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Flowering phenology of tropical-alpine dwarf trees on Mount Kinabalu, Borneo

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Abstract: The flowering phenology of five alpine dwarf-tree species was observed in the summit region (3900–3950 m elevation) of Mt. Kinabalu on Borneo Island from March 1998 to November 2001. For each target species, 20–50 individual plants were numbered in two observation plots and the number of inflorescences was monitored at 2–3-mo intervals. The flowering patterns varied among species. *Rhododendron buxifolium* bloomed extensively every March–May at the main plot but the flowering pattern at the subplot was less predictable. Mass flowering occurred in March 1998 when drought stress was very severe due to an El Niño event. *Rhododendron ericoides* showed continuous flowering throughout the year and high synchrony between the plots. Extensive flowering of *Leptospermum recurvum* occurred synchronously within and between plots in the early half of 1999, then flowering activity decreased greatly. *Photinia davidiana* showed an annual flowering cycle but the timing of the peak flowering differed between the plots. *Vaccinium stapfianum* showed synchronous flowering between the plots and the flowering peak appeared at longer than 1-y intervals. Plant size was positively correlated with mean flower production in all species, and with the flowering frequency of *R. ericoides*, *R. buxifolium*, and *V. stapfianum* at one of the plots at least. Two fleshy-fruited species, *P. davidiana* and *V. stapfianum*, had high selfing ability for fruit production and showed relatively low flowering synchrony among individuals in comparison with the other species. These results indicate that the trigger for initiation of flowering may differ among sympatric species in a tropical-alpine ecosystem at least in normal years.

Key Words: flowering synchrony, fruit set, *Leptospermum*, *Photinia*, *Rhododendron*, selfing ability, *Vaccinium*

INTRODUCTION

The phenological patterns of flower and fruit production under aseasonal conditions have received particular attention in the field of tropical ecology (Appanah 1985, Ashton *et al.* 1988, Augspurger 1981, Janzen 1974, Sakai *et al.* 1999, van Schaik *et al.* 1993, Wright & Calderon 1995). Most studies have been conducted in lowland tropical forests where species diversity is extremely high and canopy layers are often taller than 40 m, with only a few studies in montane cloud forests (Berlin *et al.* 2000, Koptur *et al.* 1988). So far, phenological studies of tropical plants in alpine regions have been completely lacking except for a pioneer work in the Andean desert Páramo by Monasterio (1986). In comparative studies of the fruiting phenology on Mt. Kinabalu in Borneo, different fruiting patterns were detected along an altitudinal gradient despite the lack of strong seasonality in the climate (Kimura *et al.* 2001, Leighton & Leighton 1983). Occurrence of mass-fruiting and fruitless periods was detected in the lowland forests, whereas continuous and irregular fruiting patterns without pronounced peaks were observed in the upper montane and subalpine forests. Such a variation in fruiting patterns among vegetation zones influences the migration of frugivorous birds (Kimura *et al.* 2001, Leighton & Leighton 1983). However, the fruiting pattern may not accurately reflect the flowering pattern because the periods of fruit development and presentation differ among species.

Species diversity of vascular plants drastically decreases with an increasing altitude in tropical regions (Aiba & Kitayama 1999). Because most plants have dwarfed forms and species composition is simple in alpine zones, this makes it a relatively easy task to quantify the reproductive outputs of individual plants. Taking

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advantage of this, we studied the flowering phenology of tropical-alpine plants on Mt. Kinabalu (4100 m elevation) over 4 y from March 1998 to November 2001. Although the air temperature constantly decreases with altitude, the annual fluctuation of the daily mean air temperature is small irrespective of altitude. Annual precipitation was also similar at all altitudes with little seasonal fluctuation (Kitayama *et al*. 1999). Under such aseasonal conditions, how do plants determine their reproductive schedules? Is the flowering pattern of tropical-alpine plants different from that of lowland plants? To answer these questions, we studied the flowering pattern of five major species at two locations in the summit region.

In this study, we evaluated the extent of flowering synchrony within a population, between populations, and among species within a community. If flowering phenology is determined by specific climatic cues, synchronous flowering is expected within and among local populations and among sympatric species. As an ecological factor affecting the flowering pattern of individual species, the mating system may be important (Bawa *et al*. 1985, Rathcke & Lacey 1985). There are several studies indicating the importance of pollinator attraction by synchronous flowering in lowland tropical forests (Appanah 1985, Augspurger 1981, Sakai *et al*. 1999). If pollinator attraction is the key determinant of flowering phenology, synchronous flowering is expected within a population and among species depending on the same pollinator type. Thus, we assessed the selfing ability of target species by comparing the fruit set under natural conditions with a net-bagging treatment. Furthermore, the effects of plant size on flowering vigour and synchrony were assessed because timing and quantity of flowering are sometimes influenced by the size of individual plants (Ollerton & Lack 1998, Rathcke & Lacey 1985). The purpose of our study is to answer the following questions: (1) Is there flowering synchrony among sympatric species or do individual species have their own reproductive pattern (i.e. interspecific synchrony)? (2) Do plants of the same species have a synchronous flowering pattern within a population (i.e. intra-population synchrony)? (3) If so, is there a synchronous flowering pattern between populations of the same species (i.e. inter-population synchrony)? (4) Are flowering frequency and synchrony influenced by the size of individual plants within a population? (5) Is there any correlation between the mating system and flowering pattern in these species?

MATERIALS AND METHODS

Study site

The research site was located near the Donkey Ears Peak on the summit region of Mt. Kinabalu in northern Borneo (6° 05′ N, 116° 33′ E). Altitudinal vegetation changes on Mt. Kinabalu were classified into the following five zones according to Kitayama (1992); lowland hill forest (< 1200 m asl), lower montane forest (1200–1800 m), upper montane forest (1800–3000 m), subalpine forest (3000–3400 m), and alpine vegetation (> 3400 m). A large part of the summit region consists of exposed granitic rocks. Compact vegetation patches are distributed among the boulder areas where weathered rocks and debris accumulate and thin organic soils are formed. Vegetation in the summit region is physiognomically characterized by the dominance of leptophyllous and nanophyllous dwarf trees and shrubs (Kitayama 1992). The height of canopy-forming trees is usually less than 2 m and vegetation cover is about 50%.

A preliminary survey was carried out in March 1998 to select the target species and research site. We established two measurement plots at 3900–3950 m altitude: a main plot (about 100 m × 80 m in size) located on a saddle between the Donkey Ears Peak and the Ugly Sisters Peak, and a subplot (about 100 m × 50 m) on a south-east-facing slope of the Donkey Ears Peak. Species composition and vegetation cover are similar between the plots. These plots were completely separated by bare rock for a distance of at least 300 m.

Meteorological observation

A climatic station was set up at the main plot (3940 m) in late June 1998, which was composed of a CR-10X data logger (Campbell Scientific, Logan, Utah, USA), a CS500-L6 probe for measuring air temperature and relative humidity, a LI-COR 190SB quantum sensor for detecting photosynthetically active radiation (PAR), and a TE525MM tipping bucket rain gauge for monitoring rainfall. Air temperature and humidity were measured at 1.5 m above the ground. Measurements of air temperature, humidity, and PAR were taken at 10-s intervals, and that of rainfall was taken instantaneously as pulse counts. Readings were reduced to 30-min means and/or totals, which were magnetically stored in the CR-10X.

Plant species and phenological survey

Five common dwarf-tree species were selected as target species: *Rhododendron buxifolium* Low ex Hooker f. (Ericaceae), *Leptospermum recurvum* Hooker f. (Myrtaceae), *Rhododendron ericoides* Low ex Hooker f., *Photinia davidiana* (Decne.) Cardot (Rosaceae), and *Vaccinium stapfianum* Sleumer (Ericaceae). All these species are dominant on the summit region and they occupy more than 80% of total vegetation cover (personal observation). Flowers of *R. buxifolium* and *R. ericoides* are visited by nectar-feeding birds, mainly the mountain blackeye *Chlorocharis emiliae* (Argent *et al.* 1998, and personal observation). Flowers of *L. recurvum* and *P. davidiana* are visited by dipteran insects (personal observation). Flower visitors of *V. stapfianum* are unknown.

At the main plot, 50 individual plants were arbitrarily selected for each target species (only 40 for *P. davidiana*) and numbered with plastic tags in late June 1998. Then, the number of flowering inflorescences (flowers for *L. recurvum*) of each marked plant was recorded at 2- or 3-mo intervals until May 2001. Additional observations were made in November 2001. For *R. buxifolium* and *P. davidiana*, the number of inflorescences in March 1998 was also estimated by counting old inflorescences in June 1998 since a quantitative observation was not carried out in March 1998. In total, 17 or 18 phenological census sessions were performed from March 1998 to November 2001 at the main plot. At the subplot, 26 plants for *R. buxifolium*, 25 each for *R. ericoides*, *L. recurvum* and *P. davidiana*, and 20 for *V. stapfianum* were numbered in mid-October 1998, and the same observation of flowering phenology was conducted until November 2001 (in total 15 sessions). We selected only adult plants at the subplot that had reproductive organs (floral buds, flowers, fruits or scars of fruits).

Flowering synchrony

The size of individual plants was expressed as a product of the canopy projection area and plant height. The major and minor diameters of the canopy projection and plant heights were measured for all marked plants in October 1998. The shape of the canopy projection was regarded as an ellipse. The frequency of flowering events, mean inflorescence (or flower) number per census (i.e. reproductive effort), and flowering synchrony within populations were calculated for individual plants selected. A flowering event was defined as an occurrence of more than 5% of the maximum flower number for each plant observed at a census throughout the research period. The proportion of flowering plants per population was compared between the plots over the research period by Spearman's rank correlation to assess the extent of flowering synchrony between the populations for each species. The effects of plant size on flower production and flowering frequency were tested by Spearman's rank correlation at each plot.

The flowering synchrony of individual plants (X_i) within a population (intra-population synchrony) was calculated according to Augspurger's method (1983) as follows:

$$X_i = \left(\frac{1}{n-1}\right)\left(\frac{1}{f_i}\right)\sum_{j=1}^{n} e_{j \neq i}$$

where, e_i = number of census sessions both individuals i and j are flowering synchronously, f_i = number of census sessions individual i is flowering; n = number of individuals observed in a population. When $X = 1.0$ and 0.0, perfect synchrony and no synchrony occurs within a population, respectively. Furthermore, the extent of flowering synchrony of individual plants was compared between the plots for each species considering the effect of plant size by ANCOVA, where plant size was treated as a covariate. Before the analysis, flowering synchrony was arcsine-square-root transformed and plant size was logarithmically transformed. Plants that did not flower throughout the census period were excluded from the analyses in this study.

Observation of fruiting

To assess the extent of selfing ability of the target species, fruit set (fruit number/flower number) under natural pollination and pollinator exclusion was compared. Pollinator visitation was excluded by a bagging treatment for inflorescences or branches having flower buds with fine-meshed bags during the flowering season. Fruit set of each species was measured in a vigorous flowering season at one of the plots; March 1999 for *L. recurvum* at the main plot, and March 2000 for *P. davidiana* at the subplot, *R. buxifolium* at the main plot, *R. ericoides* at the main plot, and *V. stapfianum* at the subplot. For each of *P. davidiana*, *R. buxifolium* and *V. stapfianum*, 20 individuals with more than five inflorescences at the bud stage were arbitrarily selected. For each tree, three inflorescences as a control and one inflorescence as a bagging treatment were arbitrarily marked, and the flower number was counted. At the fruiting season, the number of fruits containing mature seeds was counted and the fruit set was calculated. Mean values of three control inflorescences from the same plant were used for statistical comparison. For *L. recurvum*, branches having 10–30 flower buds were used for the measurement unit because flower buds were formed very densely in this species. For *R. ericoides*, fruit set under natural pollination (n = 30 individuals) and the bagging treatment (n = 24) were measured in different individuals because the number of inflorescences per plant was commonly small. Fruit set of control and bagged flowers was compared by the Mann–Whitney *U*-test in each species.

RESULTS

Climatic conditions

Daily mean air temperature during the period July 1998 to October 2001 was 5.4 °C ± 0.9 (SD) ranging from

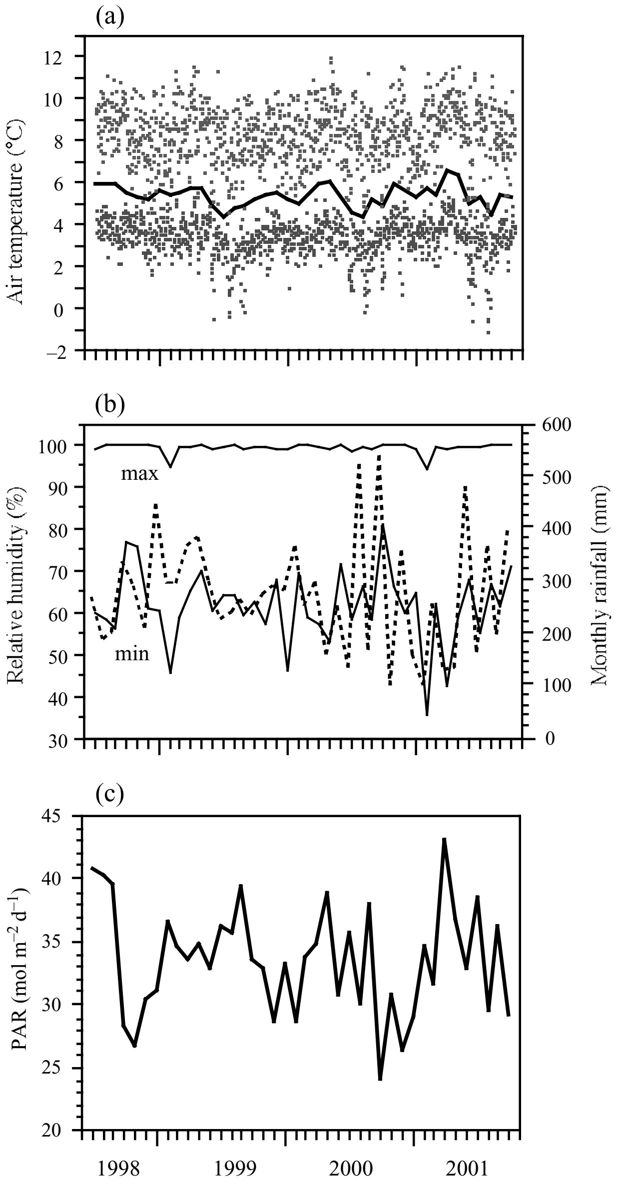


Figure 1. Transitions of (a) air temperature (monthly mean of daily mean temperature by line, daily maximum and minimum by dots), (b) relative humidity (monthly mean of daily maximum and minimum) and monthly precipitation (broken line), and (c) monthly mean of daily total photosynthetically active radiation (PAR) at the main plot from July 1998 to October 2001 on the summit of Mt. Kinabalu.

1.0–7.6 °C, daily maximum temperature ranged from 3.2–11.8 °C, and daily minimum temperature ranged from – 1.0–5.8 °C. Annual fluctuation of monthly mean temperature was about 2 °C, and monthly minimum temperature tended to decrease in June–August (Figure 1). Monthly mean values of daily maximum relative humidity (RH) were almost 100% throughout the period, whereas those of daily minimum RH fluctuated widely, ranging from 35–80% (Figure 1). Daily minimum RH decreased every January or February. Monthly mean of daily total photosynthetically active radiation (PAR) was highly variable ranging from 24–43 mol m^{-2} d^{-1}, and low PAR conditions tended to occur around October–December (Figure 1). The mean annual precipitation was 3250 mm. Monthly rainfall ranged from 100–540 mm, and increased around October to January (Figure 1). Thus, there is a mild seasonality in climatic conditions in the summit area of Mt. Kinabalu. Monthly rainfall was positively correlated with monthly mean of daily minimum RH ($r = 0.55$, $P = 0.0003$) and negatively correlated with that of PAR ($r = –0.55$, $P = 0.0002$), and monthly mean of daily minimum RH was negatively correlated with that of PAR ($r = –0.65$, $P < 0.0001$). Daily minimum temperature was independent of these variables.

Flowering pattern

Of the tagged plants, more than 90% individuals flowered during the census period for most species except for *V. stapfianum* at the main plot, where only 36% of tagged plants flowered. Two *L. recurvum* plants died at the subplot during the census, and they were excluded from the analyses. The flowering of target species varied among species and/or between plots (Figure 2). *Leptospermum recurvum* showed a high proportion of flowering individuals in 1998 and 1999 (especially in the first half of 1999) but the proportion of flowering plants became small in 2000 and 2001, especially at the main plot. In another *L. recurvum* population, the proportion of flowering individuals in 1996–1997 was about a half of that in 1998–1999 (K. Kimura, pers. comm.). This suggests that this species has a 2-y or longer cycle of vigorous flowering. An annual flowering pattern was observed in *P. davidiana* within each plot but the timing of peak flowering clearly differed between the plots. An annual flowering pattern was also observed in *R. buxifolium* at the main plot, where the flowering peak occurred from March to May every year. However, the annual pattern of flowering at the subplot was less clear. Relatively high flowering activity was maintained throughout the observation period in *R. ericoides* although the proportion of flowering decreased in the middle of 1999 at both plots. A supra-annual flowering pattern was observed in *V. stapfianum* in which widespread flowering occurred in the end of 1998 and the middle of 2000 at both plots although a small peak was also detected in the middle of 2001 only at the subplot.

Size dependency of flowering

Plant sizes selected for the monitoring were significantly larger at the subplot than the main plot for *L. recurvum*

(P < 0.001, Mann-Whitney U-test), *P. davidiana* (P = 0.001), *R. buxifolium* (P = 0.017), and *V. stapfianum* (P = 0.05), whereas there was no difference between the plots for *R. ericoides* (P = 0.68; Table 1). Plant size was positively correlated with reproductive effort, or mean flower production in all species except for *L. recurvum* at the subplot (Table 2). In addition, plant size was positively correlated with flowering frequency of individual plants in *R. ericoides* at both plots, and *R. buxifolium* and *V. stapfianum* at the main plot (Table 2). The flowering frequency, i.e. proportion of flowering occurrence during the census period, ranged from 0.18–0.41 for most species except for *R. ericoides*, which showed frequent flowering (0.59–0.73; Table 1).

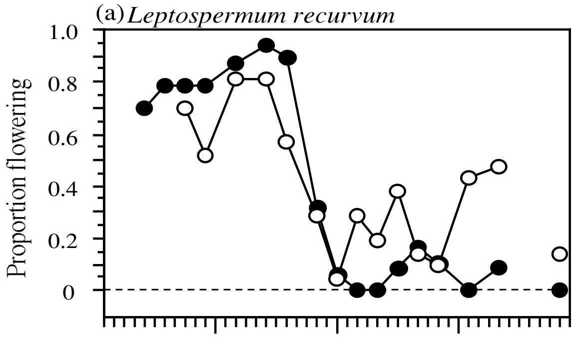
Flowering synchrony within and between populations

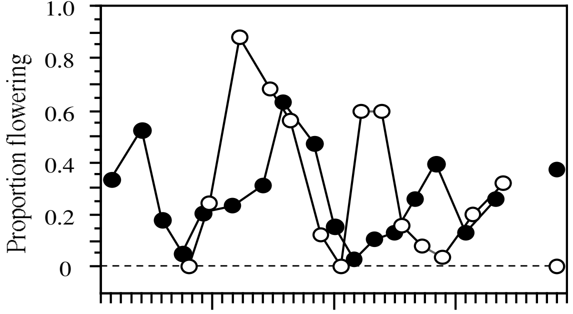
The flowering synchrony of individual plants within a population was high in *L. recurvum* at the main plot (0.74) and *R. ericoides* at the subplot (0.71; Table 1). An intensive flowering from 1998 to the middle of 1999 and a stagnant period thereafter resulted in the high synchrony of *L. recurvum* at the main plot (Figure 2). As for *R. ericoides*, continuous flowering throughout the season contributed to the high synchrony. For other species, flowering synchrony ranged from 0.33 to 0.60 (Table 1).

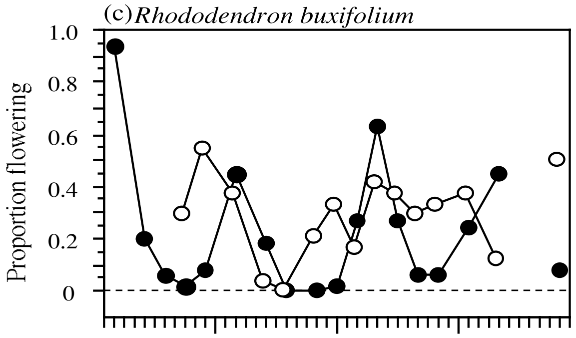
There was a positive correlation in the proportion of flowering plants between the plots in *L. recurvum* ($\rho = 0.71$, P = 0.008), *R. ericoides* ($\rho = 0.86$, P = 0.001), and *V. stapfianum* ($\rho = 0.71$, P = 0.008), indicating synchronous flowering between the populations in these species. There was no significant correlation in the proportion of flowering plants between the plots in *P. davidiana* ($\rho = -0.05$, P = 0.86) and *R. buxifolium* ($\rho = 0.29$, P = 0.28). The results of ANCOVA revealed that there were significant differences in the extent of intra-population flowering synchrony between the plots for *P. davidiana*, *R. buxifolium* and *V. stapfianum* (Table 3). In contrast, there were no differences for *L. recurvum* and *R. ericoides*, indicating again similar flowering synchrony between the populations in these species.

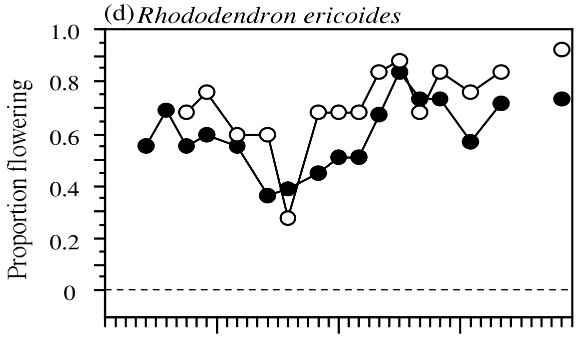
Fruit set

Exclusion of both insect and bird pollinators by the bagging treatment significantly decreased the fruit set


(a) *Leptospermum recurvum*


(b) *Photinia davidiana*


(c) *Rhododendron buxifolium*


(d) *Rhododendron ericoides*

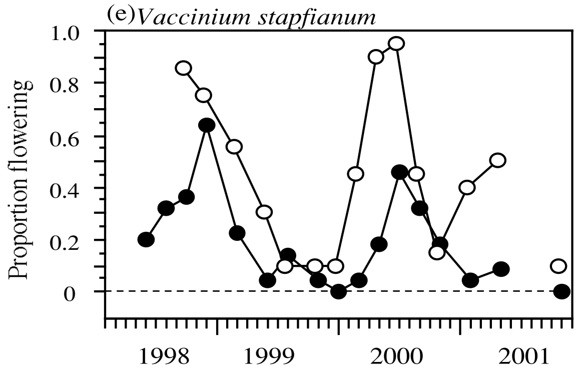

(e) *Vaccinium stapfianum*

Figure 2. Seasonal changes in the proportion of flowering individuals in target species, (a) *Leptospermum recurvum*, (b) *Photinia davidiana*, (c) *Rhododendron buxifolium* (d) *Rhododendron ericoides* and (e) *Vaccinium stapfianum* at the main plot (closed circles) and sub-plot (open circles).

Table 1. Plant size, flowering frequency, reproductive effort, and flowering synchrony of individual species at each plot. Plant size is expressed as a product of canopy projection area and plant height. Flowering frequency is expressed by the proportion of flowering occurrence throughout the phenological census, and reproductive effort by the mean inflorescence number per census of individual plants. Flowering synchrony of individual plants within a population was calculated according to Augspurger's method (for details, see text) in which synchrony ranges from 0 (no synchrony) to 1.0 (perfect synchrony). Median (above) and range (below) values are shown for each variable. Sample size (n) is shown in parentheses.

Species	Plot (n)	Plant size (m^3)	Flowering frequency	Reproductive effort	Flowering synchrony
Leptospermum recurvum	Main	0.034	0.41	5.88	0.74
	(47)	0.006–0.370	0.06–0.65	0.06–102.35	0.51–0.89
	Sub	0.104	0.40	8.67	0.52
	(21)	0.023–0.696	0.07–0.80	0.07–77.07	0.32–0.76
Photinia davidiana	Main	0.175	0.25	0.56	0.35
	(38)	0.036–0.976	0.06–0.61	0.06–3.28	0.19–0.61
	Sub	0.365	0.27	0.73	0.54
	(25)	0.120–1.440	0.07–0.67	0.13–3.73	0.38–0.74
Rhododendron buxifolium	Main	0.437	0.22	2.00	0.53
	(49)	0.027–4.005	0.06–0.56	0.11–28.39	0.24–0.92
	Sub	1.021	0.27	1.13	0.33
	(24)	0.085–9.648	0.07–0.60	0.07–8.53	0.25–0.50
Rhododendron ericoides	Main	0.019	0.59	1.59	0.60
	(49)	0.003–0.189	0.06–1.00	0.12–14.41	0.54–0.71
	Sub	0.015	0.73	2.00	0.71
	(25)	0.004–0.107	0.20–1.00	0.20–6.67	0.67–0.80
Vaccinium stapfianum	Main	0.258	0.18	0.82	0.35
	(18)	0.070–0.821	0.06–0.47	0.06–14.76	0.19–0.63
	Sub	0.467	0.40	10.37	0.60
	(20)	0.024–1.958	0.20–0.73	1.73–33.6	0.48–0.81

Table 2. Effects of plant size on flowering frequency and reproductive effort at each plot. Spearman's correlation (ρ) and significance value (P) are shown.

			Flowering frequency		Reproductive effort	
Species	Plot	n	ρ	P	ρ	P
Leptospermum recurvum	Main	(47)	0.27	0.07	0.54	<0.001
	Sub	(21)	0.02	0.91	0.17	0.44
Photinia davidiana	Main	(38)	0.25	0.13	0.45	0.006
	Sub	(25)	0.35	0.09	0.72	<0.001
Rhododendron buxifolium	Main	(49)	0.64	<0.001	0.84	<0.001
	Sub	(24)	0.20	0.35	0.72	<0.001
Rhododendron ericoides	Main	(49)	0.50	<0.001	0.64	<0.001
	Sub	(25)	0.63	0.002	0.71	<0.001
Vaccinium stapfianum	Main	(18)	0.61	0.01	0.58	0.02
	Sub	(20)	0.30	0.19	0.45	0.05

of *L. recurvum*, *R. ericoides* and *R. buxifolium* (Figure 3). In particular, the very low fruit set by the bagging of *L. recurvum* (3.5%) indicated a low selfing ability. Fruit set in the bagging treatment was less than half of the naturally pollinated inflorescences for *R. ericoides* and *R. buxifolium*, indicating the importance of pollinator visits for seed production. In contrast, other two species showed very high selfing ability. There was no significant difference in fruit set of *P. davidiana* between the control and bagging treatment. Furthermore, bagged inflorescences showed an even higher fruit set than by natural pollination for *V. stapfianum*.

Table 3. Comparison of intra-population flowering synchrony between the plots in each species. ANCOVA results are shown in which plant size is treated as a covariate. Flowering synchrony was arcsine-square-root transformed and plant size was logarithmically transformed before the analyses.

Species	Variable	df	F	P
Leptospermum recurvum	Plot	1, 64	0.40	0.53
	Size	1, 64	0.59	0.45
	Plot × size	1, 64	3.33	0.07
Photinia davidiana	Plot	1, 59	9.78	0.003
	Size	1, 59	0.88	0.35
	Plot × size	1, 59	0.29	0.60
Rhododendron buxifolium	Plot	1, 69	11.74	0.001
	Size	1, 69	4.03	0.05
	Plot × size	1, 69	2.47	0.12
Rhododendron ericoides	Plot	1, 70	0.22	0.64
	Size	1, 70	2.23	0.14
	Plot × size	1, 70	4.07	0.05
Vaccinium stapfianum	Plot	1, 34	11.63	0.002
	Size	1, 34	5.22	0.03
	Plot × size	1, 34	2.41	0.13

DISCUSSION

The phenological census of major dwarf-tree species in this study revealed that each species had its own seasonal pattern of flowering independent of each other within a community, and there was no common trigger causing the initiation of flowering for many species at least during the census period (Figure 2). Solar irradiance and rainfall are often considered as the main seasonal variables influencing the phenology of tropical plants (van Schaik *et al.* 1993, Wright 1996, Wright & van Schaik 1994). Clear annual patterns of reproductive phenology have also been reported in the montane cloud forests in tropical and subtropical regions where intensive annual fluctuations of rainfall (in Costa Rica, Koptur *et al.* 1988) or irradiance (in Hawaii, Berlin *et al.* 2000) are recognized as the major determinants of phenological events. The lack of strong seasonality in the climatic conditions on Mt. Kinabalu may be related to the individual phenological pattern of each species and/or population. In the aseasonal tropical rain forests in Peninsular Malaysia and Borneo, a drop of 2 °C in the daily minimum temperature for several days has been speculated to be a proximal cue for general flowering, which accelerates the development of floral buds for many canopy trees (Ashton *et al.* 1988, Sakai *et al.* 1999, Yasuda *et al.* 1999). We detected a decrease in the daily minimum temperature every June–August (Figure 1; except 1998 after an El Niño event, see below) and it sometimes dropped below zero at the main plot. Interestingly, such a temperature drop in July–August has not been observed at other altitudes on Mt. Kinabalu (Kitayama *et al.* 1999), thus it may be a local phenomenon specific to the summit region.

Among the target species in this study, *R. buxifolium* showed a clear flowering peak every March–May at the main plot (Figure 2). A similar flowering pattern in this species was observed widely in the summit region (Argent *et al.* 1988, G. Kudo & S. Suzuki unpubl. data) although the pattern at the subplot differed. The development of flower buds in this species usually started in July and August, and it took 8–9 mo for flowering. Thus, low night temperature seems to be related to the initiation of flowering of *R. buxifolium*. However, it is difficult to explain the interspecific variations in flowering patterns by the minimum-daily temperature hypothesis.

In addition to the mild seasonal fluctuation in climatic conditions in normal years, unpredictable drastic climatic changes, like El Niño-Southern Oscillation (ENSO) events, may also be important to trigger the phenological events in the tropical alpine communities as reported in the lowland tropical forests (Ashton *et al.* 1988, Wich & van Schaik 2000, Wright *et al.* 1999). On Mt. Kinabalu, occasional intensive droughts coincide with ENSO events (Walsh 1996). At least four ENSO events have been recorded during the last three decades in 1972–73, 1982–83, 1992, and 1997–1998, and these droughts brought severe damage to the vegetation of the summit regions (Beaman *et al.* 1985, Kudo & Kitayama 1999, Lowry *et al.* 1973, Smith 1979). The synchronous flowering of *L. recurvum* in 1998–99 might have been caused by the drought stress (van Schaik 1986) during the 1997–98 ENSO period because mass flowering was observed widely from the subalpine forests to the summit regions in this period (personal observation). Mass flowering of *R. buxifolium* was also observed widely in the summit region in March 1998 when more than 90% of adult trees flowered at the main plot (Figure 2). Because our observation started with the anomalous 1998 ENSO year, the following year may have been atypical regarding phenology. This may make it difficult to discriminate the phenological pattern in a normal year from that in an unusual year. To evaluate the significance of an unpredictable climatic impact, a long-term census is very important.

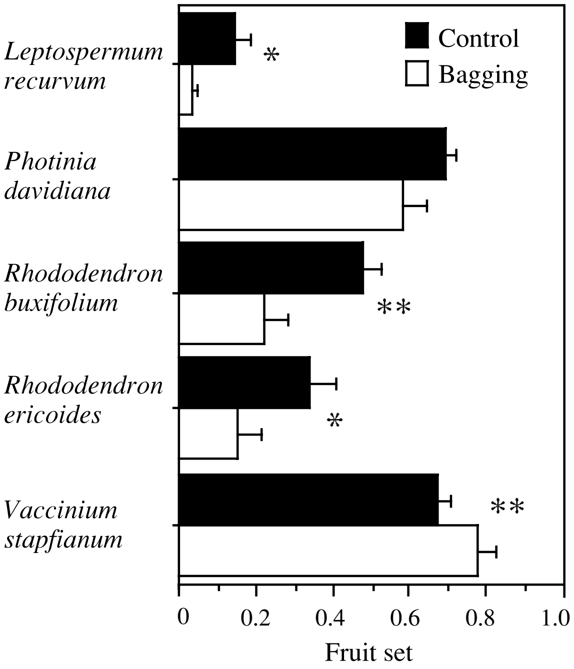


Figure 3. Fruit-set rates (i.e. proportion of flowers set fruits) of naturally pollinated (closed) and bagged (open) inflorescences in target species. Sample sizes are 20 individuals for each of *R. buxifolium*, *P. davidiana* and *V. stapfianum*, 18 (bagging) and 20 (control) for *L. recurvum*, and 24 (bagging) and 30 (control) for *R. ericoides*. Vertical bars represent SE. * $P < 0.05$, ** $P < 0.01$ by Mann-Whitney U-test.

Plant size influenced the flower production for all species and the flowering frequency of the three ericaceous species (*R. buxifolium*, *R. ericoides* and *V. stapfianum*; Table 2). Significant effects of plant size on the flowering synchrony within a population were detected in *R. buxifolium* and *V. stapfianum* (Table 3). Because these species showed a cyclic flowering pattern within populations (Figure 2), large plants having frequent flowering can bloom every flowering season resulting in higher synchrony.

The fruit set under natural pollination and the selfing ability independent of pollinator service varied among species. *Photinia davidiana* and *V. stapfianum* had very high selfing abilities and bagged inflorescences showed similar or even higher fruit sets in comparison with naturally pollinated inflorescences (Figure 3). Increased fruit set in the bagged inflorescences might be because bagged inflorescences were protected from herbivore attack before the maturation and/or physical damage such as strong wind. Another possibility is that higher temperatures inside the bags could improve pollen tube growth allowing higher rates of fertilization (Totland & Eide 1999). These species showed relatively low flowering synchrony within and/or between plots (Table 1 and Figure 2). On the other hand, *L. recurvum* and *R. ericoides* having low selfing ability (Figure 3) showed relatively high flowering synchrony within and between plots (Table 1 and Figure 2). If flowering synchrony is related to pollinator attraction (Augspurger 1981), the observed patterns seem to be reasonable. However, the flowering patterns were very different between the species having low selfing ability. Flowering of *R. ericoides* (bird-pollinated species) occurred continuously throughout the season (Figure 2) and the flowering frequency of individual plants was size-dependent (Table 2). On the other hand, *L. recurvum* (fly-pollinated species) showed mass flowering in a restricted season, i.e. the first half of 1999 (Figure 2) and flowering frequency was size-independent (Table 2). Such a difference in the flowering patterns may be related to the pollinator type of each species. However, another bird-pollinated species *R. buxifolium* showed an annual flowering cycle. Such an inconsistency between the flowering pattern and pollinator type makes it difficult to specify the ecological significance of flowering synchrony. In the comparison of flowering synchrony with fruit set of lowland neotropical shrubs, no significant correlations were detected due to the effects of other uncontrolled factors (Augspurger 1983), indicating complexity of ecological factors affecting reproductive success under natural conditions.

As mentioned before, fruiting phenology of fleshy-fruited trees was seasonally more constant in the upper-montane and subalpine forests than in the lowland forests on Mt. Kinabalu (Kimura *et al.* 2001, Leighton & Leighton 1983). Among the target species in this study, *P. davidiana* and *V. stapfianum* produce fleshy fruits suggesting bird dispersal, and the others produce dehiscent fruits that are gravity dispersed. Flowering of *P. davidiana* showed a clear annual peak within local populations but was asynchronous between the populations. Such an inter-population variation in the flowering pattern may contribute to extending the period of fruit presentation on a regional scale. Flowering of *V. stapfianum* occurred synchronously between the populations and the flowering interval was irregular, sometimes longer than 1 y. It takes almost 1 y to mature the fruits after flowering, and mature fruits remain on the plants for several months (personal observation) suggesting a scarcity of fruit dispersers in the summit region. Interestingly, only bird-dispersed species showed high selfing ability by the bagging treatment. The presentation of many fruits over a long period may be important for successful seed dispersal when dispersers are scarce (Brooke *et al.* 1996).

Under cool conditions without seasonal growth constraints, reproductive schedule (i.e. floral-bud formation, flowering, fruiting and seed dispersal) often does not follow an annual cycle but rather extends over a longer period (Monasterio 1986). If the rates of resource accumulation are influenced by the cool temperature, the flowering frequency and the interval between floral-bud initiation and anthesis should differ among species having different reproductive costs and resource conditions (Rathcke & Lacey 1985). This may restrict the occurrence of a clear seasonal pattern in the tropical alpine communities.

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LITERATURE CITED

AIBA, S. & KITAYAMA, K. 1999. Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology* 140:139–157.

APPANAH, S. 1985. General flowering in the climax rain forests of South-east Asia. *Journal of Tropical Ecology* 1:225–240.

ARGENT, G., LAMB, A., PHILLIPPS, A. & COLLENETTE, S. 1988. *Rhododendrons of Sabah*. Sabah Parks Publication No. 8, Kota Kinabalu, Malaysia. 145 pp.

ASHTON, P. S., GIVNISH, T. J. & APPANAH, S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* 132:44–66.

AUGSPURGER, C. K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62:775–788.

AUGSPURGER, C. K. 1983. Phenology, flowering synchrony, and fruit set of six neotropical shrubs. *Biotropica* 15:257–267.

BAWA, K. S., BULLOCK, S. H., PERRY, D. R., COVILLE, R. E. & GRAYUM, M. H. 1985. Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *American Journal of Botany* 72:346–356.

BEAMAN, R. S., BEAMAN, J. H., MARSH, C. W. & WOODS, P. V. 1985. Drought and forest fires in Sabah in 1983. *Sabah Society Journal* 8:10–30.

BERLIN, K. E., PRATT, T. K., SIMON, J. C. & KOWALSKY, J. R. 2000. Plant phenology in a cloud forest on the island of Maui, Hawaii. *Biotropica* 32:90–99.

BROOKE, M. DE L., JONES, P. J., VICKERY, J. A. & WALDREN, S. 1996. Seasonal patterns of leaf growth and loss, flowering and fruiting on a subtropical Central Pacific Island. *Biotropica* 28:164–179.

JANZEN, D. H. 1974. Tropical blackwater rivers, animals and mast flowering by the Dipterocarpaceae. *Biotropica* 6:69–103.

KIMURA, K., YUMOTO, T. & KIKUZAWA, K. 2001. Fruiting phenology of fleshy-fruited plants and seasonal dynamics of frugivorous birds in four vegetation zones on Mt. Kinabalu, Borneo. *Journal of Tropical Ecology* 17:833–858.

KITAYAMA, K. 1992. An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102:149–171.

KITAYAMA, K., LAKIM, M. & WAHAD, M. Z. 1999. Climatic profile of Mount Kinabalu during late 1995-early 1998 with special reference to the 1998 drought. *Sabah Parks Nature Journal* 2:85–100.

KOPTUR, S., HABER, W. A., FRANKIE, G. W. & BAKER, H. G. 1988. Phenological studies of shrub and treelet species in tropical cloud forests of Costa Rica. *Journal of Tropical Ecology* 4:323–346.

KUDO, G. & KITAYAMA, K. 1999. Drought effects on the summit vegetation on Mount Kinabalu by an El Niño event in 1998. *Sabah Parks Nature Journal* 2:101–110.

LEIGHTON, M. & LEIGHTON, D. R. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. Pp.181–196 in Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (eds). *Tropical rain forest: ecology and management*. Blackwell Scientific Publications, Oxford.

LOWRY, J. B., LEE, D. W. & STONE, B. C. 1973. Effect of drought on Mount Kinabalu. *Malayan Nature Journal* 26:178–179.

MONASTERIO, M. 1986. Adaptive strategies of *Espeletia* in the Andean desert Páramo. Pp.49–80 in Vuilleumier, F. & Monasterio, M. (eds). *High altitude tropical biogeography*. Oxford University Press, Oxford.

OLLERTON, J. & LACK, A. 1998. Relationships between flowering phenology, plant size and reproductive success in *Lotus corniculatus* (Fabaceae). *Plant Ecology* 139:35–47.

RATHCKE, B. & LACEY, E. P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16:179–214.

SAKAI, S., MOMOSE, K., YUMOTO, T., NAGAMITSU, T., NAGAMASU, H., HAMID, A. A. & NAKASHIZUKA, T. 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany* 86:1414–1436.

SMITH, J. M. B. 1979. Vegetation recovery from drought on Mt. Kinabalu. *Malayan Nature Journal* 32:341–342.

TOTLAND, Ø. & EIDE, W. 1999. Environmentally-dependent pollen limitation on seed production in alpine *Ranunculus acris. Ecoscience* 6:173–179.

VAN SCHAIK, C. P. 1986. Phenological changes in a Sumatran rainforest. *Journal of Tropical Ecology* 2:327–347.

VAN SCHAIK, C. P., TERBORGH, J. W. & WRIGHT, S. J. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353–377.

WALSH, R. P. D. 1996. Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *Journal of Tropical Ecology* 12:385–407.

WICH, S. A. & VAN SCHAIK, C. P. 2000. The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology* 16:563–577.

WRIGHT, S. J. 1996. Phenological responses to seasonality in tropical forest plants. Pp.440–460 in Mulkey, S. S., Chazdon, R. L. & Smith, A. P. (eds). *Tropical forest plant ecophysiology*. Chapman and Hall, New York.

WRIGHT, S. J. & CALDERON, O. 1995. Phylogenetic patterns among tropical flowering phenologies. *Journal of Ecology* 83:937–948.

WRIGHT, S. J. & VAN SCHAIK, C. P. 1994. Light and the phenology of tropical trees. *American Naturalist* 143:192–199.

WRIGHT, S. J., CARRASCO, C., CALDERON, O. & PATON, S. 1999. The El Niño southern oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80:1632–1647.

YASUDA, M., MATSUMOTO, J., OSADA, N., ICHIKAWA, S., KACHI, N., TANI, M., OKUDA, T., FURUKAWA, A., NIK, A. R. & MANOKARAN, N. 1999. The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula. *Journal of Tropical Ecology* 15:437–449.