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PLANT PHENOLOGICAL PATTERNS IN THE HIGH ANDEAN CORDILLERA OF CENTRAL CHILE

MARY T. KALIN ARROYO, JUAN J. ARMESTO AND CAROLINA VILLAGRAN

Departamento de Biología, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

SUMMARY

(1) Vegetative activity and flowering and fruiting records are given for ninety-seven species from three vegetational belts in the andean (alpine) zone of the Cordon del Cepo (33°17'S, 70°16'W), Cordillera de los Andes, central Chile. Comparisons of phenological behaviour and overall phenological patterns were made at six altitudes between 2320 and 3550 m, including both north- and south-facing slopes.

(2) Nine categories of phenological behaviour and their altitudinal distribution are described. The percentage of summer-dormant species (dying back before the onset of winter) reaches a maximum at 2320 m (>75% of all species), and generally decreases with altitude. More summer-dormant species are present on north-facing (equatorial) slopes than on south-facing slopes.

(3) The maximum growing season within the andean zone was 8 months at 2320 m altitude; the minimum growing season was 5 months on south-facing slopes at 3410 m. Shrubs and cushion plants had the longest period of vegetative activity, followed by perennial herbs and sub-shrubs, and then by geophytes and annuals.

(4) Flowering in some species began before snowmelt, and continued until autumn, reaching a maximum in the austral summer between late December and late February at the altitudinal extremes. Peak flowering corresponded with the period of maximum temperature at lower altitudes, but was displaced after this period at higher altitudes and on south-facing slopes.

(5) The average length of the flowering period for each species increased with altitude, approximately doubling over 1200 m altitude. Fruits of some species failed to mature both on some of the north-facing slopes and on most south-facing slopes in 1979.

(6) Slower floral development at higher altitudes accounted for about two-thirds of the difference in the lengths of the flowering periods at the altitudinal extremes.

(7) Checks in 1979–80 indicated that the phenological patterns detected in 1978–79 remained constant from one year to another.

(8) The phenological behaviour of annuals, geophytes and some perennial herbs suggests that they may have been derived from the lower mediterranean matorral flora.

INTRODUCTION

Spatial and temporal displacement by competition for light and water (Terborgh 1973), and temporal competitive adjustment for the most efficient utilization of pollinators (Levin & Anderson 1970) and seed-dispersal agents, are important factors governing niche differentiation in plant communities. Ecologists, nevertheless, have only recently paid attention to the relationships between phenological patterns, vegetative growth strategies and reproductive characteristics. During the past 10 years or so, breeding systems (Bawa 1974; Ashton 1977; Arroyo & Cabrera 1978; Ruiz & Arroyo 1978; Arroyo 1979) and phenological patterns (Janzen 1967; Medway 1972; Frankie, Baker & Opler 1974; Stiles

1978) have been studied at a community level in the tropics, yet similar studies have been attempted only occasionally in temperate areas (Simpson 1977; del Moral & Standley 1979).

High-mountain plant communities exist at the limits of tolerance for vascular plants, and, according to Mani (1962), of availability of insect pollinators. Low winter temperatures and snow accumulation restrict vegetative activity to the spring and summer months; flowering must be completed sufficiently early to permit fruit maturation and seed dispersal. It is predictable that autogamy and apomixis, which reduce dependence on external pollinators, might be more frequently encountered among species inhabiting high mountains. Abiotic factors, moreover, tend to play a more exaggerated role in determining phenological patterns in such communities.

In 1978 an intensive research programme on the reproductive biology of High Andean species was initiated in central Chile. This paper presents details of part of that research, on the phenological behaviour of ninety-seven species from the andean zone (c. 2200–3900 m) on the Cordón del Cepo (33°17'S), and compares patterns at different altitudes and on contrasting north- (equatorial) and south- (polar) facing slopes.

THE STUDY AREA

Location and vegetation

The Cordón del Cepo is a western branch of the main range of the Cordillera de los Andes, located between 33°10'S and 33°25'S in central Chile, and reaching a maximum altitude of 5430 m on Cerro Plomo. Work was conducted on a western prolongation of the Cordón del Cepo, between the catchments of the Río Molina and the Río San Francisco (33°17'S, 70°16'W), along an altitudinal gradient extending from the lower limit of the andean* (equivalent to alpine) zone at 2320 m, through the area of La Parva (2700 m), to the summit of Cerro Franciscano (3550 m).

Three distinct vegetational belts are distinguishable in the andean zone. (a) Lower andean scrub is a floristically rich formation found between 2000 and 2700 m, consisting of an open cover of low rounded shrubs, scattered perennial herbs and geophytes, and several annual herbs. Above 2700 m this scrub passes rather abruptly into (b) cushion-plant communities developed over deeper soils. From 3100 to 3500 m upward, depending on degree of exposure, slope, substrate and aspect, the cushion-plant communities intergrade into (c) impoverished subnival fellfield vegetation, with structured communities, extending up to c. 3600 m.

Climate

The High Andes of central Chile are characterized by a mediterranean-type climate in the broad sense of the term (di Castri 1973), with precipitation concentrated in the winter months, followed by progressive drying during summer and autumn. Continuously recorded climatic data are not available for the study area. The general characteristics of the climate, however, may be deduced from the records for Sewell (2134 m; 34°16'S, 70°22'W) and San José de Maipo (1060 m; 33°39'S, 70°22'W), at similar altitude and latitude, respectively, to the study area (di Castri 1973; di Castri & Hajek 1976), and from climatic data recorded at 2500 m altitude on the study area during the study period (Fig. 1).

* Vegetation above the treeline in the temperate Andes.

At Sewell and San José de Maipo, precipitation extends from April to November, with a maximum in July. The precipitation pattern observed over two years in the study area was very similar, with the exception that late summer storms were more frequent in 1980. The total of 442 mm precipitation for the 12-month period May 1978 to April 1979 in the study area was lower than the mean annual precipitation of 1052 mm at Sewell and 632 mm at San José de Maipo, suggesting that this period may have been drier than average. The respective mean maximum temperatures for Sewell and San José de Maipo are 14.5 and 21.5 °C, and the corresponding minima are 5.0 and 6.2 °C. At 2500 m altitude at the study site, for the period May 1978 to April 1979, the mean maxima and minima were 12.2 and 3.9 °C, respectively. The 1979 winter was milder than the 1978 winter.

Snow generally persists in the andean zone from July to mid-September or early October. In 1978 most of the winter snow fell in June and July. In the milder 1979 winter, although snow began to accumulate in late June, significant quantities did not fall until late August and September, and as a consequence spring snowmelt occurred about 10 days later that year. Snow also fell in late October (1978) and in late November (1978 and 1979), each fall leading to new snow accumulation above 2700 m for periods of approximately 1 week (Fig. 1). Over the two years a number of snowfalls were also recorded above 3000 m from February onwards.

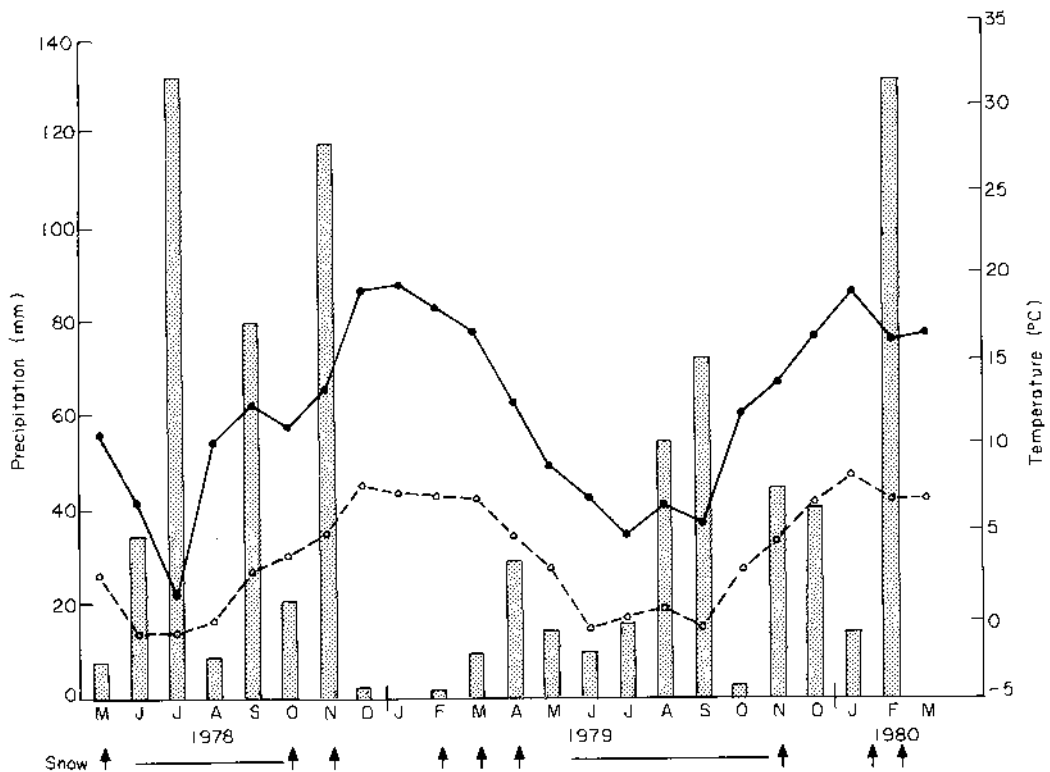


FIG. 1. Monthly precipitation (histogram), and mean monthly maximum (continuous line) and minimum (interrupted line) temperature in the area of La Parva, 2500 m altitude, Cordón del Cepo in central Chile, over the period May 1978 to March 1980. Continuous lines below the graph indicate the duration of winter snow; the arrows indicate intermittent early summer, late summer and autumn snowfalls. Total precipitation May 1978 to April 1979 was 442 mm.

METHODS

Phenological records were maintained from early October 1978, shortly after snowmelt at 2300 m, until mid-May 1979, in nine sampling sites at six different altitudes. Six of these sites (1–6) were on predominantly north-facing slopes, while three (2A, 4A, 6A) were on south-facing slopes at the same altitude as the corresponding north-facing site. Site details and snowmelt dates are given in Table 1.

TABLE 1. Characteristics of the nine sampling sites on the Cordón del Cepo (33°17'S), Cordillera de los Andes, central Chile

Station	Altitude (m)	Aspect	Slope		Vegetation	Snowmelt date (1978)
			Mean	± S.D. (n)		
1	2320	NW–W	23.2	± 10.3° (41)	Andean scrub	26 Sept.
2	2530	NW	16.7	± 6.2° (21)	Andean scrub	3 Oct.
2A	2530	S	25.6	± 8.7° (20)	Andean scrub	3 Nov.
3	2700	NW	19.9	± 4.8° (34)	Scrub–cushion communities	10 Oct.
4	2935	W	14.7	± 7.0° (20)	Cushion communities	27 Oct.
4A	2930	S	20.4	± 3.8° (15)	Cushion communities	11 Oct.
5	3200	N–NW	25.8	± 8.6° (86)	Fell-field	3 Nov.
6	3550	N–NW	24.9	± 10.4° (115)	Fell-field	27 Oct.
6A	3410	SE	30.5	± 7.4° (37)	Fell-field	3 Jan. 1979

Observations were made at intervals of approximately 2 weeks at north-facing sites and once a month at south-facing sites. This pattern was interrupted occasionally by late snowfalls. The phenophases recorded were: active vegetative growth, presence of flower buds, flowering, fruiting, and die-back of foliage or above-ground parts. Plants were considered vegetatively active at the first signs of vegetative bud break, in bloom as the first flowers opened, and in fruit as the first fruits appeared. When individual plants carried both flowers and fruits, this was noted. The results were based on observations on 10–20 marked individuals per species per site for shrub and cushion plants, and for all individuals appearing in previously-delimited transects in the case of geophytes, perennial herbs and annuals. On each observation date a total of 201 (all stations recorded) or 165 (only north-facing) species-records were made.

In order to determine whether the patterns observed over the 1978–79 period were maintained from one year to the next, observations were repeated at the north-facing sites on a number of dates in 1979–80. The degree of constancy of the phenological patterns was expressed in terms of the percentage of species with identical phenological expression over the two years on the equivalent observation dates. From January onward the comparisons are based on all phenophases; before this date only flowering activity was considered.

For comparative purposes, the lengths of the active vegetative growth period and the flowering and fruiting periods are estimated from the first and last dates on which the respective phenophases were observed in each species at the respective stations. Peak flowering and peak fruiting in this paper refer to those dates on which a maximum number of individuals of each species was active. The date of maximum flowering is considered as that upon which the greatest number of species flowered in each station.

Voucher specimens of all ninety-seven species studied* are deposited in the herbaria of the Universidad de Concepción (CONC), Concepción, Chile, and of the Missouri Botanical Garden (MO), St Louis, Missouri, U.S.A.

* A list of the species studied and their phenological behaviour-categories may be found in the Appendix.

RESULTS

Types of phenological behaviour

Nine different patterns of phenological behaviour were detected among the species studied (Table 2). Perennial herbs overwintering in a dormant state (category III; Table 2) constitute the predominant category. Many such hemicryptophytes (IIIa) die back immediately after fruiting, which may be well in advance of the onset of winter (e.g. *Cerastium arvense*). Others (IIIb) continue vegetative growth after fruiting, finally dying back at the onset of winter (e.g. *Stachys albicaulis*). A number of hemicryptophytes are facultative with respect to the timing of leaf die-back: thus *Phacelia secunda* and *Acaena pinnatifida* become dormant immediately after fruiting at 2320 m altitude, whereas at higher altitude these species continue vegetative growth throughout the summer and autumn following the reproductive period.

TABLE 2. Number of species with different types of phenological behaviour at nine sampling sites on the Cordón del Cepo in Central Chile; I = annuals; IIa = geophytes dying back after flowering and fruiting; IIb = geophytes with leaf die-back before flowering and shoot die-back after fruiting; IIc = geophytes continuing to grow for a period after reproduction and then eventually dying back; IIIa = perennial herbs and suffrutices with leaf die-back occurring before onset of winter; IIIb = perennial herbs and suffrutices continuing vegetative activity after reproduction until onset of winter; IVa = shrubs with steady growth throughout the entire growing season; IVb = shrubs with a second pronounced growth flush after fruiting; V = cushion plants

Station	Altitude (m)	I	IIa	IIb	IIc	IIIa	IIIb	IVa	IVb	V
1	2320	6	6	2	0	14	4	4	3	0
2	2530	5	2	1	1	5	6	6	3	0
2A	2530	0	1	0	0	4	6	4	1	0
3	2700	2	5	2	0	6	6	5	2	1
4	2935	0	1	1	0	6	6	4	0	4
4A	2930	1	0	0	0	6	4	3	0	1
5	3200	2	0	0	0	4	10	1	0	6
6	3550	1	1	0	0	5	12	1	0	3
6A	3410	1	0	0	0	2	2	0	0	0

Two distinct patterns of phenological behaviour were observed among shrubs. Most commonly (category IVa), flowering and fruiting were preceded by a long period of shoot and leaf growth, often apparently from pre-formed overwintering buds; after fruiting these shrubs continued growing until the beginning of winter. In others (e.g. *Nardophyllum lanatum*; category IVb) there was a second distinct growth pulse after fruit drop. The winter behaviour of shrubs, although not studied in detail, appears to be quite variable. Extensive leaf-death was seen in some shrubs after the 1978 winter, but was less pronounced in the same species in the following year. In most shrubs leaves tend to yellow towards the end of the season only to resume photosynthetic activity the following spring.

The leaves of most cushion plants died during the 1978 and 1979 winters. All cushion species continued vegetative activity throughout the entire growing season, though they were noticeably less active from late summer onward. As the behaviour of these interesting plants is intermediate between that of shrubs and hemicryptophytes, they are considered in a separate category (V).

Three different patterns of phenological behaviour characterize geophytes (category II).

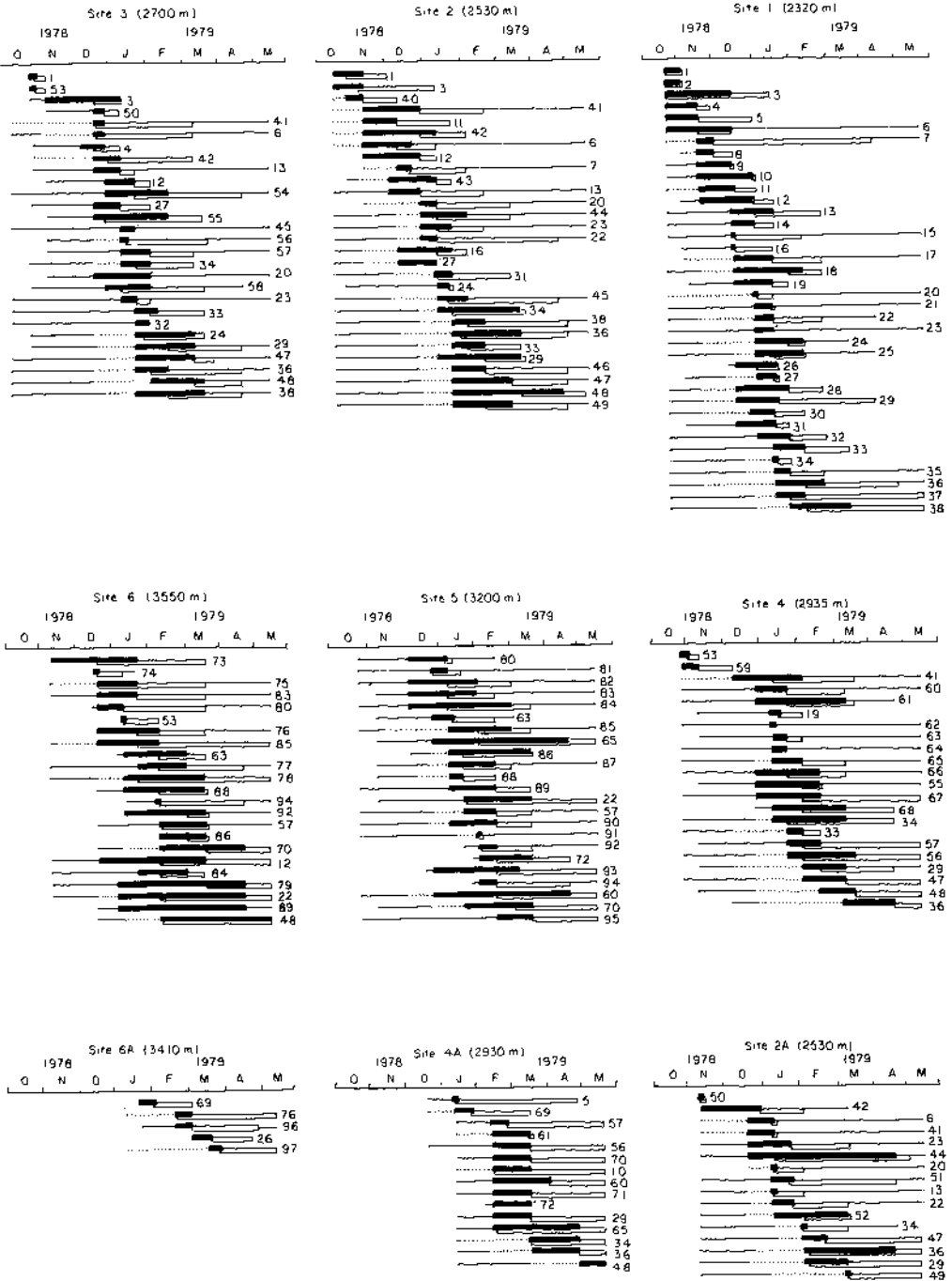


FIG. 2. Phenological records for andean species at nine sampling sites. Species are arranged in accordance with the sequence of peak flowering dates. Names and peak flowering dates are listed in the Appendix. — vegetative activity; ---- flower buds; ■■■ flowering; ▬ fruiting.

Most commonly, leaves are produced during spring, followed by flowers and fruits, after which the entire plant dies down (IIa). In some species of this kind (e.g. *Barneoudia chilensis*) the leaves are fully expanded under the snow. More typically, leaf production and flowering are gradual, temporally-separated processes, with leaves withering in late spring or early summer. In *Alstroemeria pallida* and *Rhodophiala montana*, leaves wither before the flower buds open (IIb). A third unique kind of geophyte behaviour (IIc) consists of precocious leaf production and flowering under snow, followed by fruiting, and then a second period of leaf expansion in which the original leaves elongate to approximately twice their pre-fruiting size.

Annuals (category I) constitute an interesting component of the vegetation. Most are

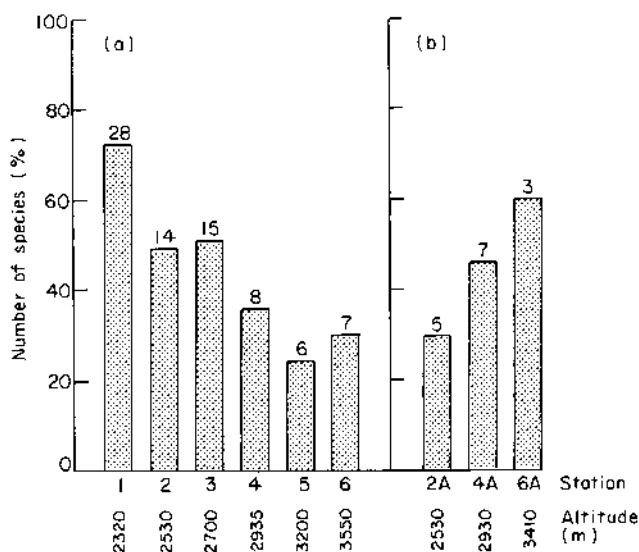


FIG. 3. The percentage of species in which the above-ground parts die back before the onset of winter on (a) north-facing and (b) south-facing sites; total number of species is shown above each histogram column.

restricted to the 2320–2700 m altitudinal range, though some extend to 3550 m. Germination of annuals occurs rather late in the season at higher altitudes.

The relative importance of the different kinds of phenological behaviour with increasing altitude may be seen in Table 2. The most evident tendencies are a decrease in the number of annual species with altitude, an abundance of summer-dormant geophytes and hemicryptophytes in the 2320–2700 m altitude range, and a restriction of shrubs having a second period of vegetative activity to altitudes below 2900 m. The total number and percentage of species dying back before the onset of winter at each site, independent of the phenological categories established above, is shown in Fig. 3. On north-facing (equatorial) slopes summer die-back is most pronounced at lower altitude; on the equivalent south-facing slopes there are comparatively few summer-dormant species, but these constitute a progressively greater proportion of the species at higher altitudes. This results from the fact that there are fewer shrubs and cushion plants on south-facing slopes, and these life-forms are entirely lacking at site 6A.

Vegetative activity

In 1978–79 the total snow-free period varied from approximately 8 months at 2320 m altitude to 7 months at 3550 m on north-facing slopes, and from approximately 7 months at 2500 m altitude to 5 months at 3410 m on south-facing slopes (Table 1). Over the study period on north-facing slopes, shrubs and cushion plants grew for an average of about 31 weeks at 2320 m, about 27 weeks at 2935 m and 24 weeks at 3550 m altitude (Fig. 4). Perennial herbs and sub-shrubs generally grew for shorter periods than did shrubs and cushion plants (differences significant at all altitudes except 3200 m; $P < 0.05$; t -test). Geophytes and annuals, growing for equivalent lengths of time, were vegetatively active for significantly shorter periods than were the above-mentioned plants ($P < 0.05$; t -test).

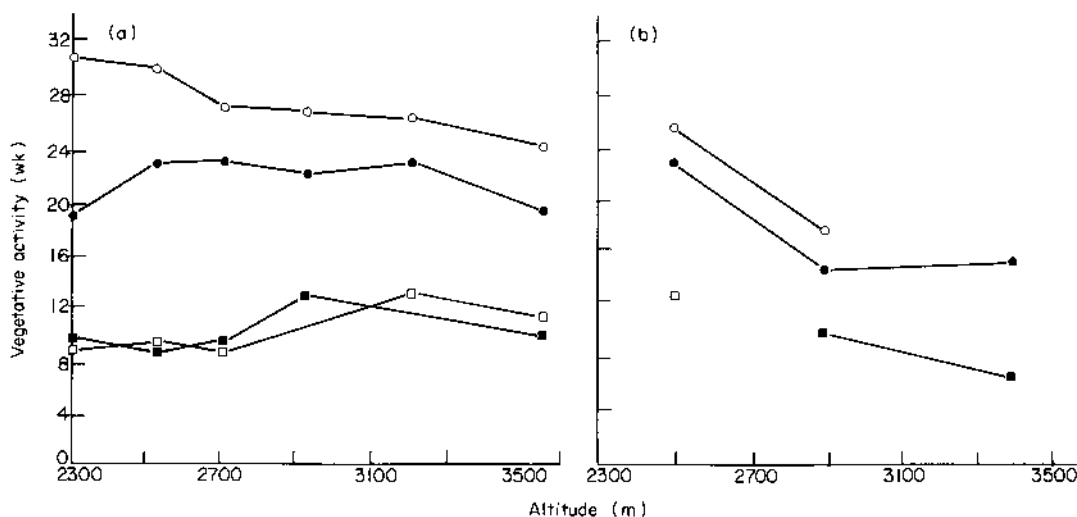


FIG. 4. Average period of vegetative activity (weeks) in different life-forms on (a) north-facing and (b) south-facing slopes. Symbols: ○, shrubs and cushion plants; ●, perennial herbs and sub-shrubs; □, geophytes; ■, annuals.

Vegetative activity was significantly shorter for shrubs on the south-facing slopes than on the north-facing slopes ($P < 0.05$; t -test). At 2500 m altitude it was reduced by 4 weeks, and at 2900 m by about 9 weeks.

Flowering activity

Flowering commenced in early spring and continued into late summer and autumn (Fig. 5). In 1979 a few species were still flowering at the higher altitudes as snow began to accumulate in late May and early June. The earliest flowering species, *Barneoudia chilensis* (Ranunculaceae), *Tristagma sessile* (Amaryllidaceae) and *Diposis bulbocastaneum* (Umbelliferae), bloomed precociously under 5–6 cm of snow and flowering was completed within 2 weeks or so of snowmelt.

Sites at all altitudes were characterized by one prominent maximum in flowering activity (Fig. 5), which in 1978–79 on north-facing slopes occurred in late December at 2320 m and in late February at 3550 m altitude. At 2530 m altitude no difference was evident between north- and south-facing slopes, but at 2930 m and 3410 m altitude maximum flowering occurred 6 weeks and 4 weeks later on the south-facing slopes. At 2930 m

altitude the displacement was roughly equivalent to that observed over a 1000-m altitudinal range on slopes of the same aspect.

The curves for 2700 m and 2930 m altitude exhibit a marked depression of flowering activity in November, followed by a rapid increase in the number of species in flower. This depression corresponds to late snow accumulation above 2700 m, which appears to have momentarily retarded flowering activity. The depression fails to show up at higher altitudes, presumably because flowering had hardly commenced at this time.

If the monthly maximum temperature curve at 2500 m altitude is compared with the corresponding flowering pattern (Fig. 6), it may be seen that maximum flowering activity occurs during the months with highest temperature. Maximum flowering continues to correspond with the period of highest temperature up to 3200 m, but above this altitude,

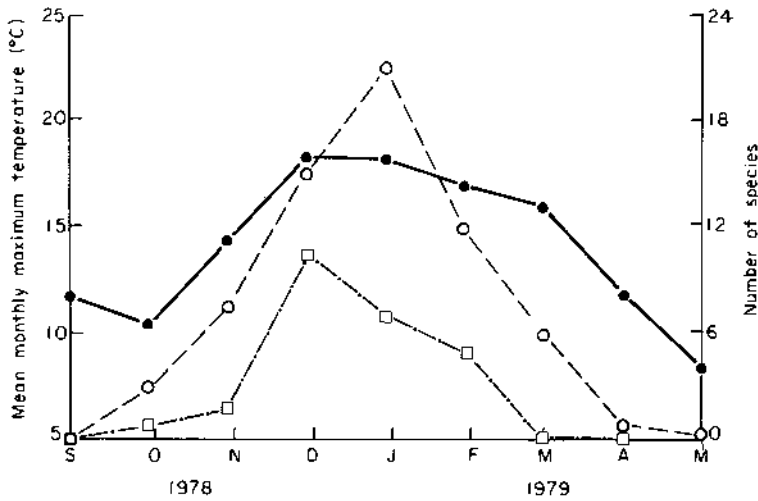


FIG. 6. Total number of species flowering in each month (○), number of species with peak flowering (□), and mean monthly maximum temperature (●) at 2500 m on the Cordón del Cepo.

sites 6 and 6A, it occurs as late as February and March respectively, and thus quite some time after the highest temperatures.

The duration of flowering tends, on average, to be longer at higher altitudes (Fig. 7). On north-facing slopes the average length of the flowering period at each station is significantly positively correlated with altitude ($r = 0.933$; $P < 0.01$), so that the flowering period increases from 4.2 weeks at 2320 m to 8.4 weeks at 3550 m altitude. The situation on the south-facing slopes is less clearly defined: here the average duration of flowering increases from 5.4 to 7.0 weeks between 2530 and 2930 m altitude, but then falls abruptly to 2.2 weeks at 3410 m.

There are several possible causes for the longer flowering periods observed at higher altitudes. If flowering were less synchronized within individual species at higher altitude, this would lead to longer overall flowering periods. Alternatively, at the higher altitudes, where temperatures are lower, the rate of floral development might be slower, in which case buds would require more time to mature and flowers would remain open for longer periods. Finally, a larger number of flowers might be produced at higher altitudes. The first

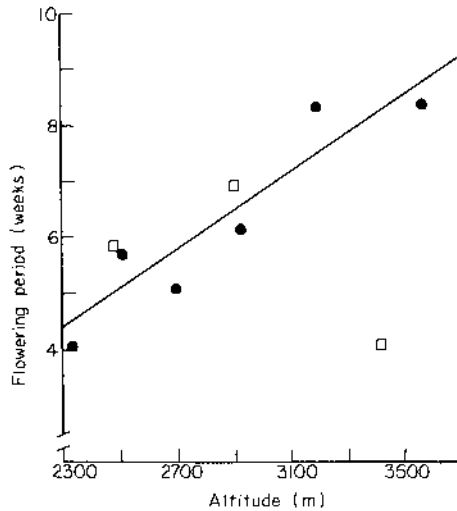


FIG. 7. Average duration of flowering at different altitudes on north-facing (●) and south-facing (□) slopes. The calculated regression line is shown.

possibility can be rejected, because when flowering is closely synchronized the percentage of individuals flowering on the peak flowering date for a given species should also be high; in contrast, when individuals are less synchronized, this percentage will be lower. However, comparison of the percentage of individuals in each species flowering on the respective peak flowering dates within and between sites (north-facing only) shows no significant differences ($F = 1.02$; $P = 0.25$).

With regard to the second alternative, Table 3 compares the life-span of individual open flowers for fifteen species at 2320 m altitude and for ten species at 3550 m, the data having been established on the basis of repeated daily observations on 5–15 flowers per species from bud stage until closing or withering. Flowers remained open for an average of 4.1 days at 2320 m altitude and for 9.0 days, or 2.2-times as long, at 3550 m (difference significant at the $P < 0.01$ level; $t = 2.9$). The average length of the flowering period for all observed species was 3.2 weeks at 2320 m and 10.8 weeks, or 3.3-times as long, at 3550 m altitude ($t = 15.6$, $P < 0.001$). Two species, *Cerastium arvense* and *Phacelia secunda*, occur at both altitudes. The life-span of flowers of these species was 2.4 and 3.2-times longer, respectively, at 3550 m altitude, while their flowering period was correspondingly 1.5 and 3.6-times as long.

Comparison of the relative values for flower life-span and length of flowering period at the two altitudes, assuming that longer life-span of flowers at the higher altitude reflects a

TABLE 3. Number of days for which individual flowers remain open on selected species at Site 1 (2320 m) (unpublished data of R. Primack) and Site 6 (3550 m), and the corresponding average flowering periods; values are mean \pm S.D.

	No. of species observed	No. of days flowers remain open	Flowering period (weeks)
Site 1	15	4.1 \pm 2.3	3.2 \pm 1.7
Site 6	10	9.0 \pm 4.1	10.8 \pm 5.4

slower rate of development, suggests that slow development accounts for about two-thirds of the difference in the average length of the flowering period between 2320 and 3550 m altitude, and for almost all the difference for one species (*Cerastium arvense*) occurring at the two altitudes.

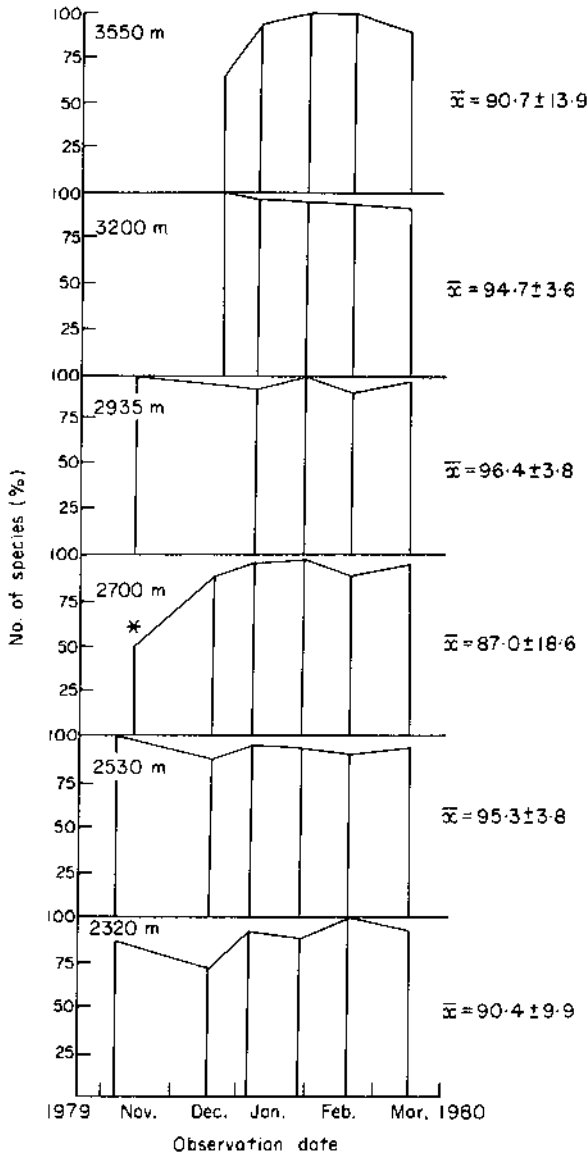


FIG. 8. Percentage of species at six sites whose phenological behaviour on specific observation dates in 1979–80 was identical with that observed on the same dates in 1978–79. November and December comparisons are based on flowering activity only; on all subsequent dates all phenophases were considered. Mean percentage \pm S.D. is given for each site. At 2700 m in Nov. (shown by an asterisk) only two species were considered.

Fruiting activity

Fruiting patterns parallel flowering patterns (Fig. 5), with maximum fruiting occurring approximately 4 weeks later than the flowering maximum. In 1979, fruiting was completed by all species at north-facing stations at 2320 m and 2700 m altitude before the winter period; above this, the first snowfalls interrupted fruit maturation and seed dispersal in a number of species, and fruiting was even less complete on south-facing slopes. Therefore, we have not attempted to correlate length of fruiting period with altitude.

Constancy of phenological patterns

A comparison of the phenological patterns recorded in 1978–79 and 1979–80 (Fig. 8) indicates that in this High Andean zone the patterns are remarkably constant from one year to the next. For dates duplicated in 1979–80, more than 90% of species had identical phenology. The deviant species were of two kinds; those with slightly later development (some annuals and geophytes), due to later snowmelt in 1979; and those with minor differences in the dates for beginning and end of flowering (some perennial herbs and shrubs). The latter differences showed no consistent direction, nor were they repeated from one altitude to another, and consequently are probably the effect of the error expected in comparing specific dates between years for patterns originally detected with a 2-week sampling-interval. The systematic variation encountered at the beginning of the season was mostly lost by early summer. Thus the phenological patterns were highly consistent from early summer onward over the two years.

DISCUSSION

In the High Andes of central Chile, phenological strategies and overall phenological patterns are governed by three considerations: the need for vegetative growth during the dry season to utilize soil moisture accumulated from winter precipitation; the pressure to flower over a relatively brief period favourable for insect activity; and need to mature fruits and seeds before the onset of winter. The total snow-free periods on north-facing slopes, with above-zero temperatures of 7–8 months, and of 5–7 months on south-facing slopes, are among the longest reported for high mountains with definable 'alpine' areas. In the northern hemisphere the growing season for such areas mostly ranges from 6 to 10 weeks (Bliss 1956; Billings & Bliss 1959; Billings 1974) and, exceptionally, extends to 12 weeks (Ellison 1954). Snow accumulation until June–July between 2800 and 3000 m in the climatically-similar Sierra Nevada in California (Klikoff 1965) suggests again that the growing season is longer in the Central Andes of Chile. Although in southern-hemisphere alpine areas the growing season is usually longer than in the northern hemisphere, 8-month snow-free periods above 2000 m altitude have not previously been described. In New Zealand, with a relatively mild oceanic climate, growth proceeds for 5 months at 1200–1300 m altitude in Central Otago (Bliss & Mark 1974), for some 6 months on Mt Ruapehu (Scott 1977) and for 7–8 months at 1220–1390 m altitude in N.W. Nelson (Clarke 1968). In the puña of N.W. Argentina (4000–5000 m, *c.* 23°S) the growing season is of 5–6 months duration (Ruthsatz 1977).

Although temperatures remain favourable for photosynthesis for a relatively long period in the High Andes, the potential for growth is counteracted from mid-summer onward by rapid soil drying. Many facets of the phenological behaviour of the high-Central-Andean species are clearly adaptations for permitting vegetative growth in spring and summer when soil moisture is abundant. Among these are precocious leaf production and flowering

under snow in many geophytes and seed germination in some annuals before snowmelt. Such precocious activity has been observed in several northern-hemisphere alpine areas (Billings & Bliss 1959; Spomer & Salisbury 1968; Kimball, Bennett & Salisbury 1973).

In the High Andean vegetation, all geophytes and many herbaceous perennials die back before the onset of winter. As outlined earlier, dormancy occurs independently of soil drought, and thus appears to be genetically determined. The abundance of such species along with many annuals is especially interesting. Annuals are generally of infrequent occurrence in high-mountain areas (c. 1–2% of the total flora: Billings & Mooney 1968; Billings 1974), because cold, erratic growing seasons make completion of an annual life-cycle uncertain. Went (1953) and Chabot & Billings (1972), however, draw attention to a higher incidence of annuals in summer-dry alpine vegetation in the Sierra Nevada of California, pointing out that many of these also occur in lower desert areas, from whence they appear to have migrated to higher altitude. Many of the High Andean annuals, as well as several geophytes and perennial species with non-facultative die-back, also appear below the andean zone as components of the matorral vegetation, extending in some cases to near sea-level. Whereas early spring die-back is clearly advantageous in lower mediterranean scrub vegetation, where summer drought occurs very early, the value of this kind of behaviour is less evident at the higher altitudes; one suggestion involves upward colonization in the past across the andean ecotone by matorral components.

In natural communities, temperature, photoperiod and soil moisture (Evans 1971), and rainfall (Opler, Frankie & Baker 1976) are important variables acting as environmental stimuli for flowering. Many angiosperms are animal-pollinated, however, so overall flowering patterns will be closely conditioned by the behavioural characteristics and abundance of the pollinators themselves. Maximum flowering activity is concentrated over periods of the year favouring pollinator-activity in several tropical communities (Janzen 1967; Frankie, Baker & Opler 1974; Stiles 1978), and this pattern should also characterize temperate plant communities. Thus, irrespective of the physiological basis for the initiation of flowering, it may be inferred that flowering patterns, and consequently internal community organization, will be strongly governed by biotic factors.

A first approximation of the degree to which the High Andean community is organized around biotic factors may be obtained by analysing overall flowering patterns. Flowering extends from the date of snowmelt through to late summer and early autumn. If allowance is made for fruit maturation, then the entire available time has been occupied in flowering. Early-flowering species bloom well before the appearance of specialized hymenopteran and lepidopteran pollinators (M. T. K. Arroyo, unpublished data); these species must therefore be utilizing reproductive methods not requiring cross-pollination, or alternatively they must have adapted to less-specialized insects which are active earlier in the season. From snowmelt onwards the number of species flowering increases rapidly until mid-summer, thereafter decreasing as autumn approaches, with the typical altitudinal displacements in peak flowering observed in other high-mountain areas (Ellison 1954; Clarke 1968; Lee 1971; Ruthsatz 1977). In both 1978–79 and 1979–80, maximum flowering in the lower andean zone corresponded with the warmest period of the year, although, interestingly, at higher altitudes it occurred somewhat later. It could be argued that the observed maximum flowering at high temperatures is a direct physiological effect, and indeed the effect which sudden low temperatures had on the otherwise smooth sequence to peak flowering in 1978–79, when more snow fell in late October and late November, is evidence that anthesis is temperature-sensitive. That temperature is not the only physiological determinant for the flowering sequence, nevertheless, may be deduced from the

observation that many species begin anthesis well after the peak temperature dates, or, in other words, fail to bloom when similar temperatures are first experienced in early summer. The correspondence between peak flowering and high temperature, the former probably physiologically maintained through selection operating on photoperiod, is thus viewed most logically as an indirect effect of selection for organizing flowering activity when pollinators are known to reach maximum abundance and diversity. The observed displacement in peak flowering beyond the maximum temperature period at higher altitudes, and especially on south-facing slopes, deserves further comment. This phenomenon is implicit in Ruthsatz's (1977) phenological records from the High Andes of N.W. Argentina (puña). Outside the Andes, there seem to be no phenological comparisons at different altitudes within the confines of alpine zones or their equivalents, so it is not clear how general this tendency really is. The late maximum flowering in the subnival zone in the High Andes of central Chile is clearly the combined effect of later initiation of vegetative activity conditioned by later spring snowmelt, slower rates of floral development, as has been demonstrated, and, probably, slower rates of vegetative activity. It is evidently too early to speculate on the significance of this displacement with respect to the availability of pollinators, as the maximum period of insect activity in the andean zone remains to be determined.

The longer flowering periods at higher altitudes are at first sight surprising. Given that the total growth period and rate of development decrease with altitude, and assuming for the moment that the relative amounts of vegetative and floral activity remain constant with altitude, then shorter and not longer flowering periods might have been predicted. It has been shown that two-thirds of the difference in average length of the flowering period between 2320 and 3550 m altitude may be attributable to slower floral development. The remaining one-third of this difference, therefore, is very likely to be the result of the production of larger numbers of flowers. This leads to the interesting and testable prediction that a greater proportion of available energy is being devoted to reproduction at higher altitudes.

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APPENDIX

List of species, their corresponding phenological behaviour (PB) and peak flowering dates in the sites where they occur. The reference numbers of the species correspond to those in Fig. 2; the order is that of peak flowering date

Ref. no.	PB		Peak flowering date and site
1.	IIa	<i>Barneoudia chilensis</i> Gay (Ranunculaceae)	13 Oct. (1); 13 Oct. (2); 26 Oct. (3)
2.	IIa	<i>Diposis bulbocastaneum</i> DC (Umbelliferae)	13 Oct. (1)
3.	I	<i>Microsteris gracilis</i> (Hook.) Greene (Polemoniaceae)	26 Oct. (1); 26 Oct. (2); 9 Nov. (3)
4.	IIa	<i>Tristagma bivalvis</i> (Lindl.) Traub. (Amaryllidaceae)	26 Oct. (1); 28 Dec. (3)
5.	IIIa	<i>Sanicula graveolens</i> Poepp. ex DC (Umbelliferae)	26 Oct. (1); 11 Jan. (4A)
6.	IVb	<i>Anarthrophyllum cumingii</i> (H. & A.) Phil. (Leguminosae)	26 Oct. (1); 8 Nov. (2); 19 Nov. (2A); 19 Nov. (3)
7.	IVb	<i>Tetraglochin alatum</i> (Gill. ex H. & A.) O. K. (Rosaceae)	11 Nov. (1); 8 Dec. (2)
8.	IIIa	<i>Calceolaria cana</i> Cav. (Scrophulariaceae)	11 Nov. (1)
9.	IIa	<i>Nothoscordum andinum</i> (Poepp.) Knuth (Amaryllidaceae)	11 Nov. (1); 21 Dec. (3)
10.	IIIa	<i>Relbunium richardianum</i> (Gill. ex H. & A.) Hick. (Rubiaceae)	11 Nov. (1); 13 Mar. (4A)
11.	IIa	<i>Sisyrinchium junceum</i> E. Mey. ex K. Presl. (Iridaceae)	8 Dec. (1); 9 Nov. (2)
12.	IIIa	<i>Cerastium arvense</i> L. var. <i>arvense</i> (Caryophyllaceae)	8 Dec. (1); 8 Dec. (2); 28 Dec. (3); 21 Feb. (6)
13.	IIIa	<i>Acaena pinnatifida</i> R. & P. (Rosaceae)	8 Dec. (1); 27 Dec. (2); 11 Jan. (3)
14.	I	<i>Tropaeolum sessilifolium</i> P. & E. (Tropaeolaceae)	8 Dec. (1)
15.	IIIb	<i>Acaena alpina</i> Poepp. ex Walp. (Rosaceae)	8 Dec. (1)
16.	I	<i>Lupinus microcarpus</i> Sims (Leguminosae)	8 Dec. (1); 27 Dec. (2)
17.	IIIb	<i>Polygonum aviculare</i> L. (Polygonaceae)	27 Dec. (1)
18.	IIIa	<i>Adesmia</i> affn. <i>aconcaguensis</i> Burk. (Leguminosae)	27 Dec. (1)
19.	IIIa	<i>Gallium eriocarpum</i> Bartl. ex DC (Rubiaceae)	27 Dec. (1); 11 Jan. (3)
20.	IVa	<i>Ephedra andina</i> Poepp. ex C. A. Mey. (Ephedraceae)	27 Dec. (1); 27 Dec. (2); 23 Jan. (3)
21.	IVa	<i>Happlopappus chrysanthemifolius</i> (Less.) DC (Compositae)	27 Dec. (1)
22.	IIIa	<i>Phacelia secunda</i> J. F. Gmel. (Hydrophyllaceae)	27 Dec. (1); 23 Jan. (5); 5 Mar. (6)
23.	IIIb	<i>Sisyrinchium arenarium</i> Poepp. (Iridaceae)	27 Dec. (1); 27 Dec. (2); 1 Jan. (3)
24.	IIIa	<i>Mutisia sinuata</i> Cav. (Compositae)	27 Dec. (1); 11 Jan. (2); 6 Feb. (3)
25.	IIIa	<i>Mutisia acerosa</i> Poepp. ex Less. (Compositae)	27 Dec. (1)
26.	I	<i>Chaetanthera pusilla</i> (D. Don) H. & A. (Compositae)	5 Jan. (1); 5 Mar. (6A)
27.	I	<i>Chaetanthera euphrasioides</i> (DC) Meigen (Compositae)	5 Jan. (1); 3 Jan. (2); 11 Jan. (3)
28.	IIIa	<i>Viviania marifolia</i> Cav. (Vivianaceae)	11 Jan. (1)
29.	IIIa	<i>Senecio bustillosianus</i> Remy (Compositae)	11 Jan. (1); 6 Feb. (2); 6 Feb. (2A); 6 Feb. (3); 21 Feb. (4); 13 Mar. (4A)
30.	IIIa	<i>Adesmia radicefolia</i> Clos (Leguminosae)	11 Jan. (1)
31.	I	<i>Madia sativa</i> Mol. (Compositae)	11 Jan. (1); 1 Jan. (2)
32.	IIb	<i>Alstroemeria pallida</i> Graham (Alstroemeriaceae)	11 Jan. (1); 6 Feb. (3)
33.	IIb	<i>Rhodophiala andina</i> Phil. (Amaryllidaceae)	11 Jan. (1); 23 Jan. (2); 23 Jan. (3); 23 Jan. (4)
34.	IIIa	<i>Perezia carthamoides</i> (D. Don) H. & A. (Compositae)	11 Jan. (1); 23 Jan. (2); 6 Feb. (2A); 11 Jan. (3) 23 Jan. (4); 13 Mar. (4A)

Ref. no.	PB	Peak flowering date and site
35.	IIIb	<i>Mutisia subulata</i> R. & P. (Compositae) 11 Jan. (1)
36.	IVb	<i>Chuquiraga oppositifolia</i> D. Don (Compositae) 23 Jan. (1); 23 Jan. (2); 6 Feb. (2A); 6 Feb. (2A); 6 Feb. (3); 21 Mar. (4); 23 Apr. (4A)
37.	IVa	<i>Mulinum spinosum</i> (Cav.) Pers. (Umbelliferae) 23 Jan. (1)
38.	IVb	<i>Nardophyllum lanatum</i> (Meyen) Cabr. (Compositae) 23 Jan. (1); 23 Jan. (2); 21 Feb. (3)
39.	IIa	<i>Solenomelus sisyrinchium</i> (Gris.) P. & D. (Amaryllidaceae) 27 Dec. (1)
40.	IIC	<i>Tristagma sessile</i> (Phil.) Traub. (Amaryllidaceae) 9 Nov. (2)
41.	IVa	<i>Berberis empetrifolia</i> Lam. (Berberidaceae) 9 Nov. (2); 19 Dec. (2A); 19 Dec. (3); 27 Dec. (4)
42.	IIIa	<i>Euphorbia portulacoides</i> L. emend. Spreng. (Euphorbiaceae) 8 Dec. (2); 19 Dec. (2A); 28 Dec. (3)
43.	I	<i>Collomia biflora</i> (R. & P.) Brand. (Polemoniaceae) 8 Dec. (2)
44.	IIIb	<i>Stachys albicaulis</i> Lindl. (Labiatae) 27 Dec. (2)
45.	IIIb	<i>Calceolaria arachnoidea</i> Graham (Scrophulariaceae) 23 Jan. (2); 11 Jan. (3)
46.	IVa	<i>Nassauvia axillaris</i> (Lag.) D. Don (Compositae) 6 Feb. (2)
47.	IIIb	<i>Nassauvia heterophylla</i> (Phil.) Reiche (Compositae) 6 Feb. (2); 6 Feb. (2A); 6 Feb. (3); 21 Feb. (4)
48.	IVa	<i>Senecio francisci</i> Phil. (Compositae) 21 Feb. (2); 21 Feb. (3); 13 Mar. (4); 23 Apr. (4A); 21 Mar. (6)
49.	IVa	<i>Haplopappus sericeus</i> Phil. (Compositae) 21 Feb. (2); 13 Mar. (2A)
50.	IIa	<i>Tristagma nivalis</i> Poepp. (Amaryllidaceae) 11 Nov. (2A); 19 Dec. (3)
51.	IIIb	<i>Perezia poeppigii</i> Less. (Compositae) 11 Jan. (2A)
52.	IIIa	<i>Moscharia</i> sp. (Compositae) 11 Jan. (2A)
53.	IIa	<i>Barneoudia major</i> Phil. var. <i>major</i> (Ranunculaceae) 26 Oct. (3); 26 Oct. (4); 11 Jan. (6)
54.	IIIb	<i>Astragalus curvicaulis</i> (Clos.) Reiche (Leguminosae) 28 Dec. (3)
55.	IIIa	<i>Oxalis geminata</i> H. & A. (Oxalidaceae) 11 Jan. (3); 23 Jan. (4)
56.	IIIb	<i>Haplopappus anthylloides</i> Meyen & Walp. (Compositae) 11 Jan. (3); 23 Jan. (4); 6 Feb. (4A)
57.	V	<i>Laretia acaulis</i> (Cav.) Gill & Hook. (Umbelliferae) 11 Jan. (3); 23 Jan. (4); 6 Feb. (4A); 6 Feb. (5); 21 Feb. (6)
58.	IIIa	<i>Adesmia exilis</i> Clos. (Leguminosae) 23 Jan. (1)
59.	IIIa	<i>Draba tenuis</i> Barn. (Cruciferae) 9 Nov. (4)
60.	IIIb	<i>Nastanthus spathulatus</i> (Phil.) Miers. (Calyceraceae) 11 Jan. (4); 13 Mar. (4A); 21 Feb. (5)
61.	IIIa	<i>Erigeron andicola</i> DC (Compositae) 11 Jan. (4); 6 Feb. (4A)
62.	V	<i>Discaria nana</i> (Rhamnaceae) 11 Jan. (4)
63.	IIIa	<i>Calandrinia sericea</i> H. & A. (Portulacaceae) 11 Jan. (4); 11 Jan. (5); 23 Jan. (6)
64.	V	<i>Azorella bolacina</i> Clos (Umbelliferae) 11 Jan. (4)
65.	IIIb	<i>Loasa caespitosa</i> Phil. (Loasaceae) 11 Jan. (4); 13 Mar. (4A); 11 Jan. (5)
66.	IIIb	<i>Calandrinia dianthoides</i> Phil. (Portulacaceae) 23 Jan. (4)
67.	V	<i>Azorella monantha</i> Clos (Umbelliferae) 23 Jan. (4)
68.	IIIa	<i>Leucheria</i> sp. (Compositae) 23 Jan. (4)
69.	IIIa	<i>Viola philippi</i> Leyb. (Violaceae) 11 Jan. (4A); 23 Jan. (6A)
70.	IVa	<i>Nassauvia pungens</i> Phil. (Compositae) 6 Feb. (4A); 21 Feb. (5); 21 Feb. (6)
71.	IIIb	<i>Perezia pilifera</i> (D. Don) H. & A. (Compositae) 13 Mar. (4A)
72.	I	<i>Chaetanthera apiculata</i> (Remy) Meigen (Compositae) 13 Mar. (4A); 6 Feb. (5)
73.	IIIa	<i>Draba gilliesii</i> H. & A. (Cruciferae) 19 Dec. (6)
74.	IIIa	<i>Viola montagnei</i> Gay (Violaceae) 19 Dec. (6)
75.	IIIb	<i>Nototriche compacta</i> (A Gray) A. W. Hill (Malvaceae) 19 Dec. (6)
76.	IIIb	<i>Nassauvia lagascae</i> (D. Don) Meigen (Compositae) 11 Jan. (6); 21 Feb. (6A)
77.	IIIb	<i>Trisetum</i> sp. (Gramineae) 23 Jan. (6)

Ref. no.	PB		Peak flowering date and site
78.	IIIb	<i>Senecio crithmoides</i> H. & A. (Compositae)	23 Jan. (6)
79.	IIIb	<i>Leucheria salina</i> (Remy) Hieron. (Compositae)	5 Mar. (6)
80.	IIIa	<i>Viola atropurpurea</i> Leyb. (Violaceae)	8 Dec. (5); 11 Jan. (6)
81.	V	<i>Calandrinia caespitosa</i> Gill. ex Arn. (Portulacaceae)	27 Dec. (5)
82.	V	<i>Oreopolus glacialis</i> (P. & A.) Ricardi (Rubiaceae)	27 Dec. (5)
83.	V	<i>Junellia uniflora</i> (Phil.) Mold. (Verbenaceae)	27 Dec. (5); 19 Dec. (6)
84.	IIIb	<i>Oxalis</i> affn. <i>compacta</i> Gill. (Oxalidaceae)	27 Dec. (5); 21 Feb. (6)
85.	V	<i>Azorella madreporica</i> Clos (Umbelliferae)	11 Jan. (5); 11 Jan. (6)
86.	I	<i>Adesmia capitellata</i> (Clos) Hauman (Leguminosae)	23 Jan. (5); 21 Feb. (6)
87.	V	<i>Adesmia glomerula</i> Clos var. <i>glomerula</i> (Leguminosae)	23 Jan. (5)
88.	IIIa	<i>Tropaeolum polyphyllum</i> Cav. (Tropaeolaceae)	23 Jan. (5); 23 Jan. (6)
89.	I	<i>Chaetanthera pentacaenoides</i> (Phil.) Hauman (Compositae)	23 Jan. (5); 21 Mar. (6)
90.	IIIb	<i>Rytidosperma virescens</i> (Desv.) Nicora (Gramineae)	6 Feb. (5)
91.	IIIb	Gramineae (unidentified)	6 Feb. (5)
92.	IIIb	<i>Pozoa coriacea</i> Lag. (Umbelliferae)	6 Feb. (5)
93.	IIIb	<i>Senecio looseri</i> Cabr. (Compositae)	6 Feb. (5); 21 Feb. (6)
94.	IIIb	<i>Stipa chrysophylla</i> Desv. (Gramineae)	21 Feb. (5); 21 Feb. (6)
95.	IIIb	<i>Nastanthus agglomeratus</i> Miers. (Calyceraceae)	5 Mar. (5)
96.	IIIa	<i>Hordeum comosum</i> Presl. (Gramineae)	5 Mar. (6A)
97.	IIIb	<i>Nassauvia pinnigera</i> D. Don (Compositae)	21 Mar. (6A)