

FACTORS CONTROLLING IRREGULAR FLOWERING IN FOUR ALPINE SPECIES OF *CHIONOCHLOA*

A. F. MARK*

Botany Department, University of Otago

INTRODUCTION

The narrow-leaved snow tussock, *Chionochloa rigida* (Raoul) Zotov,† which dominates extensively in the low-alpine zone on many mountain ranges east of the Southern Alps, does not flower annually but at irregular intervals of up to four years, when the majority of plants everywhere are in flower. This phenomenon has been discussed by several people since Barker (1953) first described differential flowering between burnt and unburnt tussocks on the Hunters Hills in South Canterbury. Only recently, however, has the basis for its control been investigated.

The results from a variety of experiments showed that the irregular flowering in *C. rigida* is largely environmentally controlled (Mark 1965b, c, d). Physiological induction of flowering occurs only in response to relatively high temperatures received during that part of summer in which day-length exceeds about 14 hours. The intensity of the flowering response, i.e. the number of tillers which are induced and in which inflorescences are subsequently initiated, is controlled partly by the duration of high temperatures and partly by the amount of reserves which the plant has available. Further, I have shown (Mark 1965c) that the species is ecotypically differentiated in temperature requirement in a way that synchronizes flowering among populations separated by 1,170 m. of altitude and up to 8°C. in mean monthly air temperatures (Mark 1965a).

The morphological initiation of inflorescences is usually apparent in autumn and a partially developed inflorescence overwinters successfully and completes its development in the following season. Thus, there is a delay of about 12 months between induction and anthesis.

Including the 1966–67 season, there have been eight rather irregularly-spaced flowering years during the past 19 years and each has followed a relatively warm summer (Connor 1966).

FLOWERING BEHAVIOUR IN OTHER SPECIES OF *Chionochloa*

Information on the flowering behaviour in the remaining 17 species described for New Zealand

(Zotov 1963) is relatively meagre, chiefly because they are either restricted in distribution or occur in fairly remote areas. However, rather sporadic field observations in the southern South Island during the past eight years indicate that at least six additional alpine species flower irregularly and, further, that their flowering seasons usually coincide with each other as well as with those of *C. rigida*. These species include three relatively widespread ones — *C. flavescens*, *C. crassiuscula*, *C. oreophila*, and three which are endemic to Fiordland — *C. acicularis*, *C. teretifolia* and *C. ovata*. All six flowered relatively profusely, wherever observed, in the 1966–67 season.

Mr C. J. Burrows (pers. comm.) reports heavy flowering in *C. oreophila*, *C. flavescens* and *C. crassiuscula*, and, in several parts of Canterbury, *C. australis* and *C. pallens*, during the 1959–60 season. He also noted light to moderate flowering in both *C. australis* and *C. oreophila* in 1962–63, and considerable flowering in 1966–67. *C. australis* also flowered heavily on Mt Arthur and Mt Robert in Nelson, during 1966–67 (Miss J. A. Wells, pers. comm.). All three seasons were flowering ones for *C. rigida*. During the five other summers in the 1959–67 period, Burrows observed very light to light flowering for most of these species. It was usually confined to sites with relatively high temperatures or fertility, or both, such as occur near lower altitudinal limits of the species, or along margins of screes or erosion patches, or around deer carcasses. Burrows considers that stimulation of flowering by high temperature may take place indirectly through an increase in availability of nutrients, especially nitrogen and phosphorus, brought about by greater mineralisation of humus.

However, this phenomenon of irregular flowering is certainly not constant for the entire genus; for example *C. rubra* appears to flower annually. No information is yet available on the remaining eight species of *Chionochloa* in New Zealand, although Connor (1966) suggests periodic flowering in *C. conspicua* ssp. *cunninghamii*.

* Miss E. L. Hellaby Grasslands Research Fellow.

† Nomenclature follows Zotov's recent treatment (1963) of *Chionochloa*.

EXPERIMENTAL

The field sites

I chose three sites on the lower slopes of Mt Brewster (2,520 m.) on the main divide near Haast Pass for study of *C. flavescens*, *C. crassiuscula* and *C. oreophila*. The lowest site (1,265 m.) is in *C. flavescens* grassland within 50 m. of the silver beech tree line, on a gentle northwest slope; *C. crassiuscula* reaches its lower limit on adjacent southern aspect slopes. The intermediate site (1,430 m.) is on a slight northwest slope within *C. crassiuscula* grassland; *C. flavescens* approaches its upper limit on adjacent moderate to steep slopes of similar aspect. The highest site (1,680 m.) is on a steep northwest slope in *C. crassiuscula* grassland near its upper limit; *C. oreophila* reaches its lower limit in adjacent depressions where snow accumulates and persists.

For the lowest site (1,265 m.) a Sumner long-term, double thermograph (Sumner 1959) has

recorded soil (-10 cm.) and air (+1.25 m. in white louvered screen) temperatures continuously since June 1966. From these records, extremes and means of daily maxima and minima and the mean temperature (mean max.+mean min./2) values were determined for each month (Fig. 1). Deviations in the three mean values from their long-term monthly values have been averaged for the two closest permanent stations, Haast and Franz Josef (both near sea level) and shown on the graphs to provide an indication of long-term values.

Average daily mean air temperatures at 1,265 m. ranged from 2.5°C. to 12.5°C., whereas the mean extreme values differed from these by $\pm 2.5^\circ\text{C}$. in winter to $\pm 6.5^\circ\text{C}$. in summer. Air temperatures remained above freezing for a three month period. Mean daily soil temperatures ranged from -1°C . to 12°C . and remained above freezing for nine months of the year; the mean extremes differed from these by only $\pm 0.5^\circ\text{C}$. in winter to $\pm 2^\circ\text{C}$. in summer.

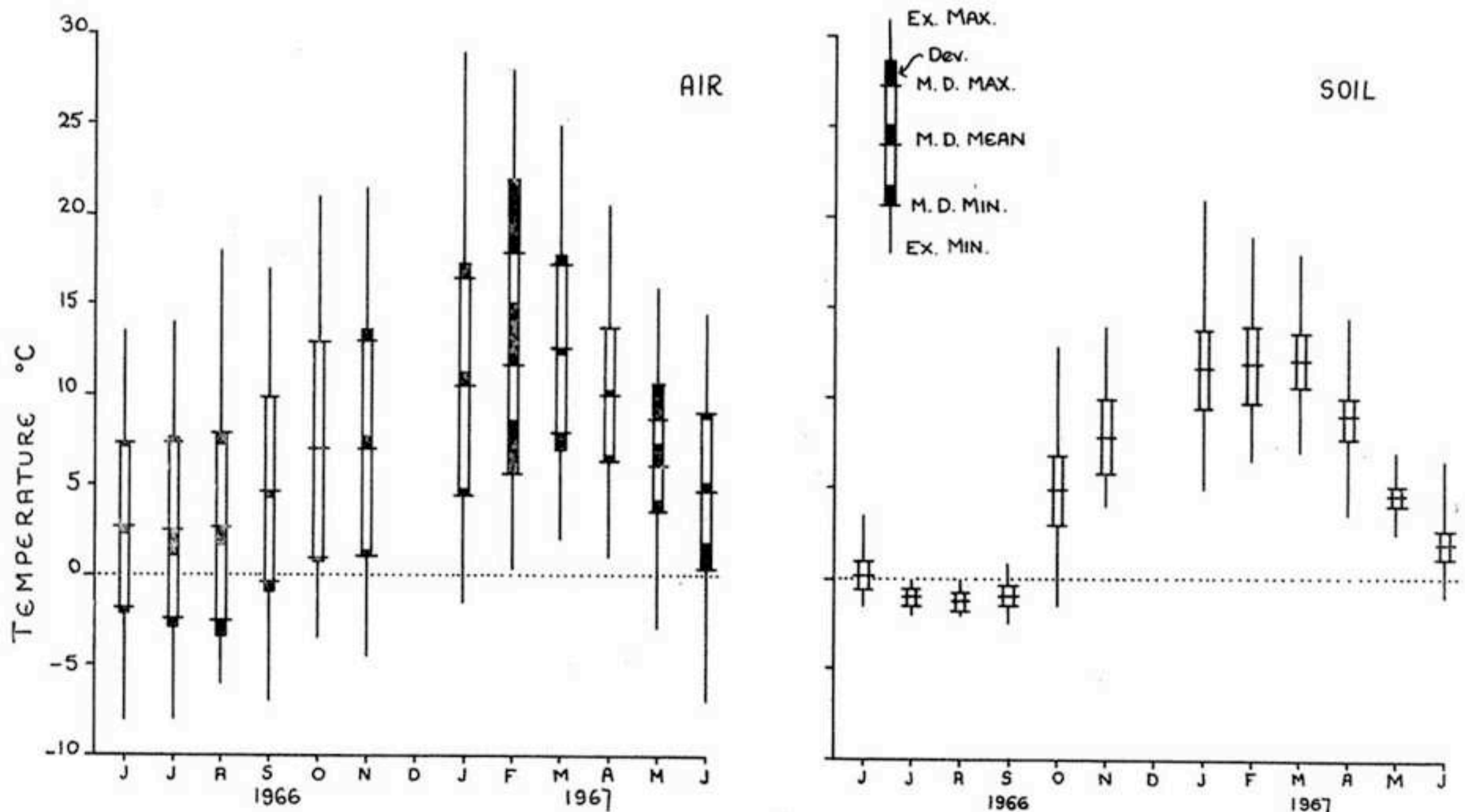


FIGURE 1. Monthly air (+1.25 m.) and soil (-10 cm.) temperatures recorded at 1,265 m. on Mt Brewster, June 1966–June 1967. Monthly extremes, mean daily maxima and minima and mean daily temperatures (=mean maximum+mean minimum/2) are shown. The black columns indicate the departures from long-term normals of mean air temperature values, averaged for Haast and Franz Josef. Freezing point is indicated by dotted lines.

U-type thermometers used to record extremes of soil (–10 cm.) and air (+1.25 m.) temperature at each site were read on seven occasions and indicate that air and soil maxima decrease by about 5°C. and minima by about 2°C. from the low to mid-altitude site, whereas the corresponding differences between the mid and high-altitude site are considerably smaller, 2°C. and 1°C., respectively.

Flowering in the field

I marked permanently 25 tussocks of *C. crassiuscula* at each of the three sites and 25 of *C. flavescens* at each of the two lower sites during February 1967 and recorded the number of inflorescences (Table 1). The values show that flowering was more abundant in the larger tussocks of *C. flavescens*. Because individual tussocks cannot be identified in *C. oreophila* I counted the number of inflorescences in 5 permanent quadrats, each of 1/16 sq. m. The mean number here was 230. Inflorescence production by these marked tussocks will be followed in subsequent seasons.

TABLE 1. Flowering during the 1966–67 season in two species of *Chionochloa* at different altitudes on Mt Brewster. Values given are the percentage of tussocks out of 25 which flowered, and the mean number of inflorescences per flowering tussock.

Altitude	<i>Chionochloa flavescens</i>		<i>Chionochloa crassiuscula</i>		
	1,265 m.	1,430 m.	1,265 m.	1,430 m.	1,680 m.
% Flowering	88	96	64	52	64
No. Infl.	52	34	11	8	12

TABLE 2. Number of initiated inflorescences and mean inflorescence length (mm.) during early April 1967, in 20 tillers from single tussocks transplanted to the Botany Department garden, Dunedin, at intervals during the 1966–67 season. Four species; two localities; five transplanting dates.

Species	Locality			Transplanting Date				
				2/XII	5/I	2/II	1/III	1/IV
<i>Ch. oreophila</i>	Mt Brewster	1,680 m.	No. Infl.	15	11	3	0	0
			Length	14.5	2.7	1.7	—	—
<i>Ch. crassiuscula</i>	,,	1,300 m.	No. Infl.	19	10	7	0	0
			Length	26.1	10.7	1.9	—	—
<i>Ch. flavescens</i>	,,	1,300 m.	No. Infl.	13	5	7	0	0
			Length	6.7	1.0	1.3	—	—
<i>Ch. rigida</i>	Old Man Ra.	1,220 m.	No. Infl.	16	2	1	0	0
			Length	30.0	0.5	0.3	—	—

Flowering following periodic transplanting to a lowland site

As in an earlier experiment involving *C. rigida* (Mark 1965b), five tussocks each of *C. flavescens* and *C. crassiuscula* from about 1,300 m. and five decimetre-square turfs of *C. oreophila* from 1,680 m. were transplanted to the Botany Department garden near sea level at Dunedin, at monthly intervals between early December 1966 and early April 1967. In addition, five tussocks of *C. rigida* were similarly transplanted from 1,220 m. on the Old Man Range, Central Otago, as a check. Soon after the last transplanting was made, 20 tillers from single tussocks in each group of five were dissected to examine their apices for the presence of initiated inflorescences. The lengths of all initials were measured. The results (Table 2) show a consistent increase both in numbers and length of inflorescences with duration in the lowland garden, except that no initials were found in plants shifted after early February.

Inflorescences were counted on all tussocks as they were becoming exposed in early October. Results from the tiller dissections made in autumn were generally confirmed (Table 3), although only in *C. flavescens* was there a consistent increase in numbers of inflorescences with duration at the Dunedin garden. However, differences in plant vigour probably explain the absence of a similar trend in the other three species. Every tussock transplanted before mid-February flowered, but flowering in plants shifted after this time occurred only in single tussocks of each species from Mt Brewster. These results are consistent with those reported earlier for *C. rigida* (Mark 1965b). They also indicate that the coming season (1967–68) will be a non-flowering one.

TABLE 3. Mean number of inflorescences produced by tussocks (and number of tussocks flowering) after transplanting from field sites to Dunedin at monthly intervals from early December 1966 until early April 1967. Four species; two localities; five tussocks per sample. Counts made on 6 October 1967.

Species	Locality		Transplanting Date				
			2/XII	5/I	2/II	1/III	1/IV
<i>Ch. oreophila</i>	Mt Brewster	1,680 m.	16.4(5)	42.2(5)	28.4(5)	1.0(1)	0.0
<i>Ch. crassiuscula</i>	"	1,300 m.	28.6(5)	24.2(5)	26.4(5)	4.0(1)	0.0
<i>Ch. flavescens</i>	"	1,300 m.	32.0(5)	19.4(5)	10.2(5)	5.0(1)	0.0
<i>Ch. rigida</i>	Old Man Ra.	1,220 m.	55.6(5)	11.0(5)	14.6(5)	0.0	0.0

Flowering following reciprocal transplanting of two *Chionochloa* species

Ten tussocks of *C. flavescens* from each of two sites (1,265 m. and 1,430 m.) on Mt Brewster and 10 of *C. crassiuscula* from the same two sites plus the 1,680 m. site, were established as transplants at all three sites during November 1965. Actually, each tussock was quartered to provide, in addition, a segment for the Botany Department garden at Dunedin. Flowering during the following (1966–67) season was complete in all tussock segments shifted to the relatively warm low-altitude garden at Dunedin (Table 4). Among the field sites, however there was differential flowering in both species, according to their altitude of origin. Compared with performances at their home site, flowering was greater at warmer sites and less or absent at cooler ones. Thus plants of both species from the low-altitude site (1,265 m.) produced relatively few inflorescences at the two higher sites; whereas those of *C. crassiuscula* from the highest site (1,680 m.) flowered heavily at both lower field sites.

DISCUSSION AND CONCLUSIONS

All nine alpine species of *Chionochloa* for which some information is available flower heavily at rather irregular intervals and, moreover, their flowering years appear to coincide. Within the

genus only *C. rubra* is known to flower annually, as is typical for perennial grasses. There are still eight species in New Zealand for which we have no information on flowering behaviour.

In the widespread eastern South Island species, *C. rigida*, it seems clear from earlier studies that the irregular flowering is largely controlled by the environment (Mark 1965b, c, d). Results of preliminary studies with the three western species described here (*C. crassiuscula*, *C. flavescens*, *C. oreophila*), suggest the operation of a similar control. As they are long-day plants, physiological induction occurs during summer, but only in response to relatively high temperatures. Differential flowering in tussocks shifted at intervals to a milder lowland site shows that the abundance of flowering varies with the duration of exposure to high temperatures and, in *C. rigida* at least, with the amount of reserves which the plant has available (Mark 1965b, c, d). Synchrony in flowering years among these four and at least five other alpine species (*C. acicularis*, *C. australis*, *C. ovata*, *C. pallens*, *C. teretifolia*), suggests a similar control for all.

Chionochloa is exceptional among perennial grasses, not only in its irregular flowering, but also in the nature of the environmental control of this, to judge from recent reviews by Evans (1964)

TABLE 4. Flowering during the 1966–67 season in two species of *Chionochloa* from Mt Brewster, reciprocally transplanted 22 Nov. '65. Values given are: percentage of the 10 clone members which flowered (% Fl.); mean number of inflorescences per flowering plant (No. Infl.). Those for segments replanted at their home sites are in bold type.

GARDEN		<i>Chionochloa flavescens</i>				<i>Chionochloa crassiuscula</i>					
		ORIGIN				ORIGIN					
		1,265 m.		1,430 m.		1,265 m.		1,430 m.		1,680 m.	
		% Fl.	No. Infl.	% Fl.	No. Infl.	% Fl.	No. Infl.	% Fl.	No. Infl.	% Fl.	No. Infl.
Dunedin	10 m.	100	10.7	100	15.0	100	9.8	100	8.7	100	13.8
Brewster	1,265 m.	40	2.5	90	18.0	60	6.5	80	3.4	100	10.9
Brewster	1,430 m.	10	2.0	100	5.3	10	1.0	60	3.0	100	12.1
Brewster	1,680 m.	0	—	0	—	20	1.5	0	—	70	4.3

and Calder (1965). Almost all perennial, temperate zone grasses that have been studied are either obligate long-day plants or their flowering is accelerated by long days. Evans reports (1964) that initiation of flowering in many long-day grasses can be considerably modified by temperature. The commonest modification is an inhibition caused by relatively high night temperatures, as in *Poa pratensis* (Evans 1960) and *Bromus inermis* (Evans and Wilsie 1946); but in *Phleum pratense* either high day or high night temperatures may be inhibitory (Cooper 1958). On the other hand, all instances reported which require high temperatures for flowering refer to short-day grasses. These are characteristic of tropical regions.

Thus, a combined daylength and temperature control of flowering, as in *Chionochloa* spp., which involves a cumulative effect of relatively high temperatures during the critical long-day period, appears to be exceptional among grasses. Moreover, differential flowering following reciprocal transplanting of altitudinal populations of *C. rigida* (Mark 1965c) and *C. flavescens* and *C. crassiuscula*, indicates ecotypic differentiation in its temperature control. Such ecotypic differentiation does not appear to have been described for altitudinal races in any other genus. If an environmentally-controlled irregular flowering has a positive selective value for these species of *Chionochloa*, this genetic variation would be adaptive by permitting synchronization of flowering years over their entire altitudinal ranges. There is some evidence to support this contention: Irregular flowering accords well with the longevity of seeds and with the reduced vigour that follows depletion of reserves caused by heavy flowering or forced regular flowering. Although recorded to date only for *C. rigida* (Mark 1965b, c, d), both of these features probably characterise other species of this genus. Irregular flowering certainly accords with the longevity of established plants in all species of *Chionochloa*. In addition, irregular seeding, by providing an unreliable food source for certain insects, such as the larvae of gall midges (Mark 1965b), would reduce their threat to seed production. In the same way it may also be an important factor in accounting for the notable rarity of native seed-eating birds in the alpine snow tussock grasslands. Further, in *C. rigida* at least, the control mechanism involved with the irregular flowering also assures a prolific seeding within two years of fire (Mark 1965d), at a time when competition would be least and therefore conditions for establishment relatively good.

Under lowland conditions, morphological *initiation* of the inflorescences in these four species occurs in the autumn, soon after induction. Autumn initiation in the field has been established only for *C. rigida* (Mark 1965b, d), but it has been demonstrated at Dunedin for all four species. The autumn initiation of inflorescences in *Chionochloa* also appears to be exceptional among the grasses. No instances were reported by either Evans (1964) or Calder (1965). Indeed, Evans suggests "that the role of vernalisation may be more to prevent initiation in the autumn than to permit it in the spring". There is no information on a need for vernalisation in *Chionochloa*, but if there is a need it must presumably be satisfied in the winter preceding induction. The only other report of autumn initiation in grasses appears to be one made recently by Hodgson (1966) for all the 13 perennial species native to Alaska which he studied. Hodgson considered that initiation in the autumn and successful overwintering of a partially developed inflorescence, although requiring very high levels of cold resistance, would have a selective advantage in both arctic and alpine environments.

The type of reproductive behaviour in which seasons of heavy flowering throughout the entire range of a species occur intermittently among seasons of light or negligible flowering appears to be quite exceptional among perennial grasses. However, it is well known in several woody genera, especially in the Fagaceae. Both in *Fagus* and in all but one of the indigenous species of *Nothofagus* there is intermittent prolific flowering which is followed by a heavy seeding or mast. Poole (1949) described late summer initiation of flowers in *Nothofagus* and suggested a causal relationship between mast years and abnormally warm summers in the preceding season. A similar relationship was also suggested for flowering years in *C. rigida* (Mark 1965b, d). Connor (1966) emphasised the complete coincidence between the eight flowering years in both *C. rigida* and *Nothofagus* spp. during the two decades for which records of both snow tussock and beech are available. Striking fluctuations of carbohydrate reserves in relation to mast years, have been described for *Fagus sylvatica* by several workers (Gäumann 1935; Murneek 1939) but depletion of reserves following prolific flowering in *C. rigida* has been inferred only, on the basis of plant performance subsequent to flowering (Mark 1965b, c, d).

Perhaps some features of the flowering behaviour in *Chionochloa* which appear to be exceptional among perennial grasses merely reflect, as

Calder (1965) points out, the emphasis given to research on the agriculturally-important, mostly lowland, grasses. However, the irregular flowering, characteristic of the alpine species of *Chionochloa*, may well prove to be unique among perennial grasses.

SUMMARY

Irregular flowering occurs in at least nine alpine species of *Chionochloa* and, moreover, their flowering seasons usually coincide. Transplanting experiments with four of these species (*C. crassiuscula*, *C. flavescens*, *C. oreophila* and *C. rigida*) indicate that their flowering is largely controlled by the environment, although availability of reserves is probably also important.

The number of tillers induced in a tussock varies with the duration of high-temperature treatment received during the summer long-day period. Such a day-length-temperature control of flowering, involving a cumulative effect of relatively high temperatures received during long days, has not been recorded in any other grasses. In three species, synchronization of flowering over their altitudinal ranges is achieved by ecotypic differentiation in the temperature requirement.

The apparently rare phenomenon among grasses of autumn initiation and successful overwintering of inflorescences occurs in the four species studied.

The possible adaptive value of irregular flowering in alpine species of *Chionochloa* is discussed.

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