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FLOWERING RECORDS OF SOME SUBALPINE TREES AND SHRUBS AT ARTHUR'S PASS, NEW ZEALAND

Summary: The flowering periodicity and intensity of some subalpine trees and shrubs at Pegleg Flat, Arthur's Pass National Park, was recorded from 1981/82 to 1984/85. Moderate to heavy flowering of most species in 1981/82 was followed by two years of little or no flowering in 1982/83 and 1983/84; almost all species observed flowered heavily in 1984/85. No clear correlation was found between flowering intensity and mean summer temperatures of the previous growing season, when flower buds were initiated. It is suggested that the extent of flower bud initiation may also depend on current carbohydrate and mineral nutrient levels in the plants, which are temporarily depleted after mass-flowering years. The observed 3-year cycle of heavy flowering coincides with previous records for many other New Zealand trees and shrubs.

Introduction

Periodic flowering, i.e., the tendency to flower moderately to heavily in some years, but only lightly or not at all in others, has been described for a number of New Zealand forest trees, e.g., *Nothofagus solandri** (Poole, 1949; Wardle, 1970), podocarps (Beveridge, 1964), southern rata *(Metrosideros umbellata)* (Wardle, 1971), and also for some alpine herbs and grasses (Connor, 1966; Mark, 1968, 1970; Clarke, 1968; Campbell, 1981). In many of the species studied, flowering appears to follow a 3-year cycle. Flower bud primordia are initiated in late summer to autumn and produce flowers in the following spring or summer after overwintering. It has been suggested that warm temperatures during the period of flower bud initiation may promote a higher flower density in the subsequent flowering season (e.g. Poole, 1949; Connor, 1966; Mark, 1968; Wardle, 1971). In several species of *Celmisia,* however, flowering intensity is also influenced by the abortion of floral primordia due to cold winter temperatures (Mark, 1970).

Correlations between flowering intensity and discrete temperature data have only rarely been sought (Poole, 1949; Connor, 1966; Mark 1968). During the present study, flowering of several species of subalpine trees and shrubs at Pegleg Flat, Arthur's Pass National Park, was observed from 1981/82 to 1984/85. The area is situated close to the upper altitudinal limit of the species studied, where both reproductive and vegetative processes may be severely affected by seasonal temperature fluctuations.

Methods

Pegleg Flat, situated near the summit of Arthur's Pass (42°54' S, 171°34' E), is a small river flat at an altitude of 830 m a.s.l. which was created by the deposition of a young river terrace of the Otira River. Older high terraces of the Otira River and Pegleg Creek and the lower slopes of the surrounding mountains support various associations of subalpine low forest and subalpine scrub up to an altitude of approximately 1000 m. A detailed description of the local forest and scrub vegetation, soils, and climate has been given elsewhere (Haase, 1985, 1986a).

In the 1981/82 season flowering intensity was only noted on a subjective basis. In the following seasons (1982/83 to 1984/85) flower panicles (corymbs) of the small epacrid tree *Dracophyllum traversii* and the composite shrubs *Senecio bennettii* and *Olearia ilicifolia* were counted, or estimated when in great numbers (Haase, 1986b, c, d). Flowering intensity of a number of other tree and shrub species was observed on a subjective basis. All flowering records were reduced to the four intensity classes: none or very little; light; moderate; and heavy flowering.

Air temperature was recorded with a Casella thermohygrograph from September 1982 to May 1984; mean monthly temperatures of previous seasons were extrapolated from records of the Otira and Arthur's Pass stations. These records were also used to calculate the 10-year mean for every month (Haase, 1985).

Results

The flowering season at Pegleg Rat is normally protracted, from September to April (Table I). The early-flowering *Pseudopanax colensoi* may commence in August during mild winters; autumn flowering species, especially *Metrosideros umbellata,* can still bear flowers in May, some individuals even in early June (Haase, 1985). The flowering times can vary up to four weeks from year to year depending on spring temperature.

Table 1: *Flowering times of 12 subalpine tree and shrub species at Pegleg Flat. *only observed in 1984.*

Species	A	S	O	N	D	J	F	M	A
*Pseudopanax colensoi**	⎯⎯⎯								
Dracophyllum traversii *Dracophyllum longifolium* *Olearia arborescens*				⎯⎯⎯					
Olearia lacunosa				⎯⎯⎯					
Olearia ilicifolia *Senecio bennettii*					⎯⎯⎯				
Hoheria glabrata *Hebe salicifolia*						⎯⎯⎯			
Metrosideros umbellata *Olearia avicenniaefolia* *Dracophyllum uniflorum*						⎯⎯⎯			

The results of the flowering records of fourteen woody and four herbaceous species are shown in Table 2.

Dracophyllum traversii flowered in all four growing seasons considered in this study. *D. traversii* produces large terminal flower panicles; the buds are probably initiated by mid to late summer and overwinter. The apical meristem of the shoot is exhausted in the process of flowering and the supporting branch usually dies back and aborts within a few years unless lateral branches arise from the axils of the remaining older leaves which did not produce flower buds (Haase, 1986b).

Senecio bennettii produces terminal flower panicles which arise only from one-year-old lateral shoots. After flowering the complete shoot aborts. The number of lateral shoots per apical shoot varies considerably from year to year and flowering intensity will thus depend not only on the climatic conditions during the time of flower bud initiation but is also regulated by the number of lateral shoots produced earlier in the season (Haase, 1986c).

Olearia ilicifolia produces flower corymbs from axillary buds. *O. ilicifolia* flowered, at least to some extent, in all growing seasons observed, but in 1982/83 and 1983/84 the flowering intensity was much reduced and some plants did not flower at all. In 1981/82 and 1984/85 the crowns of most trees appeared completely white due to high flower density (Haase, 1986d).

Hoheria glabrata develops flower buds in triple clusters in the axils of all foliage leaves except the two or three youngest leaves of the season (Haase, 1985).

Table 2: Flowering intensity of 18 subalpine species at Pegleg Flat. Symbols: -, no or very little; 0, light; $ moderate; $$, heavy flowering; * flower density mainly regulated by bud abortion during current season; ** only two trees in study area.

Species	1981/82	1982/83	1983/84	1984/85	1985/86
Dracophyllum traversii	+	0	+	++	0/-
Senecio bennettii	+	-	+	++	-
Olearia ilicifolia	++	0	0	++	0/-
*Hoheria glabrata**	++	-	++	+	++
Pseudopanax colensoi	++	-	-	++	
*Olearia lacunosa***	-	-	++	-	
Metrosideros umbellata	-	++	+	+	
Olearia colensoi	-	-	-	++	
Coprosma pseudocuneata	-	-	-	++	
D. longifolium, D. unifl.	+	+	+	+	
O. arborescens, O. avice., *Hebe salicifolia*	++	++	++	++	
Ph. cookianum, A. nervosa, *Ch. flavescens*	++	-	-	+/++	
Aciphylla horrida	-	-	-	++	

Flower buds are clearly visible in November but only open in February. Although a number of buds usually abort during further development, *Hoheria* normally flowers heavily. An exception was the cool and wet summer of 1982/83 when almost all buds were aborted (Haase, 1985).

Flowers of *Pseudopanax colensoi* are arranged in terminal umbels; new vegetative growth resumes from lateral buds after flowering. The fully developed flower buds overwinter and open in early spring (September). Flowering was not observed in 1981 but judging from the abundance of fruit later in the season, 1981 appears to have been a heavy flowering year.

Two specimens of *Olearia lacunosa* present in the study area flowered heavily in 1983/84 but not at all in the remaining three seasons.

Metrosideros umbellata, which occurs only in the northern part of the study area, did not flower in 1981/82, whereas 1982/83 was a heavy flowering year. In 1983/84 and 1984/85 flowering was moderate.

Olearia colensoi flowered heavily in 1984/85 but did not produce flowers in the three previous seasons.

The dioecious shrub *Coprosma pseudocuneata* has very inconspicuous flowers which are only noticed on close inspection, but the red berries are easily observed later in the season.

Olearia arborescens, O. avicenniaejolia, Hebe salicifolia, Dracophyl/um longifolium, and *D. uniflorum* flowered moderately to heavily in all four growing seasons. The perennial monocotyledonous plants *Phormium cookianum, Astelia nervosa,* and *Chionochloa flavescens* had moderate to heavy flowering seasons in 1981/82 and 1984/85; 1982/83 and 1983/84 were non-flowering years. *Aciphylla horrida* (Umbelliferae) only flowered in 1984/85.

Table 3 gives the mean monthly temperatures and rainfall for the summer months, together with the calculated 10-year means. The temperature data are based on direct measurements at Pegleg Flat; the rainfall figures are records from the Otira station and are closely related to the actual rainfall at Pegleg Flat (Haase, 1985). Table 4 gives the mean monthly temperatures of the winter months.

Table 4: *Mean monthly winter temperatures* (^{O}C). *.extrapolation from Otira records (1973-84)*; ***umeasured at Pegleg Flat.*

Season	June	July	August	winter mean
Mean*	3.0	2.4	3.4	2.9
1984*	5.4	4.3	5.2	5.0
1983**	3.3	2.5	4.5	3.4
1982*	3.2	1.4	3.3	2.6
1981*	3.9	2.8	2.1	2.9

Discussion and Conclusions

During the four growing seasons observed, there were two very good flowering years for most species, separated by a 2-year interval with no or considerably reduced flowering. Only *Metrosideros umbellata* and *Olearia lacunosa* were out of phase, with heavy flowering in 1982/83 and 1983/84, respectively. Comparison of the data presented in Tables 2 and 3 suggests no overall correlation between flowering intensity and summer temperature. Only the heavy flowering in 1981/82 was preceeded by a summer with higher than average temperatures and a considerable rainfall deficit; in all other years flowering intensity was not correlated with summer temperature. Neither is there any consistent effect of winter temperatures (Table 4), and abortion of the more exposed floral buds, in *Pseudopanax colensoi* and *Dracophyllum traversii,* was never observed.

Table 3: *Mean monthly summer temperatures* (^{O}C) *and rainfall (mm).* * extrapolation from Otira temperature records (1973-84); ***temperature measured at Pegleg Flat.*

Season	December		January		February		Summer mean	
	Temp.	Rain	Temp.	Rain	Temp.	Rain	Temp.	Rain
Mean*	10.3	427	11.6	426	12.5	346	11.5	1199
1984/85*	11.1	807	12.3	654	12.2	157	11.9	1618
1983/84**	8.8	549	10.1	436	13.4	211	10.8	1196
1982/83**	8.0	635	8.7	693	11.7	108	9.5	1436
1981/82*	11.8	751	11.1	906	12.9	317	11.9	1974
1980/81*	11.1	171	13.9	227	12.8	423	12.6	821

Warm and dry summers have often been associated with extensive initiation of flower buds in woody and herbaceous species (e.g. Hocking, 1936; Poole, 1949; Connor, 1966; Mark, 1968; Wardle, 1971). Warm summer temperatures are correlated with high rates of photosynthesis and carbohydrate production which increase the C/N ratio in the plant tissue. This ratio may be further increased by summer drought, because decreasing availability of water also limits the mineral uptake from the soil including nitrate, thus limiting vegetative, but promoting reproductive growth (e.g. Hocking, 1936; Poole, 1949). A well-studied example relating flower bud initiation to environmental parameters and to carbohydrate reserves is the periodically flowering grass *Chionochloa rigida*. Here summer temperature appears to be the key factor for flower initiation (Mark, 1968; Payton & Mark, 1979). However, the same may not necessarily apply to woody plants. Some of the flowering records cited appear to contain only selected heavy flowering years positively correlating with summer temperature; seasons with less spectacular flowering were not recorded.

The cost of reproduction in woody plants is illustrated by the severely reduced radial wood increment during heavy flowering seasons (e.g. Holmsgaard, 1956) which probably makes it physiologically impossible for trees to flower every year; irregular flowering may therefore be the consequence of environmental and physiological constraints on seed production (Silvertown, 1980). Tree populations usually exhibit synchronous mass-flowering; the following intermast period may constitute the time required for accumulation of nutrient reserves necessary for the next mass crop (Silvertown, 1980). During the course of evolution this synchronous flowering periodicity has also come to serve as an anti-herbivore adaptation (Janzen, 1971; Silvertown, 1980).

Applying this nutrient constraint concept to the present study, it is suggested that the heavy flowering and subsequent fruiting in 1981/82 and 1984/85 prevented or reduced renewed large scale flower bud initiation in the following years. In 1982/83, therefore, no flowering occurred in *Senecio bennettii, Pseudopanax colensoi, P. simplex, P. lineare,* the monocotyledonous *Phormium cookianum* and *Chionochloa flavescens,* and a very much reduced flowering was revealed in *Olearia ilicifolia* and *Dracophyllum traversii*. Total failure to flower in *Hoheria glabrata* and *Senecio bennettii,* however, was also due to bud abortion and morphological constraints respectively. On the other hand,

Metrosideros umbellata, which did not flower in 1981/82, flowered heavily in 1982/83.

Jackson & Sweet (1972) noted that flower buds are often initiated after shoot and leaf growth has ceased in late summer. In 1983/84 the vegetative resting buds of many species (e.g. *Hoheria glabrata* and all composites) contained a smaller number of leaf primordia than normal and only a minimum of new leaf and shoot growth was produced (Haase, 1985, 1986e). Vegetative growth other than wood increment ceased relatively early in the summer of 1983/84 and did not demand as much carbohydrate expenditure as in other seasons. As a result, a particular accumulation of carbohydrate reserves during the remaining part of the growing season was probably responsible for the heavy flowering in 1984/85.

It was noted that some species apparently produce flower buds every season. In the two shrubby species of *Dracophyllum* the always small-scale annual flowering is probably not constrained by nutrient limitations. All other annually flowering species studied, i.e. *Hoheria glabrata, Olearia arborescens,* O. *avicenniaefolia,* and *Hebe salicifolia,* are typical of disturbed habitats. For early successional species the regular production of large seed crops is an ecological necessity which can probably be maintained by the higher soil fertility normally associated with disturbed sites (Haase, 1985).

Lack of correlation between summer temperature and extent of flower bud initiation in subalpine woody plants, annual flowering of species on more fertile sites, and an apparent promotion of heavy flowering by an early cessation and/or minimum production of vegetative growth, suggest that sufficient nutrient reserves may be more important as a trigger for widespread flower bud initiation than warm summer temperatures.

Acknowledgements

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