FLOWERING PHENOLOGY AND FLORAL SUCCESS IN MONOCARPIC BARLERIA INVOLUCRATA VAR. ELATA

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Abstract

The flowering phenology and floral success of the monocarpic understorey shrub species *Barleria involucrata* var. *elata* (Acanthaceae) in a medium elevation evergreen forest in southern Western Ghats was examined. No proximate environmental cues could be identified in this study for flowering initiation. Peak flowering was observed in December. Floral predation was low and predators tracked floral availability. Early flowering individuals suffered greater floral predation. Floral success was influenced by floral display, visitation rates and pollen load deposited on stigmas. With the onset of synchronous flowering, decreased floral predation and increased fruit set was observed. Plant size influenced the relative reproductive success of individuals.

Introduction

Tropical species display a variety of flowering and fruiting patterns (Snow, 1965; Janzen, 1967; Foster, 1982; Frankie *et al.*, 1974; Opler *et al.*, 1976; Jackson, 1978; Croat, 1978; Putz, 1979; Heideman, 1989). Despite these variations, there is certain predictability about the flowering and fruiting episodes of the species (Snow, 1965; Janzen, 1967; Auguspurger, 1982). Most understorey shrub species in the southern Western Ghats exhibit a seasonal flowering (Krishnan, 1996). The only exception to this rule is the monocarpic genera *Nilgirianthus* which is known to flower synchronously (Duthie, 1890; Robinson, 1935; Steenis, 1938; Hutton, 1949; Santapau, 1950, 1952; Matthew, 1959).

Several ecological advantages have been associated with the monocarpic life history strategy. Significant of these are the selection for outcrossing as the selective force (Whitehead, 1969; Opler *et al.*, 1976), pollinator energetics (Heinreich & Raven, 1972) and pollinator attraction and seed predator avoidance (Beattie *et al.*, 1973; Auguspurger, 1981). The timing for onset of reproduction in monocarpic plants continue to be a mystery, although environmental cues (Auguspurger, 1982) or to resource availability (Harper & Ogden, 1970; Werner, 1975; DeJong *et al.*, 1986; Mooney & Chiariello, 1984) are implied the list is not exhaustive. Timing of flowering is thus crucial for maximizing reproductive gains especially in monocarpic plants which have a short, sharp flowering window. In some species, synchronous flowering is known to increase the fruit set by attracting pollinators (Auguspurger, 1980) and by predator satiation (Auguspurger, 1981). In contrast, individuals of *Polemonium folisissimum* increased their reproductive success under low floral density (Zimmerman, 1980). The relative importance of predators and pollinators determines the reproductive success of a species and cannot be generalized.

In this paper, the results of phenological observations on *Barleria involucrata* var. *elata* (Acanthaceae), a monocarpic understorey shrub, are presented. This study has the following specific objectives (1) to identify the significance of environmental cues for initiation of flowering, (2) to examine the impact of floral predation on overall fruit

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set, (3) to establish the factors that determine the floral success, and (4) to consider the effect of plant size on reproductive success.

Study Site

Kakkachi (1400 m), the study site is located in the southern end of Kalakad-Mundanthurai Tiger Sanctuary in the southern Western Ghats in Tamil Nadu, South India. The medium elevation evergreen forests are floristically classified as *Cullenia exarillata - Mesua ferrea - Palaquium ellipticum - Gluta travancorica - Diccusocarpus wallichianus* type (Ramesh *et al.*, 1999). The common canopy trees include- *Calophyllum austro - indicum, Diccusocarpus wallichianus, Cullenia exarillata,* and *Palaquium ellipticum.* The common understorey and sub-canopy trees include- *Myristica dactyloides, Artocarpus heterophyllus* and *Agrostistachys boornensis. Saprosma corymbosum, Diotacanthus grandis, Agrostistachys indica, Sarcandra chloranthoides* and many species of *Nilgirianthus* are found in the shrub layer. *Barleria involucrata* var. *elata* is a monocarpic shrub species endemic to the evergreen forests of Western Ghats (Gamble, 1967; Henry *et al.,* 1987), and was distributed in a clumped fashion in the study area (Krishnan, 1996). Rainfall occurs in 2 peaks following the northeast and the southwest monsoon. The average annual rainfall is around 3000 mm, with 4 to 5 dry months (data from Nalmukku, approximately 2 km from the study site). The environmental factors considered were monthly readings of mean maximum and minimum temperature, rainfall, soil moisture and number of bright days. The study was conducted between January, 1990 to June, 1992.

Material and Methods

Natural history : Barleria involucrata var. *elata,* is a monocarpic understorey shrub growing to a maximum height of 4 m in the evergreen forests of the Western Ghats. Genus *Barleria* is less known than the genus *Nilgirianthus* for its synchronous flowering behaviour. The species probably flowers synchronously once in 4 or 5 years, although the flowering periodicity has not been recorded.

Barleria flowers are blue and tubular (2.76 cm long), with 2 epipetalous functional anthers and 2 staminodes. The single ovary has 3 to 6 ovules. The 2-day flowers are protogynous, offering copious nectar and pollen. The major pollinators are *Apis dorsata* and *Apis cerena,* although *Xylocopa* bees and large butterflies also visit them (Personal observation). Small birds like rose finch (*Carodacus erythrinus*) and sun birds (*Nectarinia asiatica*) rob the flower of nectar by piercing the corolla tube vertically. The capsules dehisce mechanically in the dry season from April.

Plant census and size : Individuals (n= 36) marked for study were located along a 500 m x 10 m transect. Monthly census was taken to record the number of open and predated flowers, inflorescence, and fruits for the marked individuals. Every 3 months height and number of growing points were recorded for individuals. Growing points are the number of meristems available for further growth. Based on the number of growing points, plants were classified into 2 groups: Small individuals (1-30) and Large individuals (> 30). The degree of flowering and fruiting overlaps for the population was estimated with the number of open flowers recorded monthly following Ludwig and Reynolds (1988).

Flowering stages : To characterize flowering stages of the population, the flowering times were classified as- early (attained when 10% individuals were in flower), middle (reached when 50% individuals were in flower) and late (when 75% individuals were in flower). The individual flowering peaks, defined as the month in which median number of flowers were open, were assigned using the month in which the median flower opened. Individuals were further grouped into synchronous, pre-synchronous and post-synchronous flowering individuals based on the time when the median flower opened. During the synchronous flowering period, maximum number of individuals displayed their median flowers. The period before and after this was categorized as pre-synchronous and post-synchronous flowering period respectively.

Floral success : Floral success if defined as the number of flowers successfully initiating fruits. A

stepwise regression was used to estimate the relative importance of various parameters influencing the overall flora success. The parameters used to understand the floral success were, number of flowers and fruits, pollen availability and visitation rates. To estimate the relationship that explains the floral success during each phase of flowering, attributes like mean number of flowers, fruits, leaves and inflorescence were subjected to non-parametric correlation.

The visitation rates were estimated throughout the flowering period, by observing and recording the number of pollinator visits of the inflorescence. The observations were spread throughout the flowering season in 10-minute sessions totalling up to 18 hours. The visitors were broadly identified as bees, butterflies and birds, and their foraging behaviour for nectar and pollen observed. Total of 50 anthers from the whole flowering period was crushed and stained with acetocarmine to count the number of pollen grains. Pollen deposition per stigma was estimated by collecting the shriveled stigmas of 40 flowers for the entire flowering season. The stigmas were stained with acetocarmine and the number of pollen grains counted under a stereo microscope.

Results

Flowering and environmental factors : Observations from January, 1990 to July, 1991 showed that plant growth was only vegetative. Initiation of flowering was negatively correlated with temperature (mean minimum temperature $r = -0.664$, $P<0.05$; mean maximum temperature $r = -0.559$, $P<0.05$), but did not correlate with rainfall, soil moisture or number of bright days. Fruiting was mildly aided by soil moisture ($r = 0.431$, $P<0.05$) and the number of bright days ($r = 0.514$, $n = 9$, $P<0.05$). Of the 36 individuals marked for the study, 7 (20%) failed to flower and one individual that flowered failed to fruit. The individuals that failed to flower were predated by the large mammal herbivores in the dry season.

Flowering stages and fruiting : Flowering progressed slowly from August and peaked in December. During this period 28% of the total flowers were presented. Flowering intensified after December, and by March 84% of the total flowers were open. Once flowering was initiated, the participation of individuals increased by 100% from September to October (Fig. 1). It required only 2 months to attain mid-flowering phase, while 5
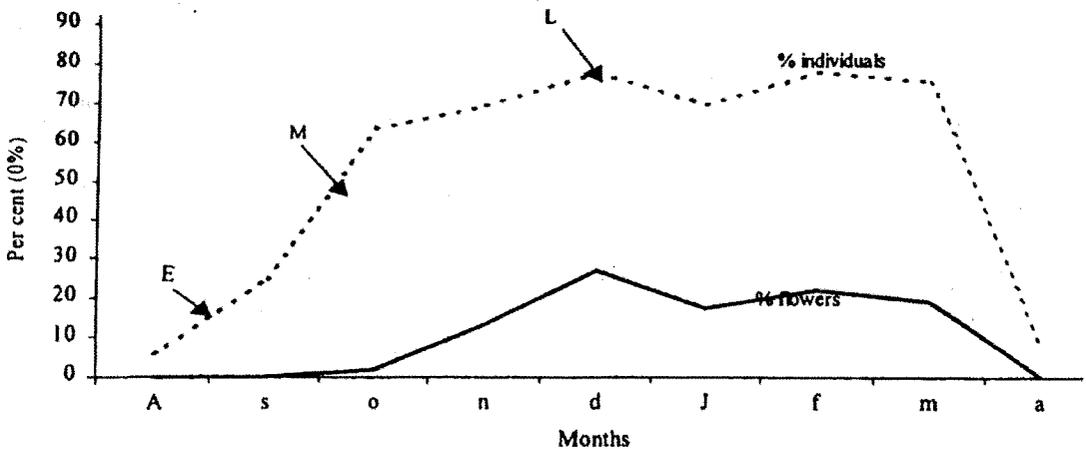

Fig.1: Flowering progression in *Barleria*.

E Early, M Mid and L Late flowering phase. The months start with August and end with April. The flowering phases are defined based on the number of individuals in flower. Early flowering phase is considered when at least 10% of the individuals are in flower, 50% of the individuals flowered during the mid-flowering phase and 75% of the individuals flowered in the late flowering phase.

months were necessary for the late flowering phase to set in. The general flowering overlap value was 0.83. The values obtained for early flowering phase and mid flowering phase were 0.72 and 0.85 respectively.

Fruit set on the other hand, was skewed to the right, beginning abruptly in October, reaching a peak in February. Fruiting ended in April with the onset of dry season. Early flowers were not very successful in setting fruits. High degree of success was observed in the late flowering phase when 72% of individuals set fruit (Fig. 2). Maximum floral success (indicated by fruit to flower ratio) was attained during mid-flowering phase, when maximum number of individuals flowered in synchrony. The general fruiting overlap was 0.85 for the entire population. The fruiting overlap for the middle and the late phase were 0.70 and 0.87 respectively.
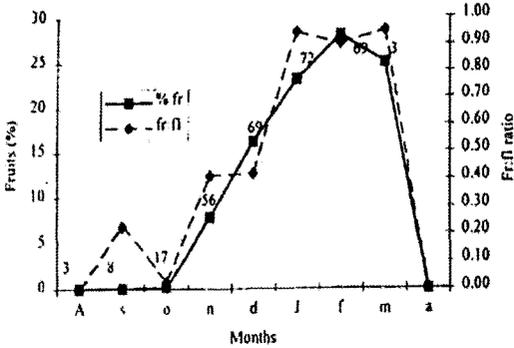

Fig.2: Fruit set in *Barleria*.

% fr. indicates the percentage of total fruits produced. The values indicated along the % fruit axis are the percentage of individuals in fruit. Fr:fl ratio indicates the fruit to flower ratio.

Floral predation : The mass flowering of *Barleria* attracted lepidopteran caterpillars. Predation of individual floral parts or the entire flower was observed throughout the flowering season. The total number of flowers predated was only 2% of the flowers produced. The predators seem to track the number of open flowers, until the beginning of synchronous flowering period, after which a drop in herbivory is observed (Fig. 3). Fruit predation was very rare.
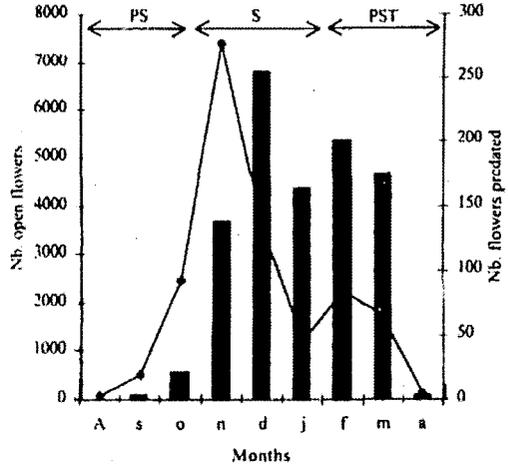

Fig.3: Floral herbivory in *Barleria*.

The proportion of open flowers predated were only 2% of the total flowers that were open. There is a steep decline in floral herbivory following the onset of synchronous flowering phase.

Floral success : Over all floral success was influenced by 3 factors, floral display, visitation rates and pollen load on stigmas (r^2= 0.93, P<0.01, Table-1). The higher visitation rate translated to increase in the number of the pollen load deposited on stigmas (r= 0.83, P<0.05), and the fruit set was correlated with the pollen availability (r= 0.78, P<0.05).

Table-1 : Factors influencing reproductive success

Variables	Reg. co-eff.	F	P	partial r^2
Pollen grain/stigma	20.11	14.84	0.011	0.75
Open flowers	0.44	15.59	0.010	0.76
Visits	-43.25	7.60	0.039	0.60

The results of the step-wise regression are tabled depicting the variables that separate out in each step. The r^2= 0.93 is significant to consider the model. Other models did not account for many variables as most of them were insignificant to be included in the successive steps. Dependant variable: Fruits.

Pollen availability differed during the flowering phases (F= 15.07, P<0.05), while the pollinator visitation rate (F= 1.06, ns) and the number of pollen

grain deposited per stigma (F= 0.99, ns) did not change during the different flowering phases.

In the mid-flowering phase, there was a strong correlation between pollinator visits and pollen grains deposited (r= 0.91, P<0.05). For the late flowering phase, a correlation between floral display and number of pollen grains deposited (r= 0.98, P<0.05) was observed. No significant correlation was obtained for early flowering phase.

Individual variation in flowering times : Individual variation in phenological behavior is depicted by differential median flowering times. During 3 months (September, October and April) none of the individuals showed median flowering. There were 3 pre-synchronous flowering individuals in the population. The individuals that flowered synchronously formed the largest group (23 individuals) while, 4 individuals were post-synchronous in their flowering behaviour (Fig. 4).
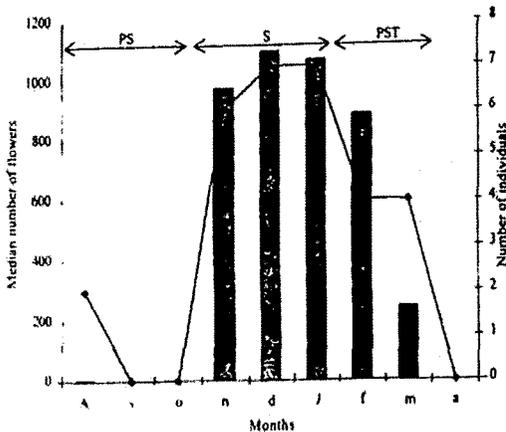

Fig.4: Variation in individual flowering times.

Depicted is the median number of flowers open for the population and the number of participating individuals. A maximum of 22% of individuals displayed the median flowers in the synchronous flowering period. During the synchronous flowering period, several individuals staggered their flowering peaks, while some individuals opened their median flowers just after the synchronous flowering phase.

Duration of the individuals flowering in and out of synchrony was not significantly different (Chi square = 11.71, ns). When the mean flowering duration's were compared, the pre-synchronous individuals were found to flower briefly (mean = 4.00 months) while the synchronous and post-synchronous individuals flowered longer (mean = 6.25 & 6.36 months respectively). The mean number of flowers and fruits produced were significantly different between the pre-synchronous and post-synchronous flowering individuals (D= 0.11, χ^2= 24.99, P<0.01), and also between synchronous and pre-synchronous flowering individuals (D= 0.14, χ^2= 54.70, P<0.01, Table-2).

Table-2: Factors success of individuals flowering in & out of synchrony

Flowering time	Flowers (mean)	Fruits (mean)
Pre-synchronous	495.30[a]	657.70[a]
Synchronous	913.50[b]	676.80[b]
Post-synchronous	386.50[b]	461.00[b]

The groups marked by the same alphabets are different from each other at P<0.01. Significant differences between pre-synchronous and post-synchronous flowering and fruiting individuals (D= 0.11, χ^2= 24.99, P<0.01), and for synchronous and pre-synchronous flowering and fruiting individuals (D= 0.14, χ^2= 54.70, P<0.01) are observed.

Plant size and flowering : Equal numbers of small and large plants were found in the population (n= 18). Three of the large plants (17%) and 4 of the small plants (22%) failed to flower. In plants of all sizes, number of mature leaves per plant influenced the number of inflorescence (r= 0.72, P<0.05) and number of fruits (r= 0.77, P<0.025). The mean number of flowers produced was 432 and 839 in small and large plants respectively. The mean flowering duration in small and large plants were 5.44 and 5.00 months respectively. Flowering and fruiting intensity was higher in the large plants than the small plants. When reproductive parameters such as number of flowers per plant, flowering synchrony, number of fruits per plant and fruiting synchrony are compared, it was evident that large plants derived only marginal advantage due to their size. When fruit set is considered, large plants had greater success than the small plants (Table-3).

Table-3: Comparison of traits and relative success of the small and large plants

Character	Small (n= 18) (mean ±Std)	Large (n= 16) (mean ±Std)
Number growing points*	11.00±8.99	43.00±14.73
Number mature leaves*	8.5±7.46	15.25±5.18
Plant height (m)*	1.38±0.056	1.96±0.43
Number of flowers per plant*	431.89±366.85	869.38±818.72
Duration of flowering (months)	5.44±2.55	5.00±3.03
Flowering overlap	0.70	0.84
Number of fruits per plant*	313.00±310.55	551.00±438.01
Fruiting overlap	0.87	0.84
Fruit : flower	0.72	0.63

The small and large plants were compared using t-test. When significantly different at P<0.05 (*), indicates that the large plants were better endowed with resources at the onset of reproduction that the small plants. Unmarked traits were not compared.

Discussion

Temperature and moisture, the two environmental cues that are known to trigger flowering in the tropics did not have any significant impact on *Barleria*. In seasonal tropics, several species respond to rainfall and temperature as cues for synchronous flowering (Fischer & Turner, 1978; Hodgkinson & Quinn, 1978; Opler *et al.*, 1976; Auguspurger, 1982; Borchet, 1983). A seasonality in the tropics, especially with respect to the flowering phenology has been reported from other forests (Putz, 1979; Primack, 1980; Krishnan, 1996). Flowering in *Barleria* is independent of the environmental factors, although the fruiting responded to soil moisture and bright days.

Mass flowering in *Barleria* accommodates a great deal of individual variation. The flowering progression indicates that the mass flowering in *Barleria* is not attained by synchronous large floral display, rather, it is accomplished in stages where increased participation by the individuals is evident. This flowering behaviour contrasts with the flowering observed for the understorey shrub *Hybanthus prunifolius*, where the flowering peak is attained in 13 days following the summer rains (Auguspurger, 1982). Flowering progression was characterized by sudden, synchronous onset of flowering by many individuals from the early flowering phase onward. This produces a skewed flowering distribution in population. When flowering is skewed to right, it increases the detectability of the species and attractiveness to pollinators (Thomson, 1980). This synchronous onset of flowering also ensures that floral predators are satiated. These results are similar to the observations made on *Hybanthus prunifolius*, where synchronous flowering reduced the damage by floral and seed predators (Auguspurger, 1981). Predator satiation in *Barleria* is not crucial once the synchronous flowering phase sets in. Increased floral density due to synchronous flowering ensures greater floral success. The fruit to flower ratio indicates that the floral success was high during the synchronous flowering phase than the early flowering phase. The increase in fruit set seemed to be achieved by the extended flowering period, so as to overlap with the synchronous individuals.

Large plants were also better endowed at the beginning of reproduction, and produced more flowers and fruits than the small plants. Despite this, flowering was not greatly extended in large plants and the floral success was not much greater than in smaller plants. Plant size has often been correlated with reproductive success of individuals (De Jong *et al.*, 1986; Harper, 1977; Herrera, 1991 and Lawrence, 1993). In other species, it has been observed that larger plants had larger floral displays and attracted more pollinators (Auguspurger, 1982; Kleinkhamer *et al.*, 1989), leading to pollen limitation in small plants with smaller floral displays (Lawrence, 1993). Plant size only marginally improved the reproductive potential of *Barleria* individuals.

The importance of the floral display, visitation rates and pollen deposition suggests that the reproductive success of the species is influenced by pollinator movements. Synchronous flowering also ensures that the pollinator service translates

into floral success. It is possible that there is reallocation of resources during the synchronous flowering phase towards maternal function to ensure that there is maximum seed set as indicated by the differences in number of pollen grains per anther over the flowering period (Llyod, 1980). Since large floral display ensures that the pollinator visitation is almost constant, floral success is ensured. Findings from other studies on mass flowering plants suggest that mass flowering endows the individuals of a species with 2 major advantages: first, it facilitates highest outcrossing rates (Appanah & Chan, 1981) and second, it increase the number of pollinator visits to the entire population (Lawrence, 1993). Reproductive success in *Barleria* population seems to be attained by balancing the role of predators and pollinators to ensure that optimal densities of flowers are presented.

Acknowledgements

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