A maximum of three inflorescences per tussock remained after thinning in the thinned density plots; super-thinned plots were left with no more than one inflorescence per tussock. The total number of inflorescences left in each plot was then counted. Thinning was carried out during the middle of February prior to anthesis, which occurred about two weeks later. Plots were checked at regular intervals following thinning in order to remove late developing inflorescences.

One possible problem is that the experimental plots were small relative to pollen dispersal distances, so that background pollen from beyond the manipulated areas could result in higher than intended local pollen densities. To calculate the magnitude of this effect we modelled local pollen densities to estimate the amount of pollen arriving at the centre of the 100 m$^2$ treatment plot from different distances out to 30 m. We calculated pollen catch as decreasing with the cube of distance (Faegri & van der Pijl 1971, p. 39) in 10 cm steps, then multiplied by the area involved at that distance and summed over all distances. For simplicity, the model used circular plots of the same area as the treatment plots (a treatment plot of 5.6 m radius, with a buffer zone extending to 16.9 m radius). When the whole area was assigned a uniform density of inflorescences, the vast majority (98.6%) of the pollen catch in the centre of the treatment plot came from within the plot and only 0.25% from beyond the buffer zone. However, when the treatment plots were thinned to lower densities than the rest of the area, background pollen became relatively more important. We compared pollen catch in the treatment plot under the thinned treatment (1 inflorescence m$^{-2}$ in the treatment plot; 0 m$^{-2}$ in the buffer zone; and 15 m$^{-2}$ beyond that) with that expected in a uniformly low year (1 m$^{-2}$ at all distances). In this case, pollen from beyond the buffer zone contributed 3.6% of all pollen, and the total pollen catch was 2.3% higher than expected compared with a uniform flowering density of 1 m$^{-2}$. Similarly, the super-thinned treatment (0.2, 0, 15) was compared with a uniformly very low year (0.2 m$^{-2}$ at all distances). In this case, 15.8% of the pollen catch came from outside the buffer zone, raising total pollen catch by 17.1%; making the pollen catch equivalent to a uniform inflorescence density of 0.234 m$^{-2}$. Since this is still much lower than the control plots, we conclude that the treatments did produce major alterations in local pollen catches similar to those experienced during low and very low flowering years.

Following anthesis and ovary development, 15 inflorescences were selected arbitrarily from throughout each plot to determine seed fate. No more than one inflorescence was collected from any tussock. Inflorescences were then stored in a freezer at -10°C until dissection began. For each inflorescence the total number of spikelets was recorded, and on 10 spikelets all florets (usually totalling 50–60 per inflorescence) were examined under a dissection microscope. Seeds were assigned to one of six categories adapted from Kelly et al. (1992) and Cone (1995). These categories described the developmental stage of the seed (seed present or absent, unfilled or developing), whether predated or not, and if possible the identity of the predator (if present, or by characteristic feeding sign).

Pollination failure was estimated following the method of Kelly & Sullivan (1997), using the proportion of ovaries which did not expand. Kelly & Sullivan (1997) excluded predated florets from their analysis. In this study, lower levels of predation were recorded and nearly all was by the late-feeding cecidomyiid, so determination of filled or unfilled ovaries was usually possible even in predated florets. Hence, predated florets were not excluded from our analysis. Although the proportion of unfilled ovaries is not a direct estimate of pollination failure, it does set an upper limit. This method is frequently used for quantifying pollination efficiency (Nilsson & Wästljung 1987; Norton & Kelly 1988; Allen & Platt 1990).

Analysis

Two logistic regressions with binomial error distributions were carried out using the S-plus statistical package (Statistical Sciences Inc. 1993) to test whether predation and the proportion of unfilled seed varied between density levels (Dobson 1990). Two predictors were included in each model: site and density. The response variables for the two models were the proportion of predated seed and the proportion of unfilled (aborted) seed, respectively. Each analysis was performed at two levels of replication, plot and inflorescence. This was done because the low number of replications at the plot level meant it was not possible to test for an interaction between the two main effects without fitting a saturated model (Crobbie & Hinch 1985). In addition, the two levels of replication (plot and inflorescence) represent extremes for assumptions of independence of data points. Although inflorescences within a plot were
of insect were recorded within florets; orange larvae of the unidentified Cecidomyiid fly species (Diptera: Cecidomyiidae) reported by previous authors (Kelly & Sullivan 1997), and an unidentified Eulophid wasp (of the Eulophinae; A. Cone pers. comm.). The wasp is probably a parasitoid of the cecidomyiid. These insects were found in 95% and 2%, respectively, of all damaged florets. The remaining damaged florets (3%) could not be attributed to any particular seed predator. Predation showed no clear relationship to flowering density (Fig. 1A) and proved to be non-significant at both plot and inflorescence levels (Table 1). The site main effect and interaction between site and density were also non-significant.

A weak negative relationship was found between the proportion of unfilled seed and flowering density (Fig. 1B) with super-thinned plots having more unfilled seeds (35%) than the thinned plots (24%) and twice as many as the controls (18%). However, these differences were not statistically significant at either the plot or the inflorescence level despite explaining up to 38% of the deviance (Table 1).

Fig. 1 The effect of flowering density on reproduction in Chionochloa macro at Mt Hutt, 1995. A, proportion of florets predated; B, proportion of florets with unexpanded ovaries (assumed to represent pollination failure). Sample sizes were 89 inflorescences for controls, 60 for thinned, and 29 for super-thinned treatments. Boxplots show median and interquartile distance (IQD); error bars indicate 1.5 × IQD and lines represent outliers.

subjected to the same density manipulation, it was considered that circumstances affecting one inflorescence were unlikely to influence neighbouring inflorescences. Inflorescences were therefore partially independent, but the degree of independence could not be determined. The inflorescence level analysis represents the most optimistic assumption of complete independence of inflorescences, and the plot level analysis represents the most pessimistic assumption of complete dependence within a plot.

RESULTS

Seed predator damage to florets ranged from 24% in the super-thinned plots to 35% in the thinned plots and 28% in the controls (Fig. 1A). Only two types

DISCUSSION

Predation

Kelly & Sullivan (1997) showed a strong effect of mast seeding on reducing predation in C. pallens at Mt Hutt, and concluded that predator satiation was providing most of the benefits of mast seeding. In this study, the proportion of seed lost to predators did not decline in low flowering density treatments, but this was not totally unexpected. Kelly & Sullivan (1997) showed that the change in flowering intensity from the previous year was a much better predictor of predation levels than the flowering intensity of the current year. They concluded that this showed that the predator satiation effect depended on the numerical response, i.e., starving of seed predators in low-flowering years so that flowers in the following year could escape predation. If that is correct, then thinning inflorescences within small plots in a single year would not necessarily reduce the number of predators or the level of predation. In fact, such thinning may even increase the level of predation, when the same number of predators is concentrated onto fewer remaining inflorescences. Another factor which may come into operation at very low inflorescence densities is that the search range of the insects may become limiting; Kelly et al. (1992) reported that in the very low flowering of 1992, some
inflorescences were heavily attacked while others had no seed predators at all, giving a moderate mean level of predation but a high variance. Such an effect could contribute to the lower levels of predation seen in this study in super-thinned plots compared with thinned plots. Other factors such as the time of insect pupation, plot and buffer size, and the predators' searching abilities may also have had an effect on the outcome. Therefore, these data do not support the predator satiation hypothesis, but they are not conclusive evidence against it because of limitations in the experimental design when used for that purpose.

Pollination

The results show a weak positive relationship between inflorescence density and pollination success. This effect explained 38% of the variance at the plot level but was non-significant because of great between-plot variation. However, the magnitude of the trend is consistent with the significant between-years effect shown in C. pallens by Kelly & Sullivan (1997), where unfilled seeds increased from about 20% in high flowering years to 30% in low years. This suggests that although pollination success may vary with flowering density, the benefits are relatively small; presumably this is because pollination is still quite efficient even at low flowering densities. We would therefore predict that the pollination benefits to be gained by following a masting reproductive strategy would be so small that they would be unlikely to compensate for the disadvantages of missing reproductive opportunities in the intervening years. This result accords well with the conclusions of Kelly & Sullivan (1997). Moreover, grasses like Chionochloa allocate relatively few resources to unpollinated florets. The models of Smith et al. (1990) show that in species which allocate few resources to unpollinated florets, the per-flower effect of pollination failure is much lower than in species (such as gymnosperms) which allocate substantial resources to unpollinated structures. Therefore, we find little evidence for an important pollination benefit from masting in Chionochloa.

However, there are two caveats that must be added. Firstly, both our two study sites and that of Kelly & Sullivan (1997) consist of continuous tussocks with high vegetative cover. This means that there are many tussocks per unit area of ground, and so even in low flowering years, there are relatively many inflorescences m\(^{-2}\). In areas where the Chionochloa plants are more widely spaced, either because of competition from other plants (such as tussocks growing along the edge of streams or bluffs adjacent to forest) or because of human activity (such as burning or animal grazing), then the same flowering effort in inflorescences per tussock will represent a lower inflorescence density m\(^{-2}\). In such cases, less efficient pollination will occur at any specified number of inflorescences per tussock, and the benefits from concentrating pollination in high flowering years may be more substantial.

Table 1  Analysis of deviance tables of proportion of predated and unfilled (unpollinated) Chionochloa macra seeds at three flowering densities, for the main effects site and density at the plot and inflorescence levels, and at the inflorescence level the site x density interaction. The lines testing for a density effect are in bold face.

<table>
<thead>
<tr>
<th>Terms added</th>
<th>Residual deviance</th>
<th>Residual degrees of freedom</th>
<th>Deviance explained</th>
<th>Degrees of freedom</th>
<th>% of deviance explained</th>
<th>Probability (/$\chi^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predated (plot level)</td>
<td>Null</td>
<td>0.206</td>
<td>11</td>
<td>0.0014</td>
<td>1</td>
<td>0.68</td>
</tr>
<tr>
<td>Site</td>
<td>0.205</td>
<td>10</td>
<td>0.00001</td>
<td>2</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>Density</td>
<td>0.205</td>
<td>8</td>
<td>0.000001</td>
<td>2</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>Predated (infl. level)</td>
<td>Null</td>
<td>25.916</td>
<td>177</td>
<td>0.035940</td>
<td>1</td>
<td>0.13</td>
</tr>
<tr>
<td>Site</td>
<td>25.880</td>
<td>176</td>
<td>0.035941</td>
<td>2</td>
<td>0.05</td>
<td>0.492</td>
</tr>
<tr>
<td>Density</td>
<td>24.461</td>
<td>174</td>
<td>1.419413</td>
<td>2</td>
<td>5.7</td>
<td>0.492</td>
</tr>
<tr>
<td>Site x Density</td>
<td>24.383</td>
<td>173</td>
<td>0.077302</td>
<td>1</td>
<td>0.30</td>
<td>0.781</td>
</tr>
<tr>
<td>Unfilled (plot level)</td>
<td>Null</td>
<td>0.444</td>
<td>11</td>
<td>0.165</td>
<td>1</td>
<td>37</td>
</tr>
<tr>
<td>Site</td>
<td>0.280</td>
<td>10</td>
<td>0.165</td>
<td>2</td>
<td>38</td>
<td>0.920</td>
</tr>
<tr>
<td>Density</td>
<td>0.112</td>
<td>8</td>
<td>0.167</td>
<td>2</td>
<td>38</td>
<td>0.920</td>
</tr>
<tr>
<td>Unfilled (infl. level)</td>
<td>Null</td>
<td>22.943</td>
<td>177</td>
<td>2.797</td>
<td>1</td>
<td>12.19</td>
</tr>
<tr>
<td>Site</td>
<td>20.146</td>
<td>176</td>
<td>2.797</td>
<td>2</td>
<td>9.78</td>
<td>0.309</td>
</tr>
<tr>
<td>Density</td>
<td>17.798</td>
<td>174</td>
<td>2.346</td>
<td>2</td>
<td>9.78</td>
<td>0.309</td>
</tr>
<tr>
<td>Site x Density</td>
<td>17.612</td>
<td>173</td>
<td>0.186</td>
<td>1</td>
<td>&lt; 1</td>
<td>0.666</td>
</tr>
</tbody>
</table>
Secondly, other work suggests that pollen quality may be important as well as pollen quantity. McKone et al. (1997) have added to Connor’s (1967) earlier work on self-compatibility in the Chionochloa genus. Self-pollen from both C. macra and C. pallens was found to be equally as viable as cross pollen at germinating on excised stigmas. Connor’s (1967) research showed that selfed florets produce numerous seeds which grow into large, fecund offspring. However, McKone et al. (1997) deduced from other information that outcrossing may be common in Chionochloa despite the high level of self-fertility. Moreover, Connor suggested that in C. conspicua selfed offspring showed inbreeding depression through a much higher death rate of selfed seedlings. This is interesting because the present study has shown that there is little advantage in masting in terms of the quantity of full seed produced, but it has not shown how the quality of that seed (selfed versus outcrossed) varies between mast and non-mast years. If the quality of seed produced during mast years is proportionally higher than that of seed produced during the intervening years, this may provide enough selection pressure to select for masting. The fraction of seeds which result from self-pollination may be much more sensitive to flowering density that the fraction of unfilled seeds. If self-pollinated seeds show significant inbreeding depression, there may be a stronger wind pollination-mediated selective benefit to mast seeding than our simple measurements of seed production have shown. Thus, before the wind pollination hypothesis can be rejected in Chionochloa, further research is required to determine how strongly seed quality in the field is affected by flowering intensity.

ACKNOWLEDGMENTS

We thank the Miss E. L. Hellaby Indigenous Grassland Research Trust for financial assistance, Angela Cone for help with insect identification, and Andrea Thom and Alan Mark for comments on an earlier draft.

REFERENCES


