

# PHENOLOGICAL INVESTIGATIONS IN ALPINE VEGETATION, CRAIGIEBURN RANGE, SOUTH ISLAND, NEW ZEALAND

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## ABSTRACT

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Phenology of selected alpine species was followed over the 1987/88 season in tussock grassland, herbfield, fellfield, and late snow communities in the Craigieburn Range, South Island. Replicate plots in each plant community showed little variation in phenological events within the same species, although strong differences occurred between communities in some species, notably in *Poa colensoi* and *Anisotome aromatica*. Correlation analyses of flowering with temperature suggest that flowering is related to patterns of snowmelt, and that responses of species within the late snow community are accelerated compared to those in other communities. Flowering peaks could not be distinguished from random patterns, lending little support to hypotheses of either pollinator competition or sharing. Fruiting peaks were also indistinguishable from random.

KEYWORDS: alpine vegetation - alpine ecology - phenology - herbfield - snowbed - tussock grassland - fellfield - Craigieburn Range.

## INTRODUCTION

Knowledge of plant phenology is necessary for elucidating causes of reproductive patterns, such as mast seeding, regular (staggered), or clumped flowering or fruiting. Phenological data may also help us to understand the effects of grazing animals on plant communities. Previous work on phenology of alpine plants in New Zealand include Scott (1960), Clarke (1968), Mark (1968, 1970), Bliss & Mark (1974), Wilson (1976), Primack (1980), and Campbell (1981). Wardle (1978) provides a general overview for the New Zealand flora. In this investigation, phenological patterns of alpine species in the Craigieburn Range were investigated over the 1987/1988 season. Three questions were specifically asked: 1) how different is the phenology of the same species in different communities; 2) is flowering of the common species clumped or regular; and 3) is fruiting of the common species clumped or segregated?

## MATERIALS AND METHODS

The study was conducted in alpine vegetation at the head of the Craigieburn catchment, northern Craigieburn Range. The general vegetation and environment of the area has been described by McIntosh (1978). Four different plant communities were investigated. Three of these were at an elevation of 1500 m in the basin directly north of the Craigieburn Skifield (*Chionochloa* tussock grassland, *Celmisia* herbfield, and *Chionochloa oreophila* snowbed), while the fourth was situated on the crest at the head of the basin at 1800 m (fellfield).

In each plant community, two 5 m x 5 m plots were located in visually homogeneous vegetation with similar aspects and elevations. Each plot was gridded into 1 m<sup>2</sup> segments and 10 of the 36 (including marginal) intersection points were randomly picked. A 25 cm x 25 cm quadrat was located at each of the 10 points, and visual estimates of cover of all plants rooted in the quadrat were made. At weekly intervals, notes were taken at each plot on the number of plants with flowers open, or fruits maturing or dispersing. If the species was abundant (e.g., *Poa colensoi*),

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then sampling of phenological stages was done using five 25 cm x 25 cm quadrats in the manner described above, and all flowering ramets were counted. For presentation of the phenological stages, the following classification system was used:

V: plant vegetative, no sign of flowering;

o: first opening of flowers:

O: at least 50% of flowers of species population in plot open;

m: first setting of mature fruit;

M: at least 50% of fruit of species population in plot mature;

d: first dispersal of seed/fruit;

D: at least 50% dispersal of seed/fruit of species populations in plot.

A mature fruit was defined by size or color change, i.e., fully developed or changing from light to dark color. Dispersal was defined as either seeds/fruits leaving the parent plant or as opening of capsules so that seeds could escape. Each month was divided into 4 approximately weekly segments. The peak flowering and fruiting times for each species were defined as the end of the weekly segment in which an "O" or an "M" respectively was first noted for that species.

Only common species, with at least 5 individuals and 25 flowers in each plot, were measured, although notes were also kept on flowering and fruiting of rare species.

Climate data for the period September 1987 to May 1988 were obtained from the Forest Re-

search Institute climate station at Broken River (914 m elevation), which is just south of the Craigieburn catchment. A mean adiabatic lapse rate of 0.66° per 100 m was used to estimate temperatures at higher elevations, based on McCracken (1980).

Nomenclature follows Allan (1961), Moore & Edgar (1976) and Connor & Edgar (1987).

## RESULTS

The 1987/1988 summer season was not a heavy flowering year for the irregularly or mast flowering species, such as the species of *Chionochloa*, *Celmisia discolor*, *C. lyallii*, *C. viscosa*, *Aciphylla similis* and *Nothofagus solandri* (Spence, in prep.). There was no flowering of *C. lyallii*, *A. similis*, *Chionochloa pallens* or *C. oreophila* in any of the plots. Light flowering (<10% of genets/ramets) occurred in *Celmisia discolor*, *C. viscosa*, and *Chionochloa macra* in some of the plots. Within the 8 study plots, 28 species flowered and were common enough to be surveyed. Table 1 presents climate data, while Table 3 presents phenological stages for these species for the four communities. Table 2 presents cover estimates of all species found in the quadrats for the four communities.

### FELLFIELD

In addition to the nine species surveyed in this community, small amounts of *Leptinella*

	Month							
	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Mean Temperature (°C)								
(1964-79)	5.5	7.5	9.5	12.0	13.2	13.9	12.3	8.9
(1987-88)	5.8	7.6	9.5	10.9	14.7	12.3	10.8	6.9
Mean Rainfall (mm)								
(1964-79)	144	174	151	112	133	69	76	130
(1987-88)	106	162	139	155	80	153	131	59
Mean Radiation (MJ.m <sup>-2</sup> )								
(1964-79)	12.0	16.9	19.7	20.9	20.6	18.6	13.4	9.6
(1987-88)	11.8	15.2	16.7	19.0	23.2	14.0	15.7	10.4

Table 1. Selected climate data from the Broken River drainage, Craigieburn Range, Canterbury. The station is at an elevation of 914 m. Data for the period 1964-1979 is from McCracken (1980).

Species	F	S	H	G
<i>Anisotome flexuosa</i>	1	-	-	-
<i>Dracophyllum pronum</i>	1	-	2	-
<i>Chionohebe pulvinaris</i>	1	-	-	-
<i>Gentiana divisa</i>	1	-	-	-
<i>Drapetes dieffenbachii</i>	1	-	-	-
<i>Poa colensoi</i>	1	21	7	15
<i>Luzula pumila</i>	1	-	-	-
<i>Phyllacne colensoi</i>	1	1	1	-
<i>Chionochloa oreophila</i>	-	28	-	-
<i>Gaultheria depressa</i>	-	10	7	-
<i>Celmisia sessiliflora</i>	-	5	1	-
<i>Forstera sedifolia</i>	-	1	-	-
<i>Celmisia haastii</i>	-	1	-	-
<i>Plantago lanigera</i>	-	1	-	-
<i>Epilobium brunnescens</i>	-	1	1	-
<i>Luzula rufa</i>	-	1	1	-
<i>Chionochloa macra</i>	-	1	4	15
<i>Anisotome aromatica</i>	-	5	4	1
<i>Celmisia viscosa</i>	-	1	6	7
<i>Celmisia lyallii</i>	-	1	1	3
<i>Lycopodium fastigiatum</i>	-	2	1	1
<i>Schoenus pauciflorus</i>	-	1	1	1
<i>Pratia macrodon</i>	-	1	-	1
<i>Microlaena colensoi</i>	-	2	1	1
<i>Raoulia grandiflora</i>	-	1	1	2
<i>Huperzia australianum</i>	-	1	-	1
<i>Celmisia discolor</i>	-	-	15	-
<i>Celmisia spectabilis</i>	-	-	3	-
<i>Geum uniflorum</i>	-	-	9	-
<i>Wahlenbergia albomarginata</i>	-	-	1	-
<i>Hebe lycopodioides</i>	-	-	1	-
<i>Blechnum penna-marina</i>	-	-	1	-
<i>Brachyglottis bellidioides</i>	-	-	1	-
<i>Ourisia sessiliflora</i>	-	-	1	-
<i>Dolichoglottis lyallii</i>	-	-	1	-
<i>Agrostis capillaris</i>	-	-	1	-
<i>Chionochloa pallens</i>	-	-	-	10
<i>Chionochloa crassiuscula</i>	-	-	2	6
<i>Aciphylla similis</i>	-	-	1	1

Table 2. Cover values for species found in the 4 different plant communities, based on visual estimates in twenty 0.125 m<sup>2</sup> quadrats per community. Cover is rounded to the nearest whole number. All values less than 1% were rounded up to 1%. F = fellfield, S = snowbed, H = herbfield, G = tussock grassland.

*atrata* were also found in one plot, with a peak in flowering during Jan(1) (the numbers 1-4 indicate the week of each month). Species found in or adjacent to these plots but not flowering included *Hebe pinguifolia* and *Gentiana divisa*. *Haastia sinclairii*, *Poa novae-zelandiae*, *Phyllacne colensoi*, and *Brachyglottis bellidioides* occurred in nearby parts of the fellfield but did not flower. Flowering commenced in early November in *Chionohebe pulvinaris*, followed by *Anisotome flexuosa* and *Hebe tetrasticha*. The last species to commence flowering was *Poa colensoi*, in Jan(3). Peak flowering of most species occurred in December and January. Fruit maturation commenced in late December for *Chionohebe pulvinaris*, with most other species maturing fruit in January and February. Most species had finished dispersing fruit or shedding seed by early March, except for *Dracophyllum pronum*, which still had many unopened dry capsules as well as green capsules by the last survey in April.

*Drapetes dieffenbachii*, despite heavy flowering in December, produced no fruit. All flowers examined appeared to be functionally male in this species. Herbivory, by either hares, keas, or grasshoppers, took a large proportion of the fruits in *Anisotome flexuosa*, with relatively few surviving to the dispersal stage. There appeared to be no differences in flowering time between male and female plants in the dioecious species.

#### SNOWBED

Flowering of ten species was recorded in the snowbed plots, out of 21 species present in the vegetation. The plots were completely free of snow by the beginning of November, although a small patch of nearby snow persisted until late November. Flowering had commenced by the last week of November in *Luzula rufa* and the first week of December in *Anisotome aromatica*, approximately 4-5 weeks after snow release. Flowering commenced last in *Pratia macrodon* (Jan(3)). By the end of February all species except *P. macrodon* and *Epilobium brunnescens* ssp. *minutiflorum* were in the dispersal phase. By the last survey date, *P. macrodon* was still maturing many capsules, none of which had yet split open. During the dispersal phase (late January-early March), studies of the seed rain (Spence, unpublished data) indicated it was

Species	Fellfield							Snowbed							Herfield							Tussock grassland						
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Oct	Nov	Dec	Jan	Feb	Mar	Apr
	34	1234	1234	1234	1234	1234	12	34	1234	1234	1234	1234	1234	12	34	1234	1234	1234	1234	1234	12	34	1234	1234	1234	1234	1234	12
<i>Anisotome aromatica</i>								V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Anisotome flexuosa</i>	V	-	o	-	o	-	-	-																				
<i>Brachyglottis bellidioides</i>																												
<i>Celmisia discolor</i>																												
<i>Celmisia laricifolia</i>								V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Celmisia sessiliflora</i>								V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Celmisia spectabilis</i>								V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Celmisia viscosa</i>								V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Chionochloa macra</i>																												
<i>Chionohebe pulvinaris</i>	V	-	o	-	-	-	-	-																				
<i>Craspedia linearis</i>																												
<i>Dracophyllum pronum</i>	V	-	-	-	-	-	-	-																				
<i>Drapetes dieffenbachii</i>	V	-	-	-	-	-	-	-																				
<i>Epilobium brunnescens</i>								V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Euphrasia revoluta</i>																												
<i>Geum uniflorum</i>																												
<i>Hebe tetrasticha</i>	V	-	o	-	-	-	-	-																				
<i>Luzula pumila</i>	V	-	-	-	-	-	-	-																				
<i>Luzula rufa</i>								V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Microlaena colensoi</i>																												
<i>Ourisia sessiliflora</i>								V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Plantago lanigera</i>																												
<i>Poa buchananii</i>	V	-	-	-	-	-	-	-																				
<i>Poa colensoi</i>	V	-	-	-	-	-	-	-	V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pratia macrodon</i>																												
<i>Raoulia grandiflora</i>								V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Schoenus pauciflorus</i>																												
<i>Wahlenbergia albomarginata</i>	V	-	-	-	-	-	-	-	V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	34	1234	1234	1234	1234	1234	12	34	1234	1234	1234	1234	1234	12	34	1234	1234	1234	1234	1234	12	34	1234	1234	1234	1234	1234	12
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Oct	Nov	Dec	Jan	Feb	Mar	Apr
	Fellfield							Snowbed							Herfield							Tussock grassland						

dominated, in order of importance, by *Poa colensoi*, *Celmisia sessiliflora*, *Anisotome aromatica*, and *Plantago lanigera*. The first three are all important components of the vegetation, while *Plantago* is a minor component (Spence, unpublished data). The most important species in the snowbed, *Chionochloa oreophila*, did not flower. The other important species, *Gaultheria depressa*, produced virtually no flowers. The 2 rare species *Gentiana corymbifera* and *Forstera sedifolia* had peak flowering in Feb(1).

#### HERBFIELD

The herbfield was the richest in number of species, with about 30, of which 14 flowered and were common enough to survey. *Celmisia discolor* was the most abundant species, but only flowered lightly in one plot. The period when the herbfield became snowfree is not known, but was probably early September. The first species to flower were *Anisotome aromatica* in Nov(2) and *Ourisia sessiliflora* in Nov(3). The last species to commence flowering were *Forstera sedifolia*, *Schoenus pauciflorus* and *Craspedia uniflora*. Minor species (and their peak flowering times) were *Plantago lanigera* (Dec(2)), *Epilobium brunnescens* (Dec(4)), *Celmisia viscosa* (Dec(4)), *Celmisia laricifolia* (Jan(1)), and *Forstera sedifolia* (Feb(2)). By middle March all species were dispersing seeds and fruits, with the seed rain dominated by *Poa colensoi* and *Geum uniflorum* (Spence, unpublished data).

#### TUSSOCK GRASSLAND

The tussock grassland examined was dominated by a mixture of *Chionochloa macra*, *C. pallens*, and *C. crassiuscula*. Small amounts of *C. flavescens*, *C. elata*, and *C. oreophila* also occurred. Of the snowgrasses, only *C. macra* flowered (<10% of whole tussocks). Light flowering occurred in *Celmisia viscosa*, but *C. lyallii*, an important component of the vegetation, did not flower. *Anisotome aromatica* was the first species to flower, in Nov(2), while *Schoenus pauciflorus* was last (Jan(2)). Dispersal began as

early as Jan(4) in *Celmisia viscosa*, although most species were dispersing in February and early March. Again, *Pratia macrodon* had not begun dispersing at the last survey date. The minor species (peak flowering) were *Euphrasia revoluta* (Dec(3)) and *Aciphylla crenulata* (Jan(1)). The single minor species for which peak fruiting was recorded was *Microlaena colensoi* (Feb(3)). The only species common in the seed rain was *Poa colensoi* (Spence, unpublished).

#### COMPARISONS WITHIN COMMUNITIES

Flowering commenced in November in all four communities, with peak flowering in December and January, and fruit maturation mainly in February and March. All but two species (*Pratia macrodon* and *Dracophyllum pronum*) were able to complete fruit maturation and dispersal by early April. Some species, including *Chionochloa macra*, *Schoenus pauciflorus*, and *Wahlenbergia albomarginata*, are likely to have continued to disperse seed up until the plants became covered with snow (Spence, pers. obs.).

Comparisons between replicate plots within each community showed that phenological stages were the same for most species. The only differences were in peak flowering (1 week difference) for *Anisotome flexuosa* in the fellfield, initial flowering (1 week) of *Epilobium brunnescens* in the snowbed, peak flowering (1 week) of *Pratia macrodon* in the tussock grassland, and initial flowering (1 week) of *Craspedia uniflora* in the herbfield. The differences in stages among replicate plots disappeared as species matured fruits.

Maximum differences in commencement of flowering between species in the same community varied from 7 weeks in the snowbed to 9 weeks in the herbfield. For peak flowering maximum differences within communities had declined to 4-6 weeks, with most change in the herbfield.

#### COMPARISONS AMONG COMMUNITIES

Differences between communities for flowering times of species that occur in more than

Table 3. Phenological patterns in the 4 communities. V = vegetative, o = first opening of flowers, O = at least 50% of flowers open, m = first mature fruit, M = at least 50% of fruit mature, d = first dispersal, D = at least 50% of fruit/seed dispersed. If the same symbol occurs twice for a species, it means that there were differences in phenology in the replicate plots. The weekly periods of each month are listed for each community across the top and bottom of the table (October - April).



one community are shown in Table 3. Initial flowering times differ the most for *Anisotome aromatica* and *Poa colensoi* (3 weeks). By the time of peak flowering, most differences had become smaller or had disappeared, except for *Poa colensoi*.

Differences in peak fruiting and dispersal for the species are also shown in Table 3. Relatively small differences are evident, except for *Poa colensoi* and *Pratia macrodon*. By the time of dispersal, there was little between-community difference for any of the species, except for *Anisotome aromatica* (2 weeks) and *Poa colensoi* (2 weeks).

#### OVERALL PATTERNS OF FLOWERING AND FRUITING

Much recent work has focused on plant competition for pollinators, and whether such interactions lead to segregation of flowering times (see review by Rathcke 1984). Other hypotheses of phenological patterns, based on sharing pollinators, have also been proposed. Relatively less attention has been given to fruiting patterns in communities and how these may relate to particular grazing pressures, although much evidence is available for individual species (Janzen 1971, Silvertown 1980, Norton & Kelly 1988).

In order to test the pattern of flowering and fruiting in each plant community, the method of Poole & Rathcke (1979) was used. They suggest that the appropriate null hypothesis is that the distribution of peak flowering (or fruiting) of the species in a community does not differ from a random pattern, i.e., with each species randomly and independently assigned a peak during the potential "flowering" or "fruiting" season. The ratio of variance of the differences in peak flowering times ( $S$ ) to one based on random distribution of peaks ( $E(S)$ ) is approximately distributed according to the  $X^2$  statistic with  $k$  degrees of freedom:

$$kS / E(S)$$

where  $k$  is the number of species. The equation for calculating the observed variance in peak events is

$$S = \sum_{i=0}^k (y_{i+1} - y_i (1 / (k+1)))^2 / (k+1)$$

where  $S$  is the observed variance,  $y_i$  is the peak flowering time (days after beginning of sea-

son) for species  $y_i$ , and  $y_{i+1}$  is the peak flowering time for the next species. Differences in flowering or fruiting peaks are first normalized to one by dividing by total number of days in season, so the start of the season is 0, and the end is 1.0. The expected variance is

$$E(S) = k / (k+1)^2 (k+2)$$

If  $S < E(S)$ , this implies regular and evenly spaced peaks, while if  $S > E(S)$  the pattern is clumped. Selection of the beginning and ending dates for the flowering or fruiting season is problematic. Poole & Rathcke (1979) and Rathcke (1984, 1988) suggest the beginning of first flowering and the ending of last flowering as reasonable endpoints (similarly with fruiting). In this study, beginning and ending of flowering was based on the first "o" in a community and the last time flowers of any of the species being studied in a plot were observed. Similarly, the first time an "m" was recorded in a community was selected as the beginning of the fruiting season. Since some species had not set mature fruit by the last observation date in early April, the end of the fruiting season was arbitrarily selected as April 15, when heavy frosts began to occur on a regular basis.

The results of these tests are shown in Table 4. For each community, the number of days in the flowering or fruiting "season", number of species, expected variance of peaks ( $E(S)$ ), actual variance ( $S$ ), and ratio of the two ( $S / E(S)$ ) is shown. In all cases, only dicot species were used. It is assumed that the monocots examined (*Poa colensoi*, *Schoenus pauciflorus*, *Luzula rufa*, *Poa buechananii*, *Chionochloa macra*, and *Microlaena colensoi*) were all wind pollinated, while all the dicot species were insect pollinated. This is a reasonable assumption, since most of the dicots studied appear to be frequently visited by insects (cf. Primack 1983). I assume, for the purposes of this analysis, that *Plantago lanigera* is also insect pollinated. Where known, peaks for rare species were also included (see comments for relevant communities).

In all cases,  $S$  is not significantly different from expectation at the 0.10 level. All values are smaller than their respective expected values, suggesting somewhat regular patterns. The larg-

Site	Days	Spp.	E(S)	S	S / E(S)
FLOWERING					
fellfield	112	7	0.096	0.007	0.073
snowbed	83	11	0.070	0.011	0.157
herbfield	112	16	0.052	0.004	0.077
tussock grassland	98	7	0.012	0.002	0.167
FRUITING					
fellfield	120	8	0.088	0.009	0.102
snowbed	105	11	0.070	0.008	0.114
herbfield	113	14	0.058	0.010	0.189
tussock grassland	98	9	0.081	0.012	0.148

Table 4. Calculated variance ( $S$ ) and expected variance  $E(S)$  values for flowering and fruiting peaks over four communities. Also listed are the number of days in flowering and fruiting "season", the number of species surveyed, and the ratio of  $S / E(S)$ . None of the  $S$  values are significantly different from random expectation at the  $P = 0.1$  level.

est departure in flowering is in the grassland and snowbed communities, while for fruiting it is the herbfield community. Nevertheless, within the constraints of the imposed assumptions, the hypotheses of segregated or clumped distributions of phenological peaks must be rejected.

#### COMPARISONS WITH CLIMATE

Variations in temperature, radiation and moisture presumably affect plant growth and timing of phenological events. Unusual events during the growing season, such as sudden freezing conditions, may affect phenology if they occur at a particularly sensitive period in plant growth. Killing of previously formed floral buds by unusually cold conditions has been documented in alpine species (Mark 1970). Relatively little work has been done on the within-season timing of phenological stages in relation to average climatic conditions, although some work has been done on subalpine shrubs (Primack 1980, Haase 1986a,b,c,d).

Cumulative number of species coming into flower and peak flower (o and O stages) were correlated with mean weekly temperature (Broken River data) at times up to 8 weeks prior to the commencement of flowering or peak flowering. Prior to approximately 8 weeks all sites but the fellfield would have been under snow. Prior

to 5 weeks the snowbed would have been under snow. Since very little difference occurred between the herbfield and grassland communities in phenological events, and because they probably became snowfree at roughly the same time, phenological data in these two communities were combined. Linear regressions of cumulative number of species coming into flower against mean weekly temperature are summarized for herbfield/grassland, fellfield, and snowbed groupings in Table 5.

For the herbfield and grassland species, mean weekly temperature 8 weeks prior to commencement of flowering is strongly correlated with number of species coming into flower. Somewhat weaker correlations also exist at 1 and 3 weeks prior to flowering. For the snowbed, strongest correlations are with the previous week. No significant relationships occur between flowering and weekly temperature for the fellfield.

For peak flowering (see Table 5), significant correlations tend to be with one, two or three weeks prior to peak flowering. For the herbfield and grassland species, strongest correlations are with the previous week, while for the snowbed strongest correlations are with three weeks. A weak correlation between peak flowering in the fellfield and temperatures 5 weeks earlier is not significant at the 0.05 level.

Model	$r^2$	F value	Significance
INITIAL FLOWERING			
Site lag (wks)			
H+G = 8	0.55	9.71	0.007
H+G = 1	0.38	4.86	0.042
H+G = 3	0.36	4.57	0.047
S = 1	0.50	6.91	0.022
FULL FLOWERING			
Site lag (wks)			
H+G = 1	0.69	15.66	0.003
H+G = 2	0.68	14.54	0.003
H+G = 3	0.43	5.23	0.041
S = 3	0.81	30.29	0.001
S = 1	0.68	12.53	0.007
S = 2	0.65	10.94	0.010

Table 5. The results of independent linear regressions between cumulative number of species coming into peak flowering and weekly mean temperatures from 1 to 8 weeks prior to flowering (1-8). Only regressions with an  $F$  probability of 0.05 or less are shown. H = herbfield, G = grassland, S = snowbed. In all cases the plant community is the dependent variable.

## DISCUSSION

The winter of 1987 was relatively dry, with early snow release. Many alpine species in the Craigieburn catchment were already flowering by early November. The overall effect of the dry winter, combined with a warmer and drier January than normal (cf. Table 1; McCracken 1980), apparently was to accelerate many phenological events. Consequently, most species had set fruit and dispersed by the end of March. Late blooming species such as *Gentiana corymbifera* and *G. bellidifolia* were in full flower by early and middle February respectively. Despite the early start, at least two species, *Dracophyllum prunum* and *Praetia macrodon*, were still maturing fruits by the time autumn conditions, with nightly frosts and intermittent snow, began (in late April). In these species, fruits overwinter on the plant and shed seed in late winter or spring.

Peak flowering in the four communities does not appear to be clumped. Based on the calculated variance in peaks, the pattern cannot be dis-

tinguished from a random one. However, not all species were surveyed in each community. Some of the more common species did not flower. It is possible that a different pattern would emerge in a mast year, with heavy flowering of all species. There is a suggestion of clumped flowering in the *Celmisia* species (see Table 3), something noted by other workers (e.g., Given & Gray 1986).

The question of fruiting patterns being clumped or segregated has not been addressed as often as flowering patterns. Clumped fruiting may evolve as a result of either generalist dispersal agents or intense grazing by generalist herbivores. In the latter situation, the massed presence of numerous fruits may satiate predators. Species that fruited earlier or later than most species would hence be more likely to suffer fruit loss to a generalist herbivore (cf. Augspurger 1981). Of the main groups of herbivores present in the Craigieburn Range that may have exerted a selective influence on the vegetation over time, relatively little information is known except for grasshoppers (White 1974, 1975). Grasshoppers tend to be generalists, although they often preferentially select certain species. White (1975) suggested that in certain communities in the Craigieburn Range, grasshoppers can exert a strong influence on the vegetation, although primarily through destruction of vegetative tissues. Important seed herbivores on alpine plants include weevils, moth larvae, and tephretid flies (Molloy 1975, White, pers. comm.), about which little is known. There is no evidence for clumped fruiting in the four communities that might lend support to this hypothesis. Again, there was some evidence that *Celmisia* species tended to have clumped fruiting (Table 3).

Overall, the problems in selection of length of flowering or fruiting season as well as the "coarse-grained" (i.e., weekly) nature of the study may limit the usefulness of the stochastic modeling of phenological patterns. A more intense study using these methods over several seasons on a group of species with similar reproductive strategies and phenologies (such as *Celmisia*, *Aciphylla*, or *Chionochoa*) may reveal interesting phenological patterns in relation to pollination, dispersal, and herbivory.

There were essentially no differences in phenology between replicate plots in the communi-



ties. However, some species found in several different communities showed striking contrasts in flowering and fruiting. *Poa colensoi* started flowering 3 weeks later in the fellfield at 1800 m compared to the lower elevation (1450-1500 m) plots. These differences were maintained throughout later stages. *Anisotome aromatica* showed differences of up to 3 weeks between the snowbed and the herbfield and grassland plots. Fruiting peaks for this species were also variable. For most other species differences were only 1 week, and most of these decreased or disappeared during the season. The *Poa* and *Anisotome* are two of the most widespread species in the area, inhabiting a variety of vegetation. These differences may result from ecotypic differentiation, and might explain the success of these two species.

Although floral bud initiation is generally in the previous year (Mark 1970, Haase 1986a), timing and extent of flowering is under control of the current growing season, and is generally controlled by climate, often temperature (moisture is rarely limiting in these communities (C.J. Burrows, pers. comm., 1988)). Regression analysis indicated that strong correlations exist between the accumulated onset of flowering in the late snow, herbfield and tussock grassland communities, and preceding average weekly temperatures. For the late snow area, initial flowering was most strongly correlated with the previous week, while peak flowering was correlated with 3 weeks. For the herbfield and grassland, these values are for 8 weeks and 3 weeks respectively. These results suggest a relatively faster response of flowering to temperature in the late snow community compared to the other two communities, especially for initial flowering. This is in accord with the shorter growing season found in snowbeds. Correlations between initial flowering and weekly temperature in the herbfield and grassland communities are strongest with the week when snow would have completely melted away. The lack of correlations between temperature and flowering in the fellfield suggests that either fellfield species are not responding to temperature as a clue for flowering, have widely different temperature requirements, or that temperatures are more variable as a result of these sites being swept free of snow much of the year.

The results reported in this paper are similar to phenological patterns in subalpine and alpine communities reported by Scott (1960), Clarke (1968), Bliss & Mark (1974), and Wilson (1976). In all studies flowering is most common in December and January, while fruiting peaks are generally in February and March. Differences in phenology within some species populations were noted at different elevations by Scott (1960), Clarke (1968), and this study. Most differences are in the order of 1-2 weeks. Aspect also affects phenology, with populations on cooler south facing slopes lagging behind those on north facing slopes (Clarke 1968). In the present study, aspect was controlled for, but differences of one week still occurred for some species in the replicate plots, a feature not reported in the other studies. These differences appeared to be most pronounced in early events (especially onset of flowering), and declined with time. Subtle differences in snow melt patterns (cf. Burrows 1977), moisture levels in the soil, and cold air drainage may account for these differences. Primack (1980), in a quantitative study on subalpine shrubs, noted that individuals in similar microsites varied considerably in flowering periods. He attributed this to either genetic control or relatively constant microhabitat factors.

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#### REFERENCES

- Allan, H.H. (1961). *Flora of New Zealand, Vol. 1*. Government Printer, Wellington.  
 Augspurger, C.K. (1981). Reproductive syn-

- chrony of a tropical shrub: experimental studies of effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62: 775-788.
- Bliss, L.C. & Mark, A.F. (1974). High-alpine environments and primary production on the Rock and Pillar Range, central Otago, New Zealand. *New Zealand Journal of Botany* 12: 445-483.
- Burrows, C.J. (1977). Alpine grasslands and snow at Arthur's Pass and Lewis Pass regions, South Island, New Zealand. *New Zealand Journal of Botany* 15: 549-564.
- Campbell, A.D. (1981). Flowering records for *Chionochloa*, *Aciphylla* and *Celmisia* species in the Craigieburn Range, South Island, New Zealand. *New Zealand Journal of Botany* 19: 97-103.
- Clarke, C.M.H. (1968). Flowering records of alpine plants at Cupola Basin, Nelson, New Zealand. *New Zealand Journal of Botany* 6: 205-220.
- Connor, H.E. & Edgar, E. (1987). Name changes in the indigenous New Zealand flora, 1960-1986 and Nomina Nova IV, 1983-1986. *New Zealand Journal of Botany* 25: 115-170.
- Given, D.R. & Gray, M. (1986). *Celmisia* (Compositae-Asteraceae) in Australia and New Zealand. In *Flora and Fauna of Alpine Australasia; Ages and Origins* (ed B.A. Barlow), pp 451-470. CSIRO, Melbourne.
- Haase, P. (1986a). Flowering records of some subalpine trees and shrubs at Arthur's Pass, New Zealand. *New Zealand Journal of Ecology* 9: 19-23.
- Haase, P. (1986b). An ecological study of the subalpine tree *Dracophyllum traversii* (Epacridaceae) at Arthur's Pass, South Island, New Zealand. *New Zealand Journal of Botany* 24: 69-78.
- Haase, P. (1986c). An ecological study of the subalpine shrub *Senecio bennettii* (Compositae) at Arthur's Pass, South Island, New Zealand. *New Zealand Journal of Botany* 24: 247-262.
- Haase, P. (1986d). Phenology and productivity of *Olearia ilicifolia* (Compositae) at Arthur's Pass, South Island, New Zealand. *New Zealand Journal of Botany* 24: 369-379.
- Janzen, D.H. (1971). Seed predation by animals. *Annual Review of Ecology and Systematics* 2: 465-492.
- McCracken, I.J. (1980). Mountain climate in the Craigieburn Range, New Zealand. *New Zealand Forest Service FRI Technical Paper No. 70*: 41-59.
- McIntosh, T.T. (1978). Snow avalanches and their effects on scrub and herbaceous vegetation. M.Sc. thesis, University of Canterbury, Christchurch.
- Mark, A.F. (1968). Factors controlling irregular flowering in four alpine species of *Chionochloa*. *Proceedings of the New Zealand Ecological Society* 15: 55-60.
- Mark, A.F. (1970). Floral initiation and development in New Zealand alpine plants. *New Zealand Journal of Botany* 8: 67-75.
- Molloy, B.P.J. (1975). Insects and seed production in *Celmisia*. *Canterbury Botanical Society Journal* 8: 1-6.
- Moore, L.B. & Edgar, E. (1976). *Flora of New Zealand, Vol. 2*. Government Printer, Wellington.
- Norton, D.A. & Kelly, D. (1988). Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu)(Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology* 2: 399-408.
- Poole, R.W. & Rathcke, B.J. (1979). Regularity, randomness, and aggregation in flowering phenologies. *Science* 203: 470-471.
- Primack, R.B. (1980). Variation in the phenology of natural populations of montane shrubs in New Zealand. *Journal of Ecology* 68: 849-862.
- Primack, R.B. (1983). Insect pollination in the New Zealand mountain flora. *New Zealand Journal of Botany* 21: 317-333.
- Rathcke, B.J. (1984). Patterns of flowering phenologies: testability and causal inference using a random model. In *Ecological Communities: Conceptual issues and the Evidence* (ed. D.R. Strong Jr., D. Simberloff, L.G. Abele and A.B. Thistle), pp 383-393. Princeton University Press, Princeton.
- Rathcke, B.J. (1988). Flowering phenologies in a shrub community: competition and constraints. *Ecology* 76: 975-994.
- Scott, D. (1960). Seasonal behavior of some

- montane plant species. *New Zealand Journal of Science* 3: 694-699.
- Silvertown, J.W. (1980). The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnaean Society* 14: 235-250.
- Wardle, (1978). Seasonality in New Zealand plants. *The New Zealand Entomologist* 6: 344-349.
- White, E.G. (1974). Grazing pressures of grasshoppers in an alpine tussock grassland. *New Zealand Journal of Agricultural Research* 17: 357-372.
- White, E.G. (1975). An investigation and survey of insect damage affecting *Chionochloa* seed production in some alpine tussock grasslands. *New Zealand Journal of Agricultural Research* 18: 163-178.
- Wilson, H.D. (1976). Vegetation of Mount Cook National Park, New Zealand. *National Parks Authority Science Series No. 1*. Department of Lands and Survey, Wellington.