

# Flowering and fruiting seasonality of eight species of *Medinilla* (Melastomataceae) in a tropical montane forest of Mount Kinabalu, Borneo

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**ABSTRACT** We studied flowering and fruiting seasonality of understory shrubs of genus *Medinilla* (Melastomataceae) in the lower montane forest on Mount Kinabalu, Borneo, in relation to seasonal change in air temperature, rainfall, and solar radiation. Eight sympatric species showed either annual or biannual patterns. The number of species bearing flower buds and flowers increased biannually, indicating that two seasons were favorable for flower budding and flowering of *Medinilla* species. Individuals of most species started flower budding during January–March, showing strongly negative correlations with seasonal patterns of mean or minimum air temperature in previous a few weeks. The number of fruiting species peaked during May–August and increased when air temperature and solar radiation were high. These findings suggested that flowering activity of most *Medinilla* species may be regulated by seasonality of air temperature through floral initiation stimulated by low temperature. In addition, the high fruiting activity during period with high temperature and insolation indicated that such climatic conditions may facilitate the development of fruits and seeds of understory plants growing in cool and poor-light conditions, because photosynthesis and other physiological reactions are activated to produce compounds necessary for the development of fruits and seeds.

## INTRODUCTION

Timing and variation in flowering and fruiting of plants are closely related with climatic seasonality (Rathcke and Lacey, 1985; van Schaik et al. 1993). Many phenological studies in tropical forests suggested that some climatic factors function as cues for reproductive activities of plants (Bendix et al. 2006; Corlett, 1990; Opler et al. 1976;

Tutin and Fernandez, 1993), and that some climatic conditions are favored at some phenophases (Anderson et al. 2005; Chapman et al. 1999; Foster, 1982; Hamann, 2004; Tutin and Fernandez, 1993; Zimmerman et al. 2007).

In seasonal tropics, important climatic factors of such favored conditions are temperature and rainfall. Generally, reproductive activities of plant community are highly seasonal apparently in areas with high seasonality in climatic conditions (Koptur et al. 1988). Plant communities in seasonal tropics showed highly seasonal flowering and fruiting related with seasonal change in rainfall (Anderson et al. 2005; Bullock and Solís-Magallanes, 1990; Foster, 1982; McLaren and McDonald, 2005) and temperature (Anderson et al. 2005; Chapman et al. 1999; Tutin and Fernandez, 1993), although some studies suggested that related climatic factors were different depending on types of pollination and seed dispersal.

In humid tropics and tropical regions such as montane and riverine where soil moisture is never seasonally limiting, temperature and rainfall rarely limit reproduction. Alternatively, a seasonal change in solar radiation regulates flowering and fruiting phenology of plant communities (Hamann, 2004; van Schaik et al. 1993; Williams-Linera, 2003; Wright and van Schaik, 1994; Zimmerman et al. 2007). Especially, the relation between flowering and fruiting seasonality of understory shrubs and seasonality in solar radiation has been emphasized (Opler et al. 1980; van Schaik et al. 1993; Williams-Linera, 2003; Wong, 1983; Wycherley, 1973; Zimmerman et al. 2007) because understory shrubs grow in a severely light-limited condition. However, there is little evidence of phenology regulated by solar radiation in Asian tropics (Corlett and Lafrankie, 1998).

In the present study, we report seasonal timing and variation in flowering and fruiting of eight sympatric species of *Medinilla*. *Medinilla* species are terrestrial or

epiphytic shrubs that commonly occur in montane cloud forests in Borneo (Beaman and Anderson, 2004; Regalado, 1990) and it has been suggested that their flowers may be insect-pollinated and their seeds may be animal-dispersed (Regalado, 1990; Tobe et al. 1989). We predicted that flowering and fruiting peaks of closely related species would occur during the sunniest period of the year because these species grew under water-rich and poor light conditions. The objectives of this study were as follows: (1) to describe seasonal variations in flower budding, flowering, and fruiting of *Medinilla* species and (2) to determine climatic factors related with phenological patterns of *Medinilla* species.

## MATERIALS AND METHODS

### Study site

We conducted a phenological investigation in forests at the altitude of 1600 m and 1800 m on the south slope of Mount Kinabalu (the summit: 6°5' N, 160°33' E, 4095 m high), northern Borneo. Both sites represent a lower montane forest, which is distributed between 1200 m and 1800 m a.s.l. at the lower altitudinal limit of cloud cover zone (Kitayama, 1992). Canopy trees are dominated by Fagaceae, Myrtaceae, and gymnosperms such as Podocarpaceae and Phyllocladaceae. In understory, shrubs and treelets of Lauraceae, Myrsinaceae, Annonaceae, Rubiaceae, Ericaceae, and Melastomataceae occur commonly.

The climate of Mount Kinabalu is humid tropical characterized by the absence of annually recurrent dry season, although droughts associated with the El Niño events occur occasionally (Kitayama, 1992; Kitayama et al. 1999). A few peaks of rainfall occur irregularly throughout the year, but an almost bimodal pattern appears in the normal years, while the reverse pattern is observed in solar radiation (Kitayama et al. 1999). Occasional droughts have substantial effects on forest dynamics through general flowering and mast fruiting (Appanah, 1985; Ashton et al. 1995; Kitayama et al. 1998; Sakai et al. 1999) and on the plant community structure through vegetation withering (Aiba and Kitayama, 2002; Kitayama, 1996; Kudo and Kitayama, 1999). The annual mean air temperature is 18.3 °C at 1560 m, and the yearly difference in monthly mean air temperature is about 2 °C in normal years (Kitayama et al. 1999).

The climate showed a normal trend during the main period of this study (Kitayama et al. 1999). Mast fruiting, a conspicuous phenological event, did not occur in the lower montane forest but occurred in the lowland hill

forest after general flowering prior to the study period (Kimura et al. 2001; Kitayama et al. 1998).

### *Medinilla* species

*Medinilla* (Melastomataceae) species are common epiphytic or terrestrial shrubs and climbers in the Paleotropics, with the center of diversity in Malesia (Regalado, 1990). Forty-eight species of *Medinilla* have been recorded from Borneo (Regalado, 1990), and 17 species of them were recorded from the region of Mount Kinabalu (Beaman and Anderson, 2004). *Medinilla* species bear brightly colored flowers and soft reddish- or purple-black berries, which are suggestive of insect-pollinated flowers and animal-dispersed seeds. Although little information is available on the reproductive system of *Medinilla* (Regalado, 1990; Tobe et al. 1989), several studies on the ecology of Melastomataceae in Paleotropics and Neotropics have revealed a strong relationship between the plants and animals, for example, insect pollination (Gross, 1993; Larson and Barrett, 1999; Momose et al. 1998; Renner, 1989), flower destruction by *Trigona* bees (Renner, 1983), and seed dispersal by birds (Loiselle and Blake, 1999; Renner, 1989).

Eight *Medinilla* species, namely, *M. amplexans*, *M. beamanii*, *M. clemensiana*, *M. crassifolia*, *M. homoeandra*, *M. speciosa*, *M. stephanostegia*, and *M. suberosa* were studied. They occur frequently or infrequently at the elevation of lower montane forest (Beaman and Anderson, 2004). *M. stephanostegia* occurred only in the 1800-m site. *M. crassifolia*, *M. homoeandra* and *M. speciosa* occurred in both 1600-m and 1800-m sites. The other four species occurred only in the 1600-m site. These species are morphologically classified into six groups designated by Regalado (1990). A conspicuous difference in reproductive organs among Regalado's species alliances is with regard to inflorescence: terminal panicles (*M. speciosa* and *M. stephanostegia*), axillary umbelliform cymes (*M. beamanii*, *M. clemensiana*, and *M. crassifolia*), and axillary fascicles of cymes (*M. amplexans*, *M. homoeandra* and *M. suberosa*). Other information on infrageneric classification and local distribution of these species has been poorly accumulated.

### Data collection and analysis

A total of 120 individuals of *Medinilla* were monitored biweekly from July 1996 to June 1997. We conducted 25 censuses and observed phenological activities of individuals by counting the number of visible flower bud, flower in bloom, immature fruit (hard, greenish or orange color), and mature fruit (soft, reddish- or purple-black

color) in each census. We focused three phenophases, that is, flower budding, flowering, and fruiting. We here regarded an individual which bore opening flowers and mature fruits as that in flowering and fruiting respectively. Consequently, an individual standing in the period between the onset of flower bud formation and flowering was regarded as that in flower budding. Additionally, we describe the period between the end of flowering and the onset of fruiting as 'premature' fruiting period. After the first observation year, we monitored the flowering and fruiting activities of these individuals by additional observations in August and December 1997; January, March, May, and September 1998; February and October 1999; July 2000; and March 2001, in order to investigate the reproductive activities of each individual in a particular year.

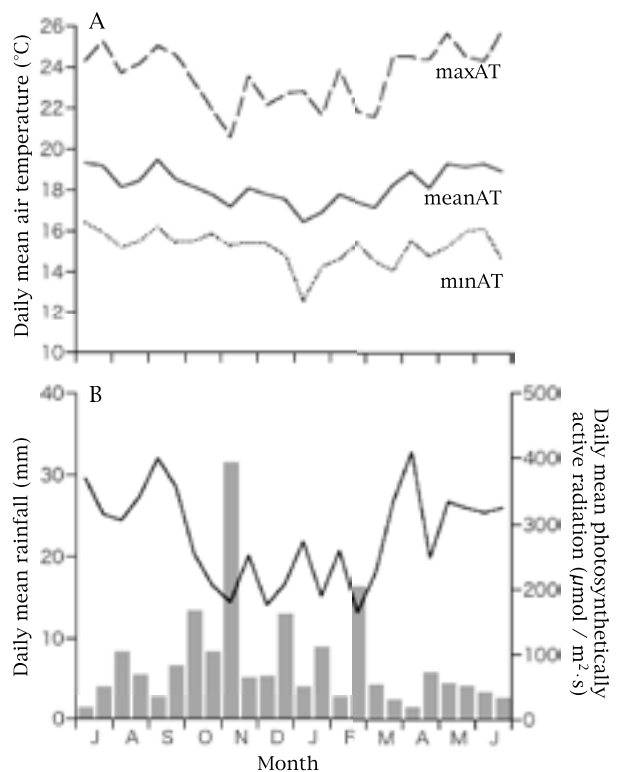
A given phenological pattern was characterized by timing of peak (hereafter referred to as peak position) and duration. The peak position was the ordered number of census (*i.e.*, from 1 to 25) in which a focused individual bore the maximum number of flowers or fruits. The duration was the number of census in which a focused individual reproduced continuously. For describing the phenological pattern of species, the mean and standard deviation were calculated from all individual values of the species.

Climatic data, air temperature, rainfall and photosynthetically active radiation (PAR), were obtained from a climatic station set up in an open place at the altitude of 1560 m. We evaluated predictable climatic cues for initiation of the phenophases of *Medinilla* species. A stepwise multiple regression analysis with the forward selection procedure was chosen because different climatic variables ought to show multicollinearity. The sequence of number of individuals which started any reproductive activity was applied as dependent variables of a given phenophase. As independent variables, we calculated average values for 14 days prior to the observation day (defined as concurrent period) for five different climatic components, namely, daily mean air temperature, daily maximum air temperature, daily minimum air temperature and daily mean PAR, and daily rainfall. To evaluate the effects of climate of the previous periods of varying time lag, we also calculated the average values with lags of one to four weeks. The Spearman rank correlation test was chosen to evaluate the relationship between climate seasonality and reproductive phenology of *Medinilla* species. All statistical analyses were performed using StatView and JMP ver.5, SAS Institute Inc.

## RESULTS

### Climate

In the first observation year, rainfall fluctuated frequently with larger peaks occurring during October–February (Fig. 1) and showed a negative correlation with the pattern of PAR (Pearson's correlation coefficient,  $r = -.610$ ,  $p = .0012$ ). PAR peaked in September and April and remained low from October to February (Fig. 1). The pattern of daily maximum air temperature was similar to that of PAR (Pearson's correlation coefficient,  $r = .834$ ,  $p < .0001$ ), which suggested that both patterns were influenced by seasonal changes in cloud occurrence through the interruption of direct rays of the sun. The daily minimum air temperature showed changes independent of the other climatic components except for the daily mean air temperature. The daily minimum air temperature decreased sharply in early January, followed by a slight decrease in March (Fig. 1). The pattern of daily mean air temperature was highly similar to those of maxAT, minAT and PAR (Pearson's correlation



**Fig. 1.** Seasonal distribution of biweekly values of (A) daily mean air temperature (meanAT), daily maximum air temperature (maxAT), and daily minimum air temperature (minAT) and (B) total rainfall (line) and daily mean photosynthetically active radiation (bar) from July 1996 to June 1997 at the altitude of 1560 m of Mount Kinabalu.

coefficient,  $r = .833$ ,  $p = < .0001$ ;  $r = .703$ ,  $p = < .0001$ ;  $r = .781$ ,  $p = < .0001$ , respectively), and was a conversely mirrored pattern of rainfall ( $r = -.473$ ,  $p = < .05$ ). An annual variation of daily mean air temperature was less than  $2.8^\circ\text{C}$ .

### Phenology

Two major seasons were favorable for flower budding and flowering of *Medinilla* species during the first observation year (Fig. 2). Individuals of *M. amplexans*, *M. crassifolia*, *M. homoeandra*, *M. speciosa*, *M. stephanostegia* and *M.*

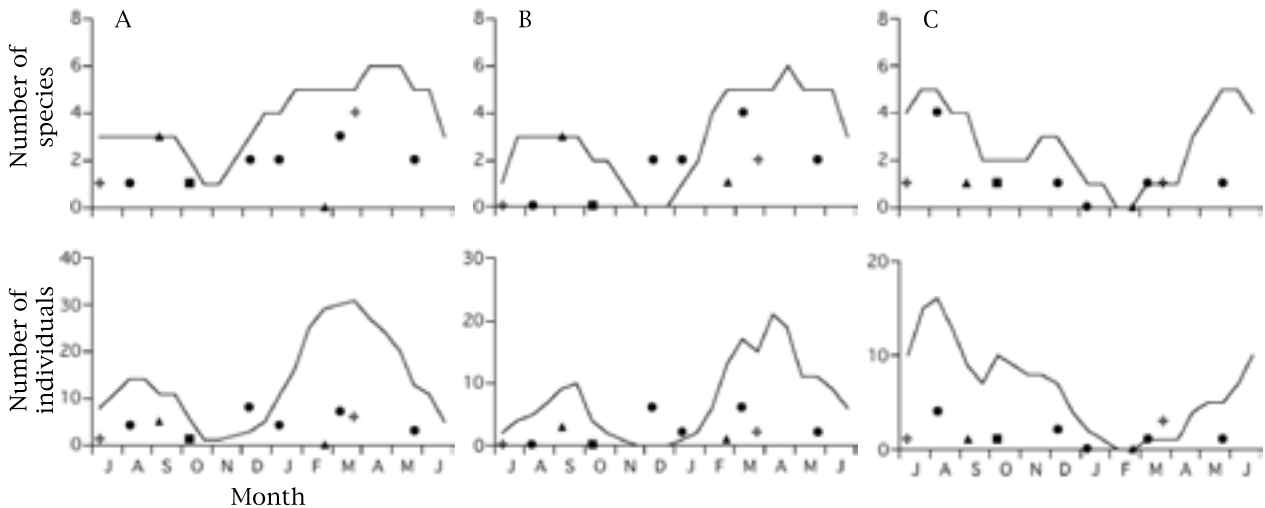


Fig. 2. Seasonal change in the number of species (left) and individuals (right) of *Medinilla* in (A) flower budding, (B) flowering, and (C) fruiting in the lower montane forest of Mount Kinabalu. The observation years are indicated as follows: biweekly change in the first year (line), second year (circle), third year (triangle), fourth year (square), and fifth year (cross).

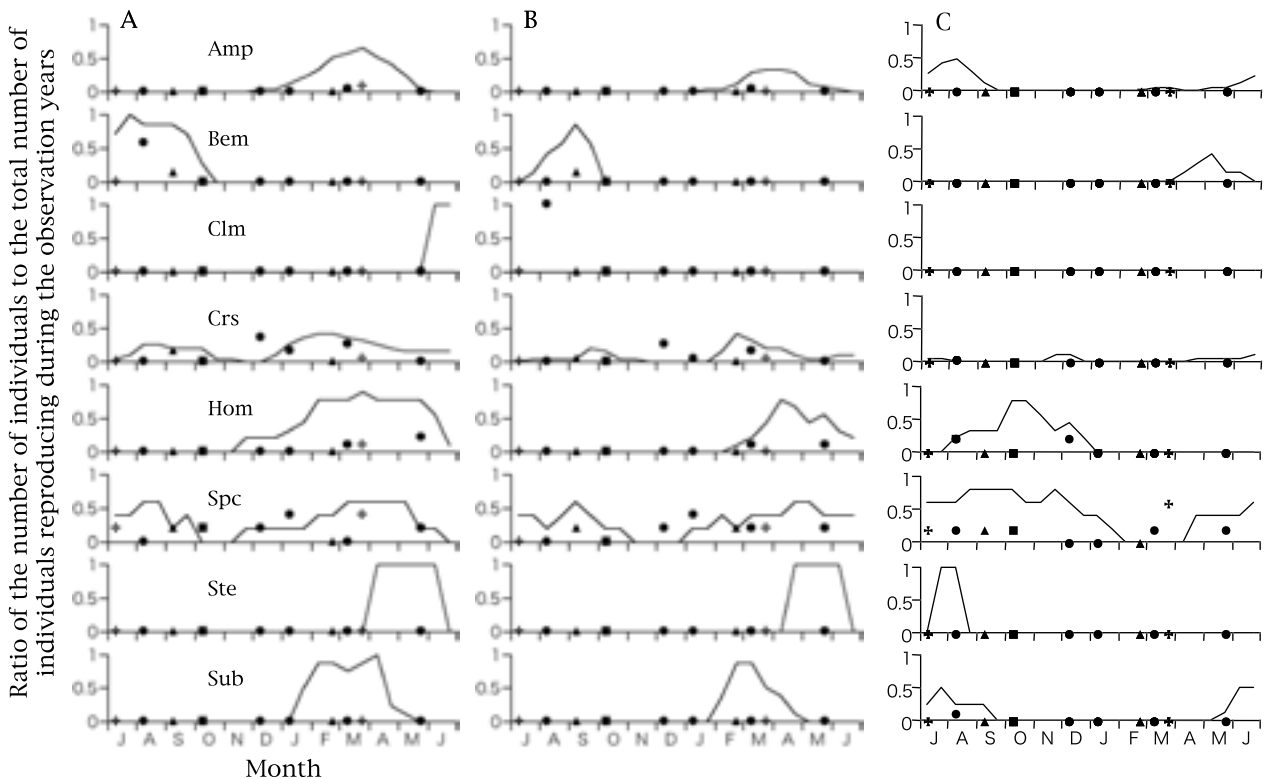


Fig. 3. Seasonal change in the proportion of individuals in (A) flower budding, (B) flowering, and (C) fruiting for eight *Medinilla* species in the lower montane forest of Mount Kinabalu. The observation years are indicated as follows: biweekly change in the first year (line), second year (circle), third year (triangle), fourth year (square), and fifth year (cross). Abbreviations for species name are as follows: Amp, *M. amplexans*; Bem, *M. beamanii*; Clm, *M. clemensiana*; Crs, *M. crassifolia*; Hom, *M. homoeandra*; Spc, *M. speciosa*; Stp, *M. stephanostegia*; Sub, *M. suberosa*.

*suberosa* flowered from January to June, while individuals of *M. beamanii*, *M. crassifolia* and *M. speciosa* did from July to early November (Fig. 3). Most of the species had annual flowering peaks; however, *M. crassifolia* and *M. speciosa* had flowering peaks occurring twice a year. No flowering species appeared from late November to December. In contrast, a biannual fruiting pattern resulting from the biannual flowering pattern was less apparent (Fig. 2). *Medinilla* species fruited sequentially almost year round (Fig. 3). All species but *M. crassifolia*

had annual fruiting peaks. *M. crassifolia* had two fruiting periods during November–December and April–July. No fruiting species appeared in February.

The mean values of duration of flower budding were similar among species (one-way ANOVA for species with more than three individuals;  $df = 7$ ,  $F = .901$ ,  $p > .05$ ). On the other hand, those of flowering and fruiting duration were significantly different among species (one-way ANOVA for species with more than three individuals; flowering,  $df = 7$ ,  $F = 3.15$ ,  $p = .007$ ; fruiting,  $df = 8$ ,  $F = 3.69$ ,

**Table 1. Timing of peak (peak position) and duration of three phenophases (flower budding, flowering, and fruiting) of eight *Medinilla* species. The value of peak position is indicated by the number of census conducted biweekly from July 1996. One duration is equivalent to 2 weeks. Values are expressed as mean  $\pm$  standard deviation.**

Species	Flower budding		Flowering		Fruiting	
	Peak position	Duration	Peak position	Duration	Peak position	Duration
<i>M. amplexens</i>						
(peak 1)	17.1 $\pm$ 2.1	4.7 $\pm$ 2.1	19.2 $\pm$ 1.7	3.6 $\pm$ 1.5	24.0	2.0 $\pm$ 1.2 <sup>†</sup>
(peak 2)	---	---	---	---	3.3 $\pm$ 0.7	3.0 $\pm$ 0.6
<i>M. beamanii</i>	3.0 $\pm$ 1.0	4.8 $\pm$ 0.8	5.3 $\pm$ 0.5	3.8 $\pm$ 1.5	19.6 $\pm$ 2.6	2.3 $\pm$ 1.9
<i>M. clemensiana</i>	23.5	2.0	---	---	---	---
<i>M. crassifolia</i>						
(peak 1)	4.0 $\pm$ 0.0	4.8 $\pm$ 1.5	6.0 $\pm$ 1.7	3.6 $\pm$ 0.9	15.0	1.5 $\pm$ 0.7
(peak 2)	15.5 $\pm$ 2.3	5.1 $\pm$ 1.5	17.9 $\pm$ 2.1	4.1 $\pm$ 1.4	22.0 $\pm$ 2.8	2.8 $\pm$ 1.3 <sup>†</sup>
<i>M. homoeandra</i>	16.1 $\pm$ 1.2	8.5 $\pm$ 2.9	20.2 $\pm$ 1.0	6.9 $\pm$ 1.1	7.2 $\pm$ 1.3	5.9 $\pm$ 3.9
<i>M. speciosa</i>						
(peak 1)	6.0	4.5 $\pm$ 2.1 <sup>†</sup>	5.8 $\pm$ 1.8	3.8 $\pm$ 2.9 <sup>†</sup>	6.8 $\pm$ 3.5	8.6 $\pm$ 3.9 <sup>†</sup>
(peak 2)	17.8 $\pm$ 3.0	6.8 $\pm$ 4.1	18.8 $\pm$ 4.1	6.3 $\pm$ 4.2 <sup>†</sup>	20.1 $\pm$ 3.8	3.0 $\pm$ 1.6 <sup>†</sup>
<i>M. stephanostegia</i>	19.0	5.0	20.5	5.0	5.0	5.0
<i>M. suberosa</i>						
(peak 1)	15.8 $\pm$ 2.0	4.9 $\pm$ 1.2	17.6 $\pm$ 2.1	5.1 $\pm$ 1.5	24.0	2.3 $\pm$ 0.5 <sup>†</sup>
(peak 2)	---	---	---	---	2.0 $\pm$ 0.0	3.8 $\pm$ 2.1 <sup>†</sup>

<sup>†</sup> the value was underestimated because the plants were not observed for the entire season

**Table 2. Total number of individuals reproducing, survival rate, and reproducing rate of eight *Medinilla* species in the observation years. The corresponding periods of each year are as follows: 1<sup>st</sup> year: July 1996–June 1997, 2<sup>nd</sup> year: July 1997–June 1998, 3<sup>rd</sup> year: July 1998–June 1999, 4<sup>th</sup> year combined with 5<sup>th</sup> year: July 1999–June 2001.**

Species	N <sup>†</sup>	Survival rate (%)				Reproducing rate <sup>§</sup> (%)			
		1 <sup>st</sup> year	2 <sup>nd</sup> year	3 <sup>rd</sup> year	4 <sup>th</sup> year	1 <sup>st</sup> year	2 <sup>nd</sup> year	3 <sup>rd</sup> year	4 <sup>th</sup> year
<i>M. amplexens</i>	23	100	100	56.5	56.5	100	4.3	0.0	23.0
<i>M. beamanii</i>	7	100	100	71.4	57.1	100	57.1	20.0	25.0
<i>M. clemensiana</i>	1	100	100	100	100	100	100	0.0	100
<i>M. crassifolia</i>	19	100	100	89.4	63.1	78.9	68.4	35.2	8.3
<i>M. homoeandra</i>	9	100	100	33.3	33.3	100	77.7	66.6	33.3
<i>M. speciosa</i>	5	100	100	100	100	100	40.0	40.0	60.0
<i>M. stephanostegia</i>	1	100	100	100	100	100	100	0.0	0.0
<i>M. suberosa</i>	8	100	25.0	0.0	0.0	100	25.0	0.0	0.0
All species	73	100	100	61.6	53.4	94.5	42.4	24.4	25.6

<sup>†</sup> the total number of individual that reproduced at least once during the observation years

<sup>§</sup> (the number of individuals reproducing/the total number of surviving individuals)\*100

$p = .002$ ). *M. speciosa* and *M. homoeandra* had longer flowering and fruiting durations at the individual level (Table 1). The flowering and fruiting period of *M. speciosa* was particularly long at the species level, extending ten months (Fig. 3).

The subsequent observations across four years revealed that the seasonal patterns of the first year were regular events for most of the species, although some individuals of *M. crassifolia* and *M. speciosa* flowered and

fructed irregularly in the second year (Fig. 3). The annual number of individuals that reproduced from the second year reduced (Table 2), and no flowering and fruiting individuals of all species but *M. speciosa* appeared in three censuses from February 1999 to July 2000. The decline in reproduction resulted from a reduction in the reproducing rate and an increase in the number of individuals which had withered after the severe drought during late 1997 – early 1998.

**Table 3. Results of stepwise multiple regression with the forward selection procedure in which the starting phenophase was regressed on average climatic variables of 14 days of the concurrent periods (prior to the census date) and the preceding periods of time lags of one to four weeks. Significant predictor variables with positive or negative signs of coefficient of multiple correlation (in parentheses), coefficient of multiple determination ( $R^2$ ), and  $F$ s and probability ( $p < .01$ ) corresponding to the ANOVA result of regression model added according to the variables are shown. Abbreviations of variables are as follows: mean air temperature (meanAT), maximum air temperature (maxAT), minimum air temperature (minAT), photosynthetically active radiation (PAR), and rainfall (RF).**

Species	Predictor variables	$R^2$	$F$ s	$p$
<u>Flower budding</u>				
<i>M. amplexans</i>	minAT(–), RF(–) [1 wk lag]	.521	13.5	< .001
	minAT(–) [2 wk lag]	.486	22.7	< .0001
	meanAT(–), RF(–) [3 wk lag]	.410	9.0	.001
	PAR(–) [4 wk lag]	.308	11.2	.002
<i>M. crassifolia</i>	minAT (–) [without lag]	.267	9.3	.005
<i>M. homoeandra</i>	meanAT (–) [1 wk lag]	.251	8.7	.007
	minAT(–) [2 wk lag]	.337	12.6	.001
<i>M. speciosa</i>	meanAT(–) [3 wk lag]	.282	10.0	.004
<i>M. suberosa</i>	minAT (–) [1 wk lag]	.525	26.3	< .0001
All species	minAT (–) [without lag]	.291	10.4	.003
	meanAT (–) [1 wk lag]	.324	12.0	.002
	meanAT (–) [2 wk lag]	.307	11.1	.002
	PAR (–) [4 wk lag]	.240	8.2	.008
<u>Flowering</u>				
<i>M. amplexans</i>	meanAT(–) [3 wk lag]	.359	13.8	.001
	minAT(–) [4 wk lag]	.424	17.9	< .001
<i>M. crassifolia</i>	minAT(–) [3 wk lag]	.240	8.2	.008
<i>M. suberosa</i>	minAT(–) [2 wk lag]	.299	10.8	.003
	minAT(–) [3 wk lag]	.291	10.4	.003
All species	minAT(–) [2 wk lag]	.307	11.2	.002
	minAT(–) [3 wk lag]	.275	9.7	.005
<u>Fruiting</u>				
<i>M. speciosa</i>	PAR(+), RF(+) [1 wk lag]	.449	10.3	< .001
	meanAT(+), RF(+) [2 wk lag]	.477	11.4	< .001
	meanAT(+) [3 wk lag]	.381	15.1	< .001
	meanAT(+) [4 wk lag]	.291	10.4	.039
All species	meanAT (+) [without lag]	.308	11.2	.002
	meanAT(+) [1 wk lag]	.410	17.0	< .001
	meanAT(+) [2 wk lag]	.312	11.4	.002

**Table 4. Spearman rank correlation test (n=24) between climate seasonality and seasonal change in the number of species of *Medinilla* in flower budding, flowering, and fruiting. Correlation coefficient (r<sub>s</sub>) and probability are shown for five climatic variables. Abbreviations of the variables are as follows: meanAT, mean air temperature; maxAT, maximum air temperature; minAT, minimum air temperature; PAR, photosynthetically active radiation; RF, rainfall.**

Climatic variable	Flower budding	Flowering	Fruiting
meanAT	– 0.17	0.12	0.75***
maxAT	– 0.03	0.20	0.57**
minAT	– 0.54**	– 0.23	0.55**
PAR	– 0.06	0.23	0.44*
RF	– 0.27	– 0.30	– 0.29

\*  $P < .05$ ; \*\*  $P < .01$ ; \*\*\*  $P < .001$

#### The relationship between climate and phenology

Flower budding of several species started, negatively corresponding with mean and minimum air temperature within the previous 3 weeks (Table 3). Individuals of *M. amplexans*, *M. crassifolia*, *M. homoeandra*, and *M. suberosa* started flower budding after the decrease in air temperature which occurred a few weeks ago. All significant correlations in the start of flowering included a negative correlation with minimum air temperature, although those were the data of more previous weeks than those of flower budding. Since the time lag of flowering response corresponds to differences in peak position between flower budding and flowering (Table 1), the predictor variables of flowering could be determined based on the response of flower budding to low temperature. Congeneric individuals started to bear mature fruits with an increase in overall mean air temperature, although only *M. speciosa* had significant predictor variables that showed positive and complicated correlations with its fruiting response.

*Medinilla* species tended to bear flower buds when minimum air temperature was low (Table 4). There was no relationship between climatic seasonality and seasonality in the number of flowering species. On the other hand, the number of species in fruiting phase correlated positively with air temperature and photosynthetically active radiation (Table 4). There were particularly strong relationships between the seasonality of air temperature and fruiting seasonality of *Medinilla* species, suggesting that *Medinilla* species tended to bear mature fruits under warm conditions.

## DISCUSSION

Flowering activities of *Medinilla* species might be regulated by the seasonal reduction in air temperature.

Flower bud formation of most *Medinilla* species seemed to have been triggered by low minimum air temperature. In the normal climatic trend of northern Borneo, the reduction in minimum air temperature appeared to occur not only during November–February when the Asian winter monsoon blew (Yasuda et al. 1999) but also June–July that is out of the monsoon season (Kitayama et al. 1999). The reproductive seasonality of *Medinilla* species must have been formed by the reciprocal climatic events in Borneo. Furthermore, the unexpected flowering event of *M. crassifolia* and *M. speciosa* which was observed in December 1997 was also explained as a response to low temperature during September–December 1997, one of periods in which the daily minimum air temperature fell below the three-year mean of daily minimum air temperature (i.e., 15.4 °C) during the observation years (Kitayama et al. 1999).

A floral initiation stimulated by low temperature has been reported in the case of mass flowering in lowland forests of Southeast Asia (Ashton et al. 1988; Sakai et al. 1999). In mass flowering, not only super-annual flowering species but also annual flowering species bloomed simultaneously. Sakai et al. (1999) suggested that non-general flowering species also utilized low temperature as a climatic cue for their flowering and had a lower threshold of temperature. In the lower montane forest of Mount Kinabalu, no event of mass flowering or mass fruiting was observed during the first observation year (Kitayama et al. 1998) and a large number of species reproduced annually or biannually (Kimura et al. 2001). These results support that the floral initiation by low temperature might be applicable to *Medinilla* species on Mount Kinabalu.

Our prediction that reproductive activities of *Medinilla* species would be related with the sunny condition was supported for fruiting phenophases. The

number of species in fruiting phase increased during the period with high temperature and insolation. In consequence of floral initiation by low temperature, the following fruiting season (including premature fruiting period) appeared to overlap with a warm period when would happen next to the period with low temperature, because air temperature changed reciprocally. However, an increase in air temperature was important for plants growing under cool condition because it promoted biotic activities and development of seeds of the plants. Simultaneously, the effect of insolation could not be negligible because air temperature and insolation were strongly correlated and because an increase in the maximum air temperature is caused largely by high insolation (Walsh, 1996). Furthermore, for understory plants exposed to poor light condition, high insolation may be more important for the development of fruit and seed because photosynthesis in plants activated by high insolation may contribute to the production of compounds related to the development of fruits and seeds (Wycherley, 1973; Zimmerman et al. 2007).

The seasonality of flowering and fruiting was regarded as an adaptation to seasonal changes in the availability of effective pollinators and seed dispersers (van Schaik et al. 1993). Many studies have shown that seasonal variations in flowering and fruiting time of animal-pollinated and animal-dispersed plants at the population or community level; these variations were related to seasonal changes in activity of available animals for pollination and seed dispersal (Elzinga et al. 2007; Ims, 1990; Kimura et al. 2001; Koptur et al. 1988; Leck, 1972; Levey, 1988; Loiselle and Blake, 1991; Marquis, 1988; Poulin et al. 1999; Sakai et al. 1999; Snow, 1965; Stiles, 1975; Waser, 1978; Wheelwright, 1985). Aggregated patterns among congeners were reported in some taxonomical groups (Poulin et al. 1999), indicating that the high synchrony among congeneric species may promote increase in visiting frequency by pollinators and seed dispersers.

However, there is no useful information about pollinators and seed disperses on Mount Kinabalu. We observed stingless bees (*Trigona* species) that infrequently visited flowers of *M. crassifolia* and *M. speciosa*. *Trigona* species was reported as an anther destroyer of Melastomataceae (Gross, 1993; Renner, 1983) and as a possible pollen vector of species belonging to Melastomataceae in Borneo (Momose et al. 1998). On the other hand, Sunda whistling-thrush (*Myophonus glaucinus*) and some flowerpeckers were observed to consume fruits of *M. speciosa* frequently. They were

resident frugivorous birds in the region of Mount Kinabalu, which were available for fruit removal of *Medinilla* species. Further observations were needed to understand the relationship between biotic factors and flowering and fruiting phenology of *Medinilla* species.

A phylogenetic constraint on phenology of plant community has been emphasized in timing of flowering (Wright and Calderon, 1995) and fruiting (Gorchov, 1990; Marco and Pérez, 2002). Wright and Calderon (1995) verified the phylogenetic hypothesis that related species have similar flowering phenologies and found strong phylogenetic patterns among congeners and confamilials. In the present study, the relationship between floral initiation/flowering and low temperature, which became characteristically apparent in *Medinilla*, may indicate that the flowering activities are phylogenetically constrained by genus *Medinilla* through physiological responses to low temperature stimulation. However, as mentioned above, the floral initiation stimulated by low temperature has been reported not only for *Medinilla* but also for many taxonomic groups of lowland dipterocarp forests in peninsular Malaysia (Ashton et al. 1988) and Borneo (Sakai et al. 1999). More comparative studies using other taxonomic groups will be required to clarify this issue.

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