

Predator satiation and extreme mast seeding in 11 species of *Chionochloa* (Poaceae)

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Variation in annual flowering effort is described for 16 long datasets from 11 species of *Chionochloa* (Poaceae) in New Zealand. All populations exhibited extreme mast seeding. The most variable species was *C. crassiuscula* (coefficient of variation, $CV = 3.02$) over 26 years at Takahe Valley, Fiordland, which is the highest published CV we know of worldwide. The other populations also had high CVs (lowest $CV = 1.42$, mean $CV = 1.84$) which were higher than for other well-studied genera such as *Picea*, *Pinus* and *Quercus*. There were also frequent years of zero flowering (mean across all populations was 37.2% zero years; maximum 53% for *C. rubra* and *C. crassiuscula* over 19 years) whereas zero years are rare in other published masting datasets.

Flowering was highly synchronous among species within a site (mean $r = 0.886$), and also (though significantly less so) among sites. Among sites, synchrony was not significantly higher within-species (mean $r = 0.711$) than between-species ($r = 0.690$). Warm summer temperatures led to heavy flowering the following summer. Flowering synchrony increased with increasing synchrony in local deseasonalised summer temperatures, and decreased with increasing distance between sites.

Mast seeding has been shown in *Chionochloa* to reduce losses to specialist flower or seed predators. Among-species synchrony may be adaptive if species share a common seed predator. Developing seeds of at least 10 *Chionochloa* species are attacked by larvae of an undescribed cecidomyiid. In Takahe Valley, where masting is most pronounced, cecidomyiids attacked all six *Chionochloa* species in all four years studied. Mean annual losses were almost constant (10.0 to 13.4%) while flowering effort varied 100-fold. The invariant losses are consistent with other evidence that the cecidomyiid may have extended diapause, which would make it harder to satiate by mast seeding. We hypothesise that one possible factor favouring such extremely high levels of mast seeding in *Chionochloa* is that its seed predator is very hard to satiate.

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Mast seeding is the intermittent synchronous production of large seed crops by a population of plants (Kelly 1994). It requires variation among years in the reproductive effort of individual plants and synchrony between individuals within a population. Mast seeding is found in plants from many different taxonomic groups

and from most parts of the world, although it seems to be especially common in temperate forest trees (Silver-town 1980) and in the New Zealand flora (Webb and Kelly 1993, Kelly 1994). From an evolutionary viewpoint, mast seeding has several clear disadvantages including: (1) increased density-dependent competition,

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seedling predation or pathogen attack (Hett 1971, Augspurger 1981, Kelly 1994); and (2) lost opportunities for colonisation when these occur in years of very low seed production or should the individual die before its next flowering episode (Waller 1979). Also, different species in the same environment often differ greatly in their degree of masting, which suggests that the variation is not purely environmentally determined (Campbell 1981, Webb and Kelly 1993, Kelly 1994). For masting to persist despite the known disadvantages, compensating economies of scale should exist (i.e. occasional large reproductive efforts are more efficient than frequent smaller ones: Norton and Kelly 1988). The two most common mechanisms proposed for this are predator satiation (Janzen 1971, Silvertown 1980) and enhanced wind pollination (Nilsson and Wästljung 1987, Norton and Kelly 1988).

Mast seeding is a quantitative phenomenon, since all plant populations vary in their reproductive outputs to some degree among years. The term mast seeding is applied to those populations at the more variable end of the continuum (Kelly 1994), measured by the coefficient of variation of seed output (CV, i.e. population standard deviation divided by the mean). Populations with greater CVs presumably will show both greater costs from masting, and stronger compensating selective benefits. Unfortunately long-term quantitative data for highly variable species are not easily obtained. Herrera et al. (1998) reviewed 296 published and unpublished datasets, 83% of which were ≤ 10 yr in length. They showed a range of CVs from 0.10 to 2.20 (given as 0.12–2.33 in Herrera et al. 1998, but see Materials and methods for correction of CVs). Their highest CV of 2.20 for *Cassia helmsii* in Western Australia (Davies 1976) is the highest published CV we know of, apart from the species in the present study. CVs ≥ 2.0 are relatively rare (4% of the 172 datasets ≥ 6 yr in Herrera et al. 1998 and 9% of the 23 in Webb and Kelly 1993).

Here we present long-term datasets (mean = 19.9 yr) on mast seeding in *Chionochloa* (Poaceae; nomenclature follows Connor 1991), a genus of perennial tussock grasses (bunchgrasses) from New Zealand. These grasses are distributed from sea level to above the tree line and are dominant in most alpine and sub-alpine grasslands (Wardle 1991, Mark 1992). All 12 *Chionochloa* species for which there are published flowering observations (Connor 1966, Mark 1968) or long-term counts (Kelly et al. 1992, Webb and Kelly 1993, Kelly and Sullivan 1997, McKone et al. 1998) exhibit mast seeding. Some of these species show very high CVs: *C. pallens* (CV = 2.02) was the second most variable species in Webb and Kelly (1993), and an earlier publication on some of the present data (McKone et al. 1998) reported CVs of 1.7 to 2.8 in *Chionochloa* populations in Takahe Valley in southwest New Zealand.

The high CVs in *Chionochloa* have been attributed to selection for predator satiation rather than enhanced

pollination, because variable flowering reduces predation markedly, but has little effect on pollination success (Kelly and Sullivan 1997, Tisch and Kelly 1998, Kelly et al. 2000). In the *Chionochloa* species for which pre-dispersal seed predation has been investigated, flowers and seeds are damaged by at least three invertebrates: *Diplo-toxa similis* (Diptera: Chloropidae); an undescribed cecidomyiid fly; and *Megacraspedus calamogonus* (Lepidoptera: Gelechiidae) (White 1975, Kelly and Sullivan 1997, Sullivan and Kelly 2000, McKone et al. 2000). The three are known solely (the cecidomyiid) or almost exclusively from *Chionochloa* florets (Hudson 1928, White 1975, Cone 1995). Mean annual losses to these three predators are often over 50% and can reach as high as 94% of florets (White 1975, Kelly et al. 1992, Kelly and Sullivan 1997, Sullivan and Kelly 2000). *C. pallens* gains large selective benefits from masting through predator satiation; when seed production is much higher than the previous year, the predators consume a smaller percentage of florets (Kelly and Sullivan 1997).

Some evidence indicates that masting may be synchronised among species of *Chionochloa* as well as among individuals within a species (Mark 1968, Kelly et al. 1992, Kelly and Sullivan 1997, McKone et al. 1998). This synchrony may be due to shared climate cues for high seed years in the different *Chionochloa* species. Synchrony among species could be adaptive if the species share common seed predators (Kelly et al. 1992, Kelly and Sullivan 1997). All three species of invertebrate predator have been reported from a wide range of sites and from several different *Chionochloa* species (White 1975, Kelly et al. 1992, Sullivan and Kelly 2000). There are previously published references to the cecidomyiid attacking at least eight different *Chionochloa* species: *C. australis*, *C. crassiuscula*, *C. flavescens*, *C. rigida*, *C. pallens* (Burrows 1961); *C. oreophila* (Burrows 1968); *C. macra* (Tisch and Kelly 1998); and *C. rubra* (Sullivan and Kelly 2000).

In this paper we use 16 long-term datasets for 11 species of *Chionochloa* to examine the following questions: 1. How variable is *Chionochloa* seed production among years? 2. Are different species in synchrony with each other? 3. Are the climatic cues associated with high seed years consistent across *Chionochloa* species? 4. How widespread are the seed predators, and is seed predation a likely selective force contributing to the high degree of masting in *Chionochloa*?

Materials and methods

Study species and sites

Chionochloa is an Australasian genus of tussock grasses (bunchgrasses) with 22 species endemic to New Zealand. In most species the plants grow as individual

tufts which are usually 0.5–1.5 m tall and up to 50 cm in basal diameter, with very little or no rhizomatous spread (Connor 1991). The flowers are wind pollinated and have dry seeds dispersed by gravity. The climate cue which triggers heavy flowering events in *Chionochloa* is high temperatures in the summer before flowering (Mark 1965, Connor 1966, 1968, McKone et al. 1998).

Four widely separated study sites were used in the South Island (Table 1) and three were essentially unmodified by humans. The Takahe Valley site is in the southwest corner of the island in a special restricted access area of Fiordland National Park (because of the presence of the endangered takahe *Notornis mantelli*). Four *Chionochloa* species were found in the grasslands at the head of the valley: *C. crassiuscula* (12% of the *Chionochloa* biomass), *C. pallens* (21%), *C. rigida* (47%) and *C. teretifolia* (20%). The two other species occurred in separate locations lower down the valley. Flowering effort (inflorescences per tussock) was measured on about 150–200 plants of each species from 1973 until 1990; thereafter, 100 tagged plants on permanently marked lines were measured for each species. Total flowering effort is the product of inflorescences per tussock \times spikelets per inflorescence \times florets per spikelet, but the overwhelming majority of the variation is at the inflorescences per tussock level (Kelly et al. 1992), so here we present data at that level.

The Mt Misery site is 560 km away at the head of Lake Rotoroa in Nelson Lakes National Park at the northern end of the South Island. The study site is in unmodified high alpine grassland above *Nothofagus* forest. *Chionochloa* inflorescences were counted in late February every 5 m along a marked transect 1 km long. At each of the 200 points every inflorescence of *C. pallens* was counted in a 1-m² plot, and those of *C.*

australis in a 0.25-m² plot. Individual plots were not permanently marked.

At Camp Creek, on the western edge of the central Southern Alps, six species were recorded in an area of unmodified subalpine and alpine vegetation above *Metrosideros*–*Weinmannia* forest. For each species, 50 permanently tagged plants were counted each year. No data were collected in 1991 for five of the species, although this was a low flowering year for all species.

The Mt Hutt site is in Canterbury on the eastern edge of the central Southern Alps, adjacent to a skifield road. This site is the only one to have suffered significant disturbance in historical times, as the grassland established within the last few hundred years after human fires cleared *Nothofagus solandri* forest from the site. Vegetation is dense *C. pallens* (94% of the tussock cover) with occasional *C. macra* (6%). Tussocks were recorded on three 20-m-long transects. Until 1989 the lines were relocated in approximately the same places and only *C. pallens* was recorded. From 1990 lines were permanently marked with metal posts, and both *C. pallens* ($n = 80$) and *C. macra* ($n = 16$ to 1994, 34 thereafter) were mapped. For more details see Kelly et al. (1992) and Kelly and Sullivan (1997).

Degree of masting and synchrony

As *Chionochloa* flowers and sets seed late in the austral summer, flowering counts were carried out in February–April, so 1986 specifies the 1985–1986 summer. The coefficient of variation of flowering intensity (CV) was calculated for each *Chionochloa* population. In calculating CVs, the population standard deviation (denominator n) was used rather than the sample standard deviation (denominator $n - 1$), as the latter inflates the

Table 1. Site data for flowering records of *Chionochloa* spp in the South Island, New Zealand.

Site	Latitude (S)	Longitude (E)	Species sampled	Altitude (m)	Years of study
Takahe Valley	45° 17'	167° 39'	<i>C. crassiuscula</i>	1200	1973–1998
			<i>C. pallens</i>	1200	1973–1998
			<i>C. rigida</i>	1200	1973–1998
			<i>C. rubra</i>	600	1973–1998
			<i>C. spiralis</i>	950	1973–1998
			<i>C. teretifolia</i>	1200	1973–1998
Mt Misery	41° 56'	172° 40'	<i>C. australis</i>	1550	1976–1998
			<i>C. pallens</i>	1550	1976–1998
Camp Creek	42° 43'	171° 33'	<i>C. conspicua</i>	900	1979–1998*
			<i>C. crassiuscula</i>	1250	1979–1998*
			<i>C. flavescens</i>	1250	1979–1998
			<i>C. oreophila</i>	1430	1979–1998*
			<i>C. pallens</i>	1250	1979–1998*
			<i>C. rubra</i>	1100	1979–1998*
Mt Hutt	43° 32'	171° 33'	<i>C. macra</i>	1070	1990–1998
			<i>C. pallens</i>	1070	1986–1998

* No data for 1991.

CVs for small datasets rather than accurately describing the variation in the data on hand. In addition, for each site, mean CVs were calculated from the mean flowering intensity over all sympatric species for each year. This was done to measure the food supply available at each site to a seed predator which was able to feed on all *Chionochloa* species equally. Where biomass data were available (Takahe Valley and Mt Hutt) the means were weighted by the biomass of each species at the site, so that the CVs were based on the total biomass of *Chionochloa* florets available each year. All regressions against flowering intensity used $\log(\text{flowering intensity} + 1)$.

To measure synchrony between populations, we standardised all masting data before analysis. First, all measurements were transformed by taking the natural logarithm. If the data set contained zeroes, then the smallest positive value in that data set was added to all values before log-transformation. After log-transformation, the mean was subtracted from all values, and then all values were divided by their sample standard deviation (SD). The resulting data sets all had mean = 0 and SD = 1. We then characterised the degree of masting synchrony among species and sites by the Pearson correlation coefficient (r). Cross-correlations were tested for significance after adjusting degrees of freedom according to the autocorrelation functions (ACFs) of the two series (Sciremammano 1979). The standard test for significance of a correlation ($r \geq Z_{1-\alpha}(n-1)^{0.5}$) assumes that all observations are independent, which is not the case for autocorrelated variables such as masting. If two autocorrelated time series have similar ACFs, then the sample cross-correlation will exceed $Z_{1-\alpha}(n-1)^{0.5}$ at a much higher frequency than the nominal α level. We reduced degrees of freedom from $n-1$ to n_{adj} to account for this lack of independence.

The magnitude of the CVs and the percent of years when no flowering was observed were compared to data for other species from the literature. A total of 335 datasets were collated from various sources (Waldron 1965, Alexander et al. 1982, Hickey et al. 1983, Graber and Leak 1992, Pucek et al. 1993, Kelly 1994, Fitzgerald et al. 1996, Herrera et al. 1998, Wilson et al. 1998, Hickey and Wilkinson 1999) of which only those of 6 yr or longer were used ($n = 210$). CVs from Herrera et al. 1998 were based on $SD(n-1)$ and so were corrected to $SD(n)$ for consistency. Curran et al. (1999) give a CV of 2.22 based on 14 yr data for dipterocarps in Borneo, but this number is based on only undamaged fruit rather than all fruit so is not included here. Davies (1976) gives a dataset for *Acacia aneura* at Ejah with $CV = 2.83$ but this appears to be the site where all five sampled plants suffered hail damage, so is excluded. For 74 of these datasets the percentage of years of zero flowering was also available and this was examined separately.

Climate

As floral induction occurs in *Chionochloa* during the summer before flowering (Mark 1965, 1968), climate data from the previous summer were regressed against flowering intensity. Mean values for December, January, February, December–January, January–February, and December–February were calculated for local air temperature and rainfall data. The temperature data used for Takahe Valley were from the valley itself, and rainfall data were from Te Anau; for Mt Misery, we used temperatures from Motueka and rainfall from Lake Rotoiti; for Camp Creek, temperatures from Hokitika and rainfall from Inchbonnie; and for Mt Hutt, temperatures from Christchurch and rainfall from Lake Coleridge (National Institute of Water and Atmosphere Research). Mean monthly temperature data for each site were deseasonalised to avoid spuriously high correlations among sites caused by synchronous seasonal changes in temperature. Temperature data were deseasonalised by subtracting from each monthly datum the monthly average temperature for that site from October 1972 until December 1997 (Takahe Valley), or January 1950 until December 1997 (all other sites). As January and January–February temperatures were the best predictors of flowering intensity, deseasonalised mean January and deseasonalised mean January–February temperatures were correlated among sites. Although some temperature records were from lower altitudes than the study sites, resulting in higher absolute temperatures, this effect was also removed by deseasonalising and the deseasonalised monthly temperatures were highly correlated within regions (data not shown).

Seed predation

Pre-dispersal predation levels were measured in all six *Chionochloa* species from Takahe Valley from 1995 to 1998. Approximately 15 inflorescences per species were collected from separate tussocks annually, late in the flowering season (see Table 5). In years of low or zero flowering on our flowering transects, wherever possible we located inflorescences nearby at the site in order to estimate predation at the site. In some years, fewer than 15 inflorescences could be collected due to very sparse flowering. The inflorescences were placed in plastic bags and frozen as soon as possible (usually 2–3 d after collection). The florets of 10 spikelets per inflorescence were dissected (or all spikelets, if the inflorescence contained less than 10). Between 215 and 838 florets were examined per species per year, except for *C. teretifolia* in 1998 (Table 5). The presence of predators within the florets was noted, as was the condition of anthers and ovary and damage to the lemma or palea. Predation levels by each known *Chionochloa* pre-disper-

Table 2. Degree of mast seeding (CV of flowering intensity), and percentage of years in which zero flowering was recorded, in *Chionochloa* species and for combined site totals for the genus. For Takahe Valley and Mt Hutt site totals were weighted by biomass of each species. Headbasin = for all species occurring together at the head of Takahe Valley (*C. crassiuscula*, *C. pallens*, *C. rigida* and *C. teretifolia*).

Species	Site	CV	% zero-flowering years	Years of data
<i>C. crassiuscula</i>	Takahe Valley	3.02	42	26
<i>C. teretifolia</i>	Takahe Valley	2.57	50	26
<i>C. rigida</i>	Takahe Valley	2.18	46	26
<i>C. australis</i>	Mt Misery	1.94	30	23
<i>C. rubra</i>	Camp Creek	1.91	53	19
<i>C. crassiuscula</i>	Camp Creek	1.81	53	19
<i>C. pallens</i>	Camp Creek	1.80	47	19
<i>C. flavescens</i>	Camp Creek	1.73	45	20
<i>C. pallens</i>	Mt Hutt	1.73	0	13
<i>C. rubra</i>	Takahe Valley	1.69	38	26
<i>C. pallens</i>	Takahe Valley	1.63	27	26
<i>C. conspicua</i>	Camp Creek	1.58	42	19
<i>C. oreophila</i>	Camp Creek	1.51	37	19
<i>C. pallens</i>	Mt Misery	1.52	17	23
<i>C. spiralis</i>	Takahe Valley	1.44	33	6
<i>C. macra</i>	Mt Hutt	1.42	33	9
All headbasin spp.	Takahe Valley	2.07	27	26
Both spp.	Mt Hutt	1.67	0	9
Both spp.	Mt Misery	1.62	17	23
All spp.	Camp Creek	1.56	32	19

sal predator were calculated as florets containing the predator plus florets containing characteristic signs of that predator, following White (1975), Kelly et al. (1992), Cone (1995), Kelly and Sullivan (1997), Sullivan and Kelly (2000), and McKone et al. (2000). The only seed predator found, an unidentified cecidomyiid, is thought to move between florets and destroy approximately 2–3 florets per larva (Cone 1995), but the number of eggs produced per female cecidomyiid is unknown. A two-way Anova with inflorescences as replicates was used to test overall levels of cecidomyiid predation among years, host species, and the year by species interaction. As there were numerous inflorescences with zero predation, a binomial GLM on predation present/absent was also calculated but this gave identical results and is not presented.

Results

Flowering variability

There was wide variation in flowering effort between years in all studied species. The most variable species was *C. crassiuscula* (CV = 3.02) over 26 yr at Takahe Valley, Fiordland and the mean CV across all datasets was 1.84 (Table 2 and Appendix 1). Even the combined CVs for total flowering by all *Chionochloa* species at a site (which would represent the food supply for a seed predator which attacked all *Chionochloa* spp.) were between 1.56 and 2.13. Most species had numerous years without flower production in our transects, and two species at Camp Creek did not flower in 53% of years. In some of these zero years there were occasional

inflorescences on plants outside the transect. Because about 100 plants were monitored at most sites, a flowering effort of zero implies only that less than ca 1% of the total population was flowering, assuming our monitored plants were representative of the entire population. If we had monitored 1000 or 10 000 plants, some of the “zeros” would have been recorded as very low but non-zero flowering efforts; this criticism is true of all datasets on mast seeding to some degree. However, in some years (especially at Camp Creek and Takahe Valley), there were no flowering plants of that species visible anywhere at the site. Only *C. pallens* at Mt Hutt did not have any years of zero flowering, although it came close in 1994 when there were only 11 inflorescences on the entire slope (ca 100 × 150 m). Thirteen of the 16 datasets had two or more consecutive years when no flowering was recorded, the maximum being *C. teretifolia* at Takahe Valley which did not flower for four consecutive years (1991–1994). Because of extensive synchrony between the species (see below), in Takahe Valley in 27% of years none of the four *Chionochloa* species present in the headbasin produced flowers.

When the highest CVs from all data in the literature were tabulated (Table 3), *Chionochloa* spp. from three sites (Takahe Valley, Mt Misery and Camp Creek) took five of the top 20 places, including the top two places by a huge margin. The table also confirms the contention of Webb and Kelly (1993) that New Zealand plants show especially strong masting, with three species of *Nothofagus* (Fagaceae) contributing to 40% of the worldwide top 20 coming from New Zealand. Moreover, many of the datasets in Table 3 from other

Table 3. Most variable cases of mast seeding (highest coefficients of variation) from the literature. "Years" is the number of years of data; only datasets ≥ 6 yr are included. CVs are based on the population standard deviation.

CV	Species	Years	Site	Reference* (site)
3.017	<i>Chionochloa crassiuscula</i>	26	New Zealand	this paper (Takahe Valley)
2.571	<i>Chionochloa teretifolia</i>	26	New Zealand	this paper (Takahe Valley)
2.200	<i>Cassia helmsii</i>	9	Western Australia	Davies 1976
2.185	<i>Fraxinus excelsior</i>	11	Britain	Flowerdew and Gardner 1978
2.182	<i>Chionochloa rigida</i>	26	New Zealand	this paper (Takahe Valley)
2.150	<i>Quercus prinus</i>	12	USA	Beck 1977
2.107	<i>Acacia sp.</i>	9	Western Australia	Davies 1976
2.105	<i>Cassia helmsii</i>	8	Western Australia	Davies 1976
2.072	<i>Nothofagus cunninghamii</i>	22	Tasmania	Hickey and Wilkinson 1999
2.042	<i>Nothofagus truncata</i>	28	New Zealand	Fitzgerald et al. 1996*
2.027	<i>Quercus robur</i>	15	Poland	Pucek et al. 1993
2.020	<i>Phillyrea latifolia</i>	12	Spain	Herrera et al. 1998
2.007	<i>Nothofagus solandri</i>	30	New Zealand	Allen and Platt 1990*
2.006	<i>Picea abies</i>	8	Finland	Sarvas 1968
1.982	<i>Sorbus aucuparia</i>	7	Spain?	Herrera et al. 1998
1.944	<i>Chionochloa australis</i>	23	New Zealand	this paper (Mt Misery)
1.937	<i>Abies concolor</i>	14	California	Fowells and Schubert 1956
1.936	<i>Acacia craspedocarpa</i>	8	Western Australia	Davies 1976
1.924	<i>Nothofagus menziesii</i>	20	New Zealand	Wilson et al. 1998*
1.906	<i>Chionochloa rubra</i>	19	New Zealand	this paper (Camp Creek)

* Data updated since publication.

parts of the world suffered from various limitations. Half were for < 10 yr, making their CV more liable to reflect only a few unusual years. The three datasets from Davies (1976) are all based on only five (or four) plants per dataset, which makes them much more likely to record zeros in low flowering years, inflating the CV. Some report seed counts and/or exclude insect predated seeds which are likely to magnify the CV compared to counts at the flowering stage such as those in *Chionochloa*. It is also noteworthy that few of the classical Northern Hemisphere masting tree genera make the top 20 list; only two *Quercus*, one *Fraxinus*, one *Abies*, and one *Picea* species are included. *Chionochloa* not only had the highest CVs, but also had few low CVs relative to other well studied genera (Fig. 1). All other groups had some or many CVs below 1.0, whereas the lowest for *Chionochloa* was 1.42.

When the 74 available datasets from the literature were ranked by percent zero years, the *Chionochloa* datasets in Table 2 took 14 of the top 18 places. The only other species in the top 18 were three species of *Nothofagus* from Mt Misery, New Zealand (Wilson et al. 1998 and unpublished data) and *Quercus robur* from Poland (Pucek et al. 1993). Only one of the 16 *Chionochloa* datasets (6%) had no zeros, whereas 62% (36/58) of the other datasets had no zero years.

Flowering synchrony

There was a high level of synchrony among *Chionochloa* populations, shown for example in Fig. 2 for *C. pallens* at all four sites. In 1984 none of the 13 monitored populations produced any flowers at all. In 1994, 14 of the 16 populations produced no flowers, and the other two produced very few; in contrast, 1995

was a high flowering year for all species (Appendix 1). Overall, correlation coefficients for flowering intensity between species pairs ranged from 0.43 to 1.00. The correlation was significant (after correcting for autocorrelation) in 71 of the 120 pair-wise comparisons. The number of years in the correlation strongly influenced the magnitude and significance of the correlation coefficient, as would be expected given the effect of sample size on critical values. The three shortest datasets (*C. spiralis* (6 yr), *C. macra* (9 yr), and *C. pallens* (13 yr) at Mt Hutt) contributed many of the non-significant val-

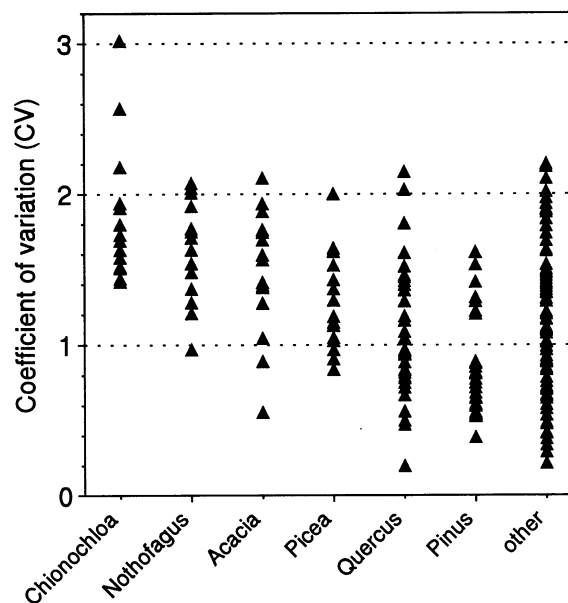


Fig. 1. Degree of masting (CV) for 210 datasets from the literature of 6 yr or more in length. Genera are plotted separately if they had at least 14 cases.

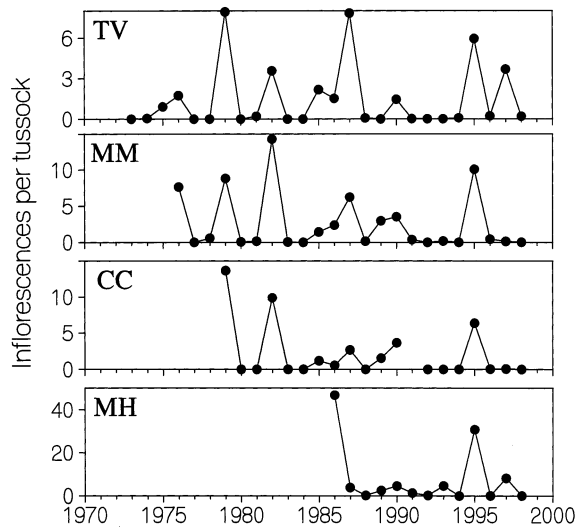


Fig. 2. Synchrony of mast flowering (inflorescences per tussock) for *Chionochloa pallens* at four sites in the South Island of New Zealand. All sites are highly correlated with each other ($0.491 \leq r \leq 0.933$; all are significant after adjusting for auto-correlation [see Materials and methods] except for TV-MH). TV, Takahe Valley; MM, Mt Misery; CC, Camp Creek; MH, Mt Hutt.

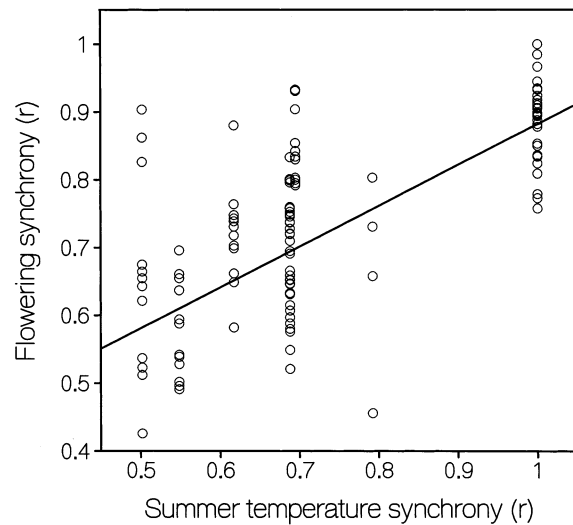


Fig. 3. Degree of synchrony in *Chionochloa* flowering patterns among populations, versus degree of synchrony in deseasonalised summer temperatures for the sites. The regression is significant, and this is still true even if within-site correlations (temperature synchrony = 1.0) are excluded (see text).

ues, and when these were excluded 75% (57/76) of the pair-wise correlations were significant.

The magnitude of the correlation coefficients decreased with increasing distance between sites ($P < 0.0001$, $F = 53.43$, $y = 0.836 - 0.00037x$). Within-site synchrony was significantly higher (mean $r = 0.886$, $n = 32$) than between-site synchrony, whether within a single species (mean $r = 0.711$, $n = 8$) or between species (mean $r = 0.690$, $n = 80$) according to a one-way ANOVA ($F_{2, 117} = 41.38$, $P < 0.0001$). Between-site synchrony was not significantly higher within a species than between species ($F_{1, 86} = 0.25$, $P = 0.621$).

Climate cues for flowering

Mean temperatures the previous summer were strongly related to flowering intensity. Twelve populations had significant regressions ($P < 0.05$), and the other four were nearly significant ($0.05 < P < 0.10$; Table 4). January alone was the best predictor for six populations, January–February was best for nine populations, and February alone for one (the marginally non-significant *C. conspicua*). In contrast, only one of the 96 different regressions of flowering intensity against previous summer rainfall for various months was significant, and as this was the shortest dataset (*C. spiralis*, $n = 6$) little emphasis can be placed on this relationship.

Table 4. Climate predictors of log flowering intensity among years for 16 *Chionochloa* datasets. Site: TV = Takahe Valley, MM = Mt Misery, MH = Mt Hutt, CC = Camp Creek. The predictor used was the best selected from local mean air temperatures averaged over December, January, February, December–January, January–February, or December–February. Where the regression is significant at $P < 0.05$ the R^2 is in bold.

Species	Site	Predictor	R^2	F	df	P	Equation
<i>C. crassiuscula</i>	TV	Jan.	0.340	11.8	1,23	0.002	$-0.670 + 0.073x$
<i>C. pallens</i>	TV	Jan.–Feb.	0.348	11.2	1,21	0.003	$-1.582 + 0.182x$
<i>C. rigida</i>	TV	Jan.	0.422	16.8	1,23	0.0004	$-1.260 + 0.146x$
<i>C. rubra</i>	TV	Jan.–Feb.	0.459	17.8	1,21	0.0004	$-2.167 + 0.245x$
<i>C. spiralis</i>	TV	Jan.	0.593	5.83	1,4	0.073	$-1.491 + 0.165x$
<i>C. teretifolia</i>	TV	Jan.	0.408	15.9	1,23	0.0006	$-1.704 + 0.190x$
<i>C. australis</i>	MM	Jan.–Feb.	0.405	14.30	1,21	0.001	$-4.31 + 0.265x$
<i>C. pallens</i>	MM	Jan.–Feb.	0.339	10.78	1,21	0.004	$-4.22 + 0.263x$
<i>C. macra</i>	MH	Jan.	0.340	3.60	1,7	0.0995	$-3.665 + 0.233x$
<i>C. pallens</i>	MH	Jan.	0.379	6.73	1,11	0.025	$-4.80 + 0.303x$
<i>C. conspicua</i>	CC	Feb.	0.195	4.12	1,17	0.058	$-3.929 + 0.285x$
<i>C. crassiuscula</i>	CC	Jan.–Feb.	0.257	5.89	1,17	0.027	$-2.58 + 0.182x$
<i>C. flavescens</i>	CC	Jan.–Feb.	0.203	4.57	1,18	0.047	$-1.74 + 0.124x$
<i>C. oreophila</i>	CC	Jan.–Feb.	0.173	3.56	1,17	0.076	$-1.223 + 0.0904x$
<i>C. pallens</i>	CC	Jan.–Feb.	0.217	4.71	1,17	0.044	$-2.733 + 0.197x$
<i>C. rubra</i>	CC	Jan.–Feb.	0.219	4.78	1,17	0.043	$-3.62 + 0.257x$

All deseasonalised local mean January temperatures were highly correlated between sites ($P \leq 0.006$), as were all deseasonalised site mean January–February temperatures (all $P < 0.0001$). This shows that summers were warmer or cooler than average in synchrony across the whole South Island. The degree of synchrony of flowering was significantly related to the degree of synchrony in January–February temperatures among sites (Fig. 3; $n = 120$, $R^2 = 0.467$, $F = 103.4$, $P < 0.0001$, $y = 0.356 + 0.527x$) and this was true even if the within-site comparisons were excluded ($n = 88$, $R^2 = 0.103$, $F = 9.88$, $P = 0.0023$). When both temperature synchrony and distance between sites were used to predict flowering synchrony in a stepwise regression, temperature was far more important, although distance was still significant ($P = 0.012$) when added to the model after temperature.

Seed predation, Takahe Valley

Seed ripening per floret varied greatly in Takahe Valley among years and among species due to predation and abortion of ovaries (Table 5). The percentages of healthy seed observed in florets ranged from 0.8% (*C. spiralis* 1998) to 77.8% (*C. pallens* 1995). An average of 9.3% (maximum 28.3%) of florets were empty with no sign of floret damage; it is not known whether these

had successfully dispersed seeds or had suffered cryptic predation. An average of 2.2% (maximum 21.5%) of the florets had definitely suffered predation, but the predator could not be identified. Floret contents were infrequently damaged by fungi, or contained pseudococcid individuals which inflicted ovary damage (cf. Cone 1995). No sign was seen of either *Diplotoxa similis* or *Megacraspedus calamogonus*, both of which attack *Chionochloa* florets at a range of other South Island sites.

The majority of floret damage (mean of 11.5% of all florets) was caused by cecidomyiid larvae. These larvae were found in the florets of all Takahe Valley *Chionochloa* species in all years and according to R. J. Gagné (pers. comm.) are apparently the same as the undescribed cecidomyiid species found feeding on *C. pallens* at Mt Hutt. A two-way Anova showed significant variation among species in mean levels of cecidomyiid predation ($F_{5, 310} = 27.9$, $P < 0.0001$), and a significant year \times species interaction ($F_{15, 310} = 4.23$, $P < 0.0001$) but no significant difference among years ($F_{3, 310} = 0.61$, NS). Mean predation each year was 10.0, 11.0, 13.4 and 11.7% in 1995–1998, respectively. Regressions of the percentage of cecidomyiid damaged florets, against the current year's flowering intensity, the previous year's flowering intensity, and the change in flowering intensity from the previous to the current year, were all non-significant.

Table 5. Fates of florets (%) of *Chionochloa* species at Takahe Valley, 1995–1998. *Cecid* = attacked by cecidomyiid, *Unid Pred* = unidentified predator; *Fate Unknw* = fate unknown, *Other* includes thrips, ergot, mould, and pseudococcids. The number of plants sampled and florets examined each year is also shown.

Species	year	Ripe Seed	Aborted	Cecid	Unid Pred	Fate Unknw	Other	No. plants	No. florets
<i>C. crassiuscula</i>	1995	45.6	36.3	5.3	0.0	13.3	0.0	15	500
	1996	28.1	44.1	8.3	0.0	19.1	0.4	16	339
	1997	51.2	33.2	13.1	0.0	2.3	0.2	12	250
	1998	38.3	27.8	0.5	21.5	11.5	0.4	15	560
<i>C. pallens</i>	1995	77.8	20.5	0.9	0.2	0.6	0.0	17	838
	1996	33.6	37.0	2.7	0.6	25.7	0.4	15	333
	1997	50.6	44.7	3.7	1.0	0.0	0.0	15	495
	1998	39.4	53.8	4.2	1.4	1.2	0.0	15	697
<i>C. rigida</i>	1995	47.8	47.0	1.8	0.2	3.2	0.0	15	805
	1996	24.4	66.2	1.0	0.0	8.0	0.4	14	549
	1997	29.8	65.0	2.8	1.2	0.5	0.6	15	603
	1998	53.3	42.0	0.7	3.9	0.1	0.0	12	568
<i>C. rubra</i>	1995	16.9	59.0	16.3	0.0	6.4	1.5	15	727
	1996	21.1	44.0	20.5	0.6	13.4	0.4	15	650
	1997	12.2	72.8	6.9	4.7	3.3	0.0	15	367
	1998	15.6	50.6	18.7	4.8	4.2	6.3	15	710
<i>C. spiralis</i>	1995	18.3	36.6	16.7	0.0	28.3	0.1	15	659
	1996	21.3	54.5	12.8	0.0	10.3	1.1	17	670
	1997	20.0	55.0	20.4	0.0	4.6	0.0	7	215
	1998	0.8	35.8	42.4	6.8	13.8	0.4	10	379
<i>C. teretifolia</i>	1995	54.7	19.4	19.1	0.1	4.5	2.1	16	662
	1996	22.4	28.6	20.4	0.0	27.2	1.5	16	396
	1997	37.8	12.9	33.4	0.0	15.4	0.4	15	483
	1998	16.7	69.2	3.7	5.0	5.4	0.0	3	68
Mean (total)		32.4	44.0	11.5	2.2	9.3	0.7	(335)	(12 523)

Discussion

Degree of mast seeding

CVs for all *Chionochloa* populations are very high, particularly for the Takahe Valley populations. Both *C. crassiuscula* (3.02) and *C. teretifolia* (2.57) considerably exceed the highest previously published CV (Table 3). Moreover the *Chionochloa* datasets are based on flowering effort, and are reliable because they span many years and sampled large numbers of plants. Data based on counts of seeds which have survived frosts, insect seed predators, etc. are likely to exaggerate the CV compared to measures of flowering effort. Short datasets may be atypical if a period of unusual weather disrupts flowering during a large part of the sampling period, and this may give a higher CV than the long-term value for that site. Datasets based on few plants are likely to exaggerate the effect of low years which also inflates the CV. The four datasets from arid Western Australia (length 8–9 yr, each based on 4–5 plants) in Table 3 are susceptible to all these effects. The CV for *C. crassiuscula* is nearly equivalent to the CV of a plant producing flowers only once every 16 yr (which would give CV = 3.08); in fact over 26 yr the species expended 79% of its flowering effort in only two years (1979 and 1987). To create a higher CV than *C. crassiuscula* may require a synchronised monocarpic flowering pattern (e.g. Foster 1977). Even the least variable *Chionochloa* species, *C. macra*, is twice as variable as published masting datasets like *Fraxinus excelsior* (CV = 0.69, Tapper 1996) and *Fagus grandifolia* (CV = 0.73, Graber and Leak 1992), and the mean CV for all *Chionochloa* species (1.84) is more than twice that for all *Pinus* spp (CV = 0.91).

Chionochloa also has much more frequent zero years than other studied taxa. Zero years are affected by sample size, as a small sampling effort may record zeros in years that are merely very low flowering. However since zeros are uncommon in other studies, we need only consider whether the sampling effort in *Chionochloa* was sufficient. Most of these datasets included 50–100 tussocks, each with hundreds of potentially reproductive tillers, and the smallest recordable non-zero flowering effort (a single inflorescence on a single monitored tussock) represents from 1/200 to 1/5000 of the maximum seen (Appendix 1). In other words, the sample sizes were large enough to document a 200- to 5000-fold range in flowering effort, yet *Chionochloa* exceeded this range.

Chionochloa is a herbaceous monocot with extreme masting, whereas most attention in masting has been on woody perennials (but cf. Janzen's (1976) work on monocarpic bamboos, and Brockie (1986) on *Phormium* spp.). Moreover, *Chionochloa* occurs in New Zealand, where the temperatures are oceanic and the climate is relatively moist and equable among years, compared to

semiarid Western Australia where *Cassia helmsii* grows. We would not have predicted that the Takahe Valley environment would produce the most variable seedfall patterns documented to date worldwide.

Flowering in *Chionochloa* is synchronous within sites, and between sites both within and between species, because all species respond to a similar temperature cue for flowering. As a result, flowering is synchronous at large taxonomic and spatial scales, and is not confined to within-population synchrony. Our observations support those of Koenig and Knops (1998) who showed synchrony of seed production within and among genera of Northern Hemisphere coniferous trees up to 2500 km apart, and Curran et al. (1999) who showed widespread synchrony among dipterocarps in Borneo. However, in the Koenig and Knops study no adaptive value in inter-taxon synchrony was apparent, whereas the synchrony among *Chionochloa* species at a site is probably beneficial because the *Chionochloa* species apparently share at least three seed predators (Kelly et al. 1992). Shared predators also seemed to make synchrony adaptive in Borneo (Curran et al. 1999).

Predation and mast seeding

The undescribed cecidomyiid fly which has been previously reported feeding on the seeds of a wide range of *Chionochloa* species was found in all six *Chionochloa* species from Takahe Valley in all four years of searching. The amounts of seed lost to this predator averaged 11.5% with a maximum of 42.4%, which is lower overall than seed losses at other *Chionochloa* sites (Kelly and Sullivan 1997, Sullivan and Kelly 2000) but still considerable. Most remarkably, there was no significant difference among years in levels of cecidomyiid seed predation, with means in a narrow range between 10.0 and 13.4%. This is despite the fact that there was very wide variation in flowering intensity over the four years (from 0.04 to 3.37 inflorescences per tussock, a 96-fold range). Moreover, 1991–1994 was the longest period of sparse flowering in Takahe Valley in the 26-yr dataset (Appendix 1). *C. teretifolia* did not flower at all in 1991–1994, *C. rigida* did not flower in 1992–1994, the other species flowered only very lightly in 1991–1993, and in 1994 only *C. pallens* flowered (very lightly). Despite this long period of near-zero flowering followed by a high flowering year in 1995, the cecidomyiid emerged in large enough numbers to destroy 10% of the florets in 1995. These cecidomyiids could not have been raised locally in such numbers in the previous year and must either have immigrated, been reared on an alternate host plant, or emerged from extended diapause. Immigration is unlikely both because the high level of local synchrony in *Chionochloa* means there were almost certainly few inflorescences in adjacent catchments in 1991–1994, and because the insect is small and seems

likely to have a limited flight range. An alternate host plant for the cecidomyiid could account for the constant predation rate, but the insect has only ever been reported from *Chionochloa*, and in any case there are few other large-seeded grasses at the Takahe Valley site. In contrast, extended diapause seems likely in the cecidomyiid (McKone et al. 2000). Extended diapause is well known in cecidomyiid seed predators, and in Douglas fir (*Pseudotsuga menziesii*), the cecidomyiid *Contarinia oregonensis* synchronises its emergence to match high seed years (Hedlin 1964). Other dipteran seed predators also show extended diapause: *Strobilomyia anthracina* (Diptera: Anthomyiidae) uses predictive diapause to cope with variable seed crops on its host plant, *Picea abies* (Brockerhoff and Kenis 1997).

Extended diapause in the undescribed cecidomyiid is supported by data from the Mt Hutt *C. pallens* population, where the highest cecidomyiid losses (43.5%) were in 1986 (Kelly et al. 1992, M. J. McKone pers. comm), despite this being the highest-flowering year in the dataset (Fig. 2). Moreover, in Takahe Valley, 1996 was a relatively low flowering year following abundant flowering in 1995. *Chionochloa* did not suffer the heavy predation (mean losses were only 11.0%) that would be expected if the cecidomyiids raised in 1995 were competing for a reduced food supply. This suggests that not all the offspring of the 1995 cecidomyiids emerged in 1996. Finally, there were no significant associations between cecidomyiid predation levels and flowering effort in the current or previous years. It would seem that the cecidomyiid population size is largely uncoupled from variations from year to year in its only known food supply, *Chionochloa* florets. In order to attack a constant 10–13% of florets while the plant varies by two orders of magnitude in flowering effort, we predict that the cecidomyiid has extended diapause which is broken in response to the same cue that triggers flowering in its host plant. We were not able to test how the cecidomyiid population in Takahe Valley varied with respect to previous summer temperature as we were not able to directly measure cecidomyiid population size.

The lack of satiation of the cecidomyiid does lead to the question of whether *Chionochloa* in Takahe Valley is gaining anything from mast seeding, if the cecidomyiid is able to track changes in flowering effort and skip a number of low flowering years by extended diapause. There may be several ways in which masting does still help *Chionochloa*. Firstly, the other two widespread *Chionochloa* flower predators (*Diplotoxa similis* and *Megacraspedus calamogonus*) have not been seen in Takahe Valley. These insects occur at similar altitudes in other parts of the South Island (Sullivan and Kelly 2000, McKone et al. 2000), so may have been eliminated from Takahe Valley by the frequent zero years. Their elimination would be consistent with the prediction of McKone et al. (2000) that *Diplotoxa* would be much more susceptible to predator satiation than the

cecidomyiid, because *Diplotoxa* apparently has lower fecundity and no extended diapause. The absence of two predators could be of considerable benefit to *Chionochloa* as each of *Diplotoxa* and *Megacraspedus* can alone destroy more than 50% of florets at a site (White 1975). Secondly, in Takahe Valley seed losses to the cecidomyiid averaged 11.5%; it is possible that this level would be higher if the cecidomyiid population could increase on a more predictable food source. Finally, masting to escape seed predation by predator satiation could be a coevolutionary arms race, which we would not expect the plants to always be winning.

In conclusion, species of *Chionochloa* in New Zealand have the most variable documented flowering schedules for any perennial plants in the world. There are high levels of synchrony among plants within a population, among species at a site, and among widely separated sites. Synchrony is achieved by use of a common weather cue to trigger flowering. Synchrony within a site is probably adaptive, as the main seed predators are apparently shared by all species of *Chionochloa*. In Takahe Valley, *Chionochloa* shows extreme variation in flowering intensity, and two of the three main seed predators are absent, possibly because they cannot persist on such an unreliable food supply. The third predator, a cecidomyiid fly, consumes a constant proportion of the hugely variable food supply, perhaps by means of extended diapause and by responding to the same weather cues as the plants. This would make the cecidomyiid harder to satiate by normal levels of masting, and could have contributed to producing or maintaining the extreme masting shown by *Chionochloa*. If this is so, the observed huge variation in flowering effort among years occurs not because New Zealand has a harsh physical environment, but because of biological interactions between *Chionochloa* and its seed predators.

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Appendix 1. Raw data for all *Chionochoa* species used in this study. Abbreviations indicate sites (TV = Takahe Valley, MM = Mt Misery, CC = Camp Creek, MH = Mt Hutt) and species (the first three letters of the species names; see Table 1 for full names). All data are inflorescences per tussock, except for MM pal (inflorescences per m²) and MM aus (inf/0.25 m²). Blank means no data.

Site and species	TV cra	TV rub	TV ter	TV rig	TV pal	TV spi	MM pal	MM aus	CC pal	CC com	CC fla	CC cra	CC ore	CC rub	MH pal	MH mac
1973	0	0	0	0	0	0										
1974	0	0.956	0	0.272	0.049	0										
1975	0.031	3.748	0.250	0.929	0.903	0										
1976	0.506	3.670	5.121	7.670	1.737	0	7.630	4.650								
1977	0	0	0	0	0	0	0	0								
1978	0	0	0	0	0	0	0.580	0.530								
1979	2.005	13.600	22.559	1.469	7.930	0	8.810	6.640	13.680	15.160	4.440	7.860	1.580	11.220		
1980	0	0	0	0	0	0	0.080	0	0	0.020	0	0	0.020	0		
1981	0.010	0.010	0.010	0.280	0.200	0	0.170	0.050	0	0.600	0.020	0	0.380	0		
1982	0.073	1.889	0.258	3.313	3.577	0	14.290	15.620	9.880	36.340	1.760	3.280	1.260	23.100		
1983	0	0	0	0	0	0	0.060	0.020	0	0	0	0	0	0		
1984	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
1985	0.005	1.716	1.715	2.371	2.183	0	1.430	1.030	1.160	15.760	0.500	0.140	0.140	0.320		
1986	0.080	1.720	0.049	0.081	1.530	0	2.370	0.390	0.540	0	0.180	0.040	0.980	0.040	46.800	
1987	5.463	11.585	31.149	15.670	7.829	0	6.240	0.400	2.660	10.880	3.780	1.100	0.640	6.980	3.900	
1988	0.005	0	0.006	0	0.067	0	0.170	0.050	0	0	0	0	0	0	0.270	
1989	0	0	0	0	0	0	2.960	1.370	1.540	18.960	0.620	1.340	2.080	0.640	2.460	2.190
1990	0.907	3.702	7.727	2.543	1.454	0	3.520	5.730	3.620	1.640	1.280	4.180	0.670	6.900	4.560	2.190
1991	0.004	0.026	0	0.013	0.016	0	0.380	2.190	0	0	0	0	0	0	1.312	0.560
1992	0.004	0.044	0	0	0.010	0	0	0	0	0	0	0	0	0	0.247	0.380
1993	0	0.010	0	0	0.010	0	0.190	0	0	0	0.020	0	0	0	4.610	4.560
1994	0	0	0	0	0.080	0	0	0	0	0.800	0	0	0.210	0.160	0.039	0
1995	0.292	7.910	3.350	1.560	5.940	0.722	10.070	1.930	6.330	27.580	2.700	6.800	3.940	22.100	30.780	13.200
1996	0.010	0.248	0.050	0.308	0.210	0.094	0.450	0.250	0.040	0	0	0.220	0	0	0.088	0
1997	0.104	4.600	1.260	2.730	3.690	1.470	0.140	0.470	0.060	0.740	0.020	0	0.380	0	8.175	5.030
1998	0	0	0	0	0.198	0.009	0.020	0	0	0	0	0	0	0	0.125	0