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THE POLLINATION ECOLOGY, BREEDING SYSTEMS AND PHENOLOGY OF BLAKEA AND TOPOBEA (MELASTOMATACEAE) IN MONTEVERDE, COSTA RICA

City University of New York PH.D. 1982

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THE POLLINATION ECOLOGY, BREEDING SYSTEMS AND PHENOLOGY OF BLAKEA AND TOPOBEA (MELASTOMATACEAE) IN MONTEVERDE, COSTA RICA

by

CECILE LUMER

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy, The City University
of New York.

1982

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirements for the degree of Doctor of Philosophy.

Sept 13, 1982
Date

Chairman of the Examining Committee

13 Sept 1982
Date

Executive Officer

Dominick V. Basile, Ph.D.	Herbert H. Lehman College, The City University of New York
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Arthur J. Cronquist, Ph.D.	New York Botanical Garden, Bronx
Peter K. Nelson, Ph.D.	Brooklyn College, The City University of New York
John J. Wurdack, Ph.D.	U. S. National Herbarium, Smithsonian Institution, Washington

ABSTRACT

The Pollination Ecology, Breeding Systems and Phenology of _Blakea_ and _Topobea_ (Melastomataceae) in Monteverde, Costa Rica

by CECILE LUMER

Thesis advisor: Dr. Ghillean T. Prance

The neotropical tribe Blakeae (Melastomataceae) is composed of two genera, _Blakea_ and _Topobea_. Five species of _Blakea_ and three species of _Topobea_ grow in Monteverde, Costa Rica: six in the cloud forest and two in the lower wet montane forest. Two types of floral morphology were observed, which correlated with two pollination syndromes. Seven species are pollinated by pollen-collecting bees which use the vibratile method to eject pollen from the anthers. These species have large showy flowers, sweet scent and lack nectar. One species, _Blakea chlorantha_, has hidden green flowers, purple anthers, produces copious nectar at night and lacks detectable scent. This species is pollinated nocturnally by at least three species of rodents which visit the flowers for nectar.

All species studied are self-compatible to varying degrees and three are capable of autogamy. Seventeen species of bees were observed on the bee-pollinated plants, ranging from large bees (_Xylocopa_, _Euleama_, _Bombus_ queens) to small _Trigona_ and halictid species. On a single visit to a plant the large bees visit 4 to 10 flowers and remain on a flower 3 to 15 seconds, whereas the smaller bees spend up to 30 minutes on an individual plant, often returning

to the same flower more than once. Since the plants are self-compatible, bees of all sizes are effective as pollinators. The large bees are probably more effective in cross-pollination and the smaller bees in self-pollination.

Three species of bee-pollinated Blakea are sympatric and share the same pollinators. These species minimize competition for pollinators by their flowering phenologies.

Floral and mature fruit phenology, as well as observations, indicate that together the species studied provide food for their pollinators and dispersal agents throughout most of the year and are an important component of their ecosystem.

ACKNOWLEDGEMENTS

Many people assisted and supported my research, both in New York and Costa Rica. I am indebted to the Tropical Science Center in Costa Rica for allowing me to conduct my research in the Monteverde Cloud Forest Reserve, as well as to J. & D. Campbell, W. & M. James, M. & P. Fogden, P. Smith, T. & L. Guindon and S. Wallace for allowing me to work on their property. Special appreciation is due J. Campbell for use of his darkroom, technical advice and weather data, to Drs. H. Baker, G. Frankie and W. Haber for loan of field equipment and advice and Dr. L. D. Gomez for helping with a variety of problems.

The eighteen months in Costa Rica would have been very difficult without the ongoing support I received from S. Koptur in the form of advice, encouragement, equipment and field assistance. I would also like to thank the many people of the Monteverde community who were supportive and helpful. Invaluable field assistance was given by L. Mertens and R. Schoer. I am grateful to D. Carmichael and B. Burns who helped with analysis of the rodent guts, to D. Carmichael who assisted with acetolysis of the pollen and Dr. L. Staiano-Colco for her permission to use the Coulter Counter and her help in counting pollen grains. I am indebted to Drs. R. Dressler, W. Haber, D. Roubik and A. Wille for identifying the bees, to Drs. A. Gardner and G. Musser for identifying the rodents, to Dr. J. J. Wurdack for plant identification and to I. Baker for chemical analysis of the nectar.

During the time I was in Costa Rica I leaned heavily on

F. Maroncelli and S. Neville who together handled my New York affairs.

I could never have completed this thesis without my friend B. Alkana, who lived with me and cared for me during the months after my accident, and the many friends who acted as my legs during this time. In this regard, special thanks are due M. Wetter and B. Braun who were aided by H. C. Hopkins, M. J. G. Hopkins, L. Atehortua, R. Callejas, L. Lynas, S. Crisafulli, L. Marschner, F. Maroncelli and J. Grimes. In addition, I would like to thank M. J. G. Hopkins for help with the graphics, M. Wetter for photographic assistance, Dr. D. Kincaid for help with the statistics and A. Rubinsztejn and the many workers at Lehman College Computor Center who patiently guided me as I learned enough word-processing to produce this document. I appreciate the help given me by Dr. W. Lehman and the nursing staff at Orthopedic Institute who "aided and abetted" my use of the terminal. My parents, Herbert and Clara Nagler were supportive and helpful throughout all phases of this research.

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INTRODUCTION

Most studies of the reproductive biology of neotropical plants have been conducted in lowland forests (Baker et al, 1980; Bawa, 1974, 1977; Bawa & Opler, 1975; Janzen, 1967). In these studies out-crossing has been found to be prevelant with a high number of dioecious species. However, little research has been done in the area of the reproductive biology of plants in neotropical montane areas (Arroyo, 1979; Lumer, 1980; Sobrevila & Arroyo, 1982) and although hemi-epiphytes are common cloud forest species almost nothing is known of their reproductive biology and pollination ecology.

Therefore, I chose to study the reproductive biology and pollination ecology of the eight species of Blakea and Topobea (Melastomataceae) in the cloud forest and wet montane forest at Monteverde, Costa Rica. Both genera are basically hemi-epiphytic montane genera with scattered lowland species.

Although the Melastomataceae are a fairly large tropical family (~4500 species) very little is known about the reproductive biology of its members. When I conceived this project in 1978, the only published accounts were of general floral observations such as those of Forbes (1882) and Pijl (1954). The exception was Almeda's monograph on Central American species of Monochaetum (1978), which contained limited information about the breeding systems and some floral observations. Recently, Buchmann and Buchmann (1981) reported on the pollination ecology of Mouriri and I have learned of studies being conducted by S. Renner (pers. comm.) in Brazil on the pollination ecology of several species of melastomes.

Blakea and Topobea are the only genera in the tribe Blakeae. With the exception of the anthers, the floral and vegetative characters of the two genera are identical. Consequently, various taxonomists (Don, 1823; Gleason, 1945; Almeda, 1974) have questioned whether the two genera should be maintained or whether they should be united under Blakea.

Because floral morphology is often correlated with the class of pollinator and/or mode of pollination (Faegri & Pijl, 1966), I was interested in whether this single difference between the genera, anther shape, would be reflected in differences in their pollination ecology. Furthermore, I was interested in how the more subtle differences in floral morphology within the genera, such as flower size and petal texture would be reflected in pollinator size or pollination mode. For instance, I expected that the large flowers of B. tuberculata would be visited by large bees, such as Xylocopa, and the smaller more delicate flowers of B. anomala and B. gracilis by smaller bees.

To investigate these ideas and to gain as wide a knowledge as possible of the reproductive biology of these plants, I planned a project which would cover at least one year. Almost nothing was known of the biology of Blakea and Topobea when I began this research. Therefore, this project included phenology studies, floral observations, collection of floral visitors, controlled pollinations to determine their breeding systems and seed germination.

Because Cruden (1977) has shown that differences in breeding systems between related taxa are often reflected in differences in pollen-ovule ratios (P/Os), I determined the P/O of the species studied.

Early in this research I became aware that seed set was low relative to the number of ovules per fruit. Therefore, seeds and ovules were counted and analyzed statistically to determine whether seed set was pollinator limited (Bierzychudek, 1981) and/or if there was a correlation between seed set and breeding systems.

STUDY SITES

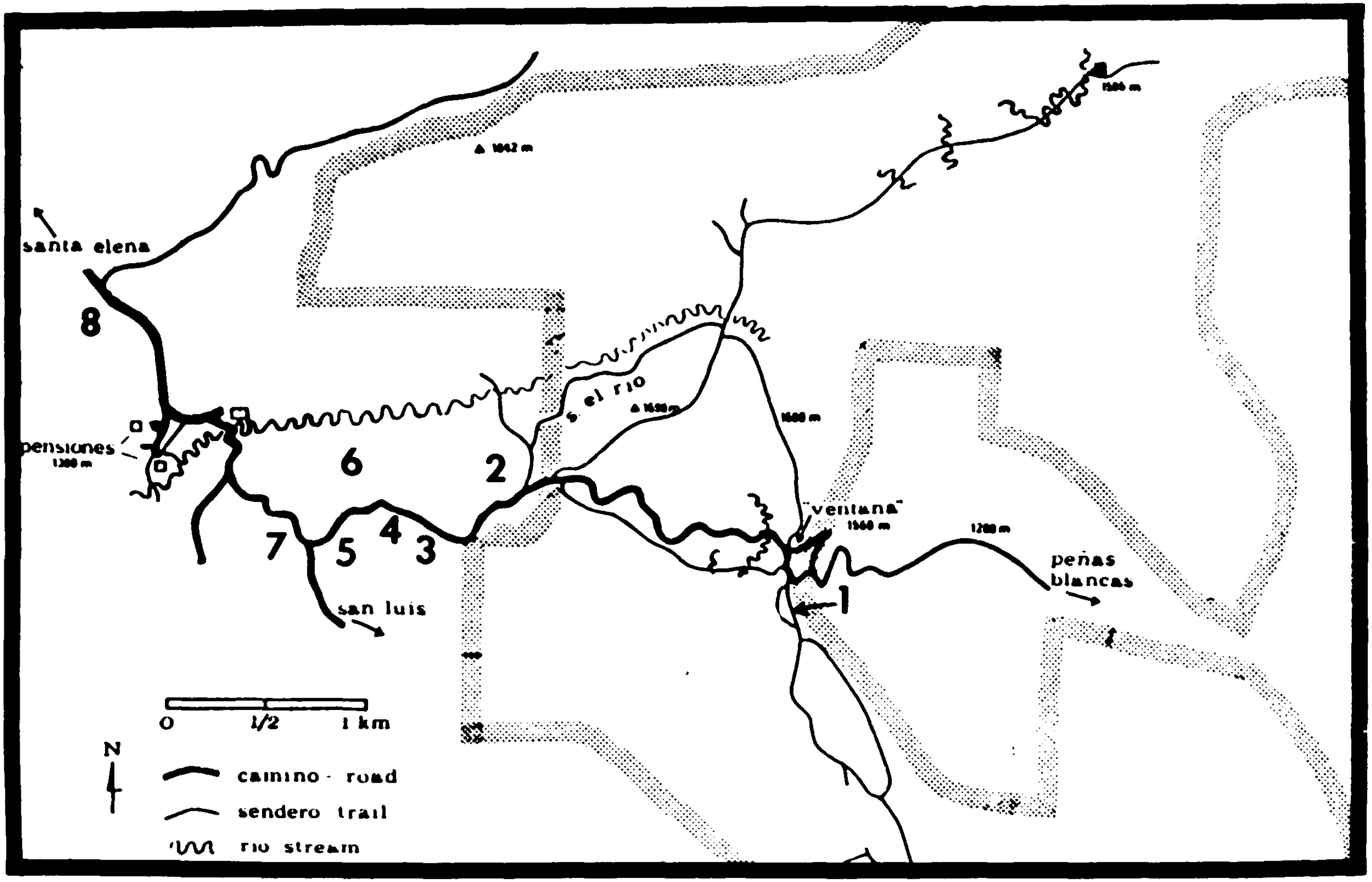
The Monteverde Cloud Forest Reserve is a mid-elevation cloud forest located along the continental divide of the Tilleran Mountains in Puntarenas Provence, Costa Rica. While the highest point reaches 1850 meters, most of the area lies between 1540 and 1650 meters. Under the Holdridge life zone system the Reserve is classified as lower montane rain forest (Holdridge et al., 1971), However, if the definition of a cloud forest is that of a forest which is bathed in clouds year-round (Lewis, 1971; Myers, 1969), then the entire Reserve deserves to be classified as cloud forest.

The Reserve encompasses approximately 5000 hectares and includes land on the Atlantic and Pacific slopes of the continental divide. The varying exposures make this an ecologically diverse and species-rich area (see Lawton & Dryer, 1980, and Powell, 1977 for a detailed history and description of the Monteverde Cloud Forest Reserve).

Below the Reserve, on the Pacific side, is the dairy farm community of Monteverde, which was established in the late 1940s and early 1950s by a small group of American Quakers. Much of the cloud forest adjoining the Reserve was cleared at that time for pasture. The forest at the lower end of the community is wet montane forest (following Holdridge, 1971). While the cloud forest itself receives moisture in the form of rain and/or mist year round, the lower wet montane area ordinarily experiences a definite dry season from February through April.

This research was carried out in the Monteverde Cloud Forest Reserve, and below the Reserve in the Quaker community of

Fig. 1. Map of Study Area. 1. Continental divide. 2. Fogden property. 3. Campbell's woods. 4. Guindon property. 5. Campbell lawn and pasture. 6. James property. 7. Smith property. 8. Wallace property.


santa elena
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"ventana"
1500 m
1200 m
1
peñas
blancas
0
1/2
1 km
N
camino - road
sendero trail
rio stream

Monteverde (Fig. 1). A total of eight species were studied, six of which grow in the Reserve and in cloud forest remnants bordering the Reserve (*Blakea anomala*, *B. chlorantha*, *B. grandiflora*, *B. tuberculata*, *Topobea brenesii* and *T. pittieri*). *Blakea gracilis* is common in the Monteverde community as well as in the wet montane forest, and *T. durandiana* was found growing along the Rio Guacimal at the lower limits of Monteverde. Plants in the Reserve were used for phenological studies and all phases of this research.

Adjoining the Reserve is the property of Michael and Patricia Fogden. This area is essentially cloud forest although it has been partially cleared. Here I found large accessible plants of *T. brenesii*, *B. grandiflora* and *B. tuberculata* which were included in this study.

The property of John and Doris Campbell is at the lower edge of the cloud forest. While part of their land has been cleared for pasture the Campbells have maintained a large tract in forest. Although this area has been selectively logged it has been the site of many biological studies. Part of this forest is true cloud forest, while the lower section is a transition toward the wet montane forest. *Blakea anomala*, *B. grandiflora*, *B. tuberculata* and *T. brenesii* grow here. Due to their inaccessibility, these plants were not used in most of the study, but were included in phenological records.

Many of the original trees still stand in a pasture locally called "Campbell's Bullpen". *Blakea anomala*, *B. gracilis* and *T. brenesii* are found here and several plants of each species were included in this study.

Many large individuals of _B. gracilis_ grow on the front lawn and pasture of the Campbell house. These were used for mark and recapture experiments with bees, as well as for collecting phenological data and for breeding systems tests.

The property of Walter and Mary James is also at the lower limit of the cloud forest. A large specimen of _T. brenesii_ growing on their front lawn was important in this study.

Two individuals of _T. brenesii_ grow on the property of Tomas and Lindy Guindon. They were also included in this project.

Lower down in the Monteverde community I studied various individuals of _B. gracilis_ growing on the roadside and on the property of Paul Smith. Towards the end of this research two individual plants of _T. durandiana_ were found growing along the Rio Guacimal on the property of Stella Wallace. Only one was accessible and this individual was added to the study.

Rainfall and Temperature

Unfortunately, this information is not available for the Reserve itself. Towards the end of my residence in Monteverde, the collection of weather data by the Tropical Science Center had just begun. However, this information is available for an area just below the Reserve at approximately 1380 meters. Here, rainfall averaged 2450 mm/year over a ten year period (Lawton & Dryer, 1980). During the time of this study 2873.9 mm fell between June 1, 1979 and May 31, 1980 (Table 1). In my experience, precipitation in the Reserve was considerably higher.

Table 1

Rainfall (mm.) at Monteverde

	1978	1979	1980	1981
January	58.	67.	122.5	95.
February	86.	35.5	58.3	55.4
March	27.1	54.	45.	52.
April	15.6	190.1	45.1	76.
May	358.	126.3	244.1	460.
June	304.	375.	359.	586.
July	317.	273.	315.	265.
August	247.	385.	316.	476.
September	283.	702.	489.	260.
October	336.	382.	433.4	-
November	202.	225.	467.	-
December	196.	134.8	157.	-

As in most tropical areas, temperature fluctuations are greater during a 24 hour period than on a seasonal basis. As Table 2 shows, from June 1, 1979 to May 31, 1980, the mean daily temperature was 18.5 C, with a high of 23.8 C for March, 1980 and a low of 13.2 C for February, 1980 (This information was collected by J. Campbell for the Instituto Meteorologico).

Table 2

Average Monthly Temperature (°C) at Monteverde

		1978	1979	1980	1981
January	max.	21.5	22.45	20.51	19.67
	min.	13.14	13.11	13.98	12.79
February	max.	21.28	21.85	20.91	21.67
	min.	13.32	14.34	13.18	13.80
March	max.	23.01	23.25	22.83	21.90
	min.	14.32	13.88	14.13	14.85
April	max.	24.28	22.63	23.11	22.06
	min.	14.5	15.56	14.68	14.93
May	max.	23.29	23.01	23.53	22.11
	min.	15.4	15.85	16.09	15.69
June	max.	21.56	21.41	22.55	21.61
	min.	15.3	15.48	16.16	15.71
July	max.	22.11	22.09	22.75	21.88
	min.	14.74	15.66	15.72	15.27
August	max.	22.27	21.59	22.59	21.29
	min.	15.53	15.54	15.53	14.96
September	max.	22.33	21.06	22.65	21.90
	min.	15.03	15.26	15.61	15.11
October	max.	21.41	21.54	22.01	-
	min.	15.09	15.58	15.53	-
November	max.	21.8	21.97	21.65	-
	min.	15.1	15.25	15.40	-
December	max.	21.7	21.40	20.13	-
	min.	14.50	14.51	14.00	-

DESCRIPTION OF THE GENERA

Both *Blakea* and *Topobea* are considered identical in all morphological characters with the exception of anther shape (Gleason, 1945; Almeda, 1974). *Blakea* has squat, wedge shaped anthers with prominent connectives (Fig. 2), while in *Topobea* the anthers and the connectives are narrower (Fig. 3). The flowers of both genera are 6-merous, with 6 petals, 6 sepals and 12 anthers and a single pistil. The flowers are subtended by two pairs of decussate bracts which vary greatly in size. In some species they are large, even showy (*B. gracilis*), while in other species they are extremely small (*B. anomala*, *T. pittieri*).

In both genera the pollen is released through terminal pores. The pollen of all eight species is extremely small, from 11 to 21 microns in diameter and tricolporate.

The species studied normally have an inferior ovary with six locules, each of which has numerous ovules. Exceptions were *T. pittieri* which often had four locules and one individual of *B. gracilis* which usually had 8 locules. The fruit is baccate, and deep red when mature, with the exception of the deep pink fruit of *T. pittieri*. A sweet scent is characteristic of these species, except for *B. chlorantha* and *T. pittieri*, whose flowers lack any scent detectable to humans.

In six of the species studied, the stamens position themselves toward the rear of the open flowers, and the pistil curves toward the anthers. These flowers have a zygomorphic appearance. In the other two species, *B. chlorantha* and *B. tuberculata*, the stamens

Fig. 2. Anthers of *Blakea sp*.

Fig. 3. Anthers of *Topobea sp*.

②

③

remain in a circle around the pistil, and the flowers are actinomorphic.

In bud the anthers are folded and form a ring around the centrally located pistil. The day before the flowers open the anthers begin to move. With the exception of B. chlorantha, the flowers open slowly through the night and are almost fully open by dawn (5:30-6:00 a.m. CST), with the stamens expanded and in place. In the zygomorphic species the movement begins within the closed bud, but is completed as the petals open. During the day the petals continue to move so that by evening the flowers are a flat dish-shape.

Scent production begins at dawn and ends at dusk, except for B. turberculata whose flowers continue to produce scent the second day. The seven bee-pollinated species (i.e. except for B. chlorantha) have functionally one day flowers, although they remain on the plant for two days. On the second day the petals and stamens fall at the slightest touch and the flowers are ignored by bees.

The individual flowers of B. chlorantha open slowly over a period of about two days. The stigma is exserted from the tightly closed bud from three to four days before the flower opens. The petals often open in the morning, but the stamens remain reflexed until late afternoon. At dusk the stamens unfold, pollen becomes available and nectar flow begins. The flowers last for two nights, producing nectar both nights, after which the petals and stamens abscise.

Although both Blakea and Topobea have been described as having some members that are small trees and others that are epiphytes (Gleason, 1945; Almeda, 1980), all species in the Monteverde area are hemi-epiphytes. They grow on trees (Fig. 4), fallen logs (Fig. 5) and tree stumps (Fig. 6). At first glance a plant may appear to be a small to medium tree, but upon examination of the substrate I have always found it to be growing on a fallen log. The exception is an individual of _T. brenesii_ growing in the front yard of Mary and Walter James, which was planted by Mary as a young seedling.

The _Blakea_ and _Topobea_ in Monteverde are sun-loving. Those growing in the shade do not flower, or have very few flowers.

Fig. 4. Blakea gracilis growing on tree.

Fig. 5. Topobea brenesii growing on log. Clusia sp. at left.

Fig. 6. Blakea gracilis growing on tree stump in pasture.

DESCRIPTION OF THE SPECIES STUDIED

Blakea cf anomala Donn. Smith

This species grows in the middle and upper canopy of the cloud forest and on fallen logs along trails and other open areas. It is also found in an area which is now pasture, "Campbell's Bullpen". This is a transition area between the cloud forest and wet montane forest environments.

The leaves and flowers of *B. anomala* (Fig. 7) are somewhat similar to those of *B. gracilis* and they are often mistaken for one another. However, the white zygomorphic flowers of *B. anomala* are smaller (~3 cm. wide) and lack the striped pattern on the dorsal side of the petals. In addition, the bracts are small and insignificant, unlike the large showy bracts of *B. gracilis*. The anthers are yellow, the filaments are pink and the pistil is white. The scent is light and sweet.

When growing in the open sun the leaves are a burnished red, which together with the showy flowers and red fruits makes this a distinctive plant.

Blakea gracilis Hemsley

Blakea gracilis does not grow in the cloud forest, but in the wet montane forest below. It is very common in pastures and along roadsides in the Monteverde community. Throughout Costa Rica this species is called San Miguel. The entire plant, leaves, flowers, buds and fruits, is eaten by cattle and humans.

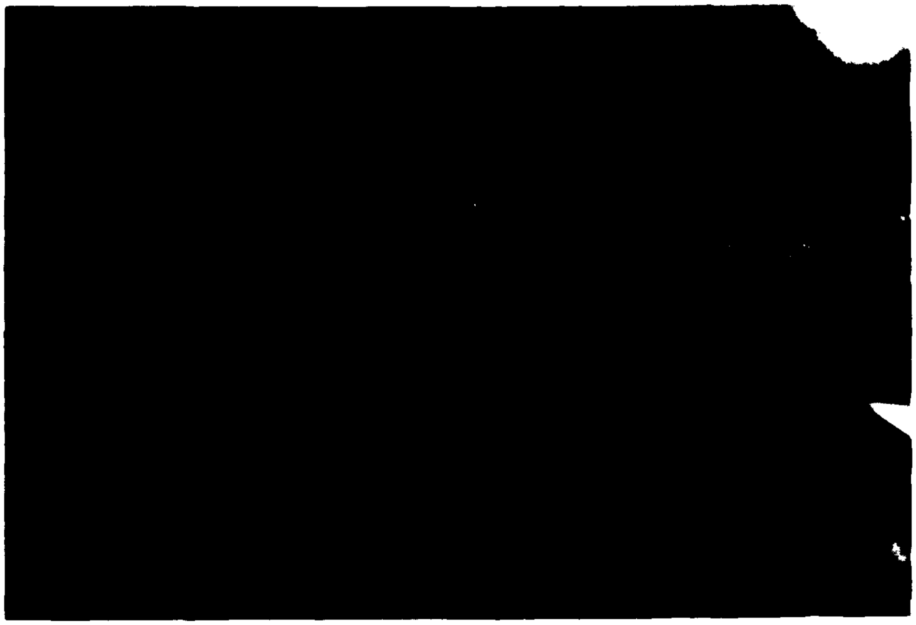


Fig. 7. Flower of *Blakea anomala*

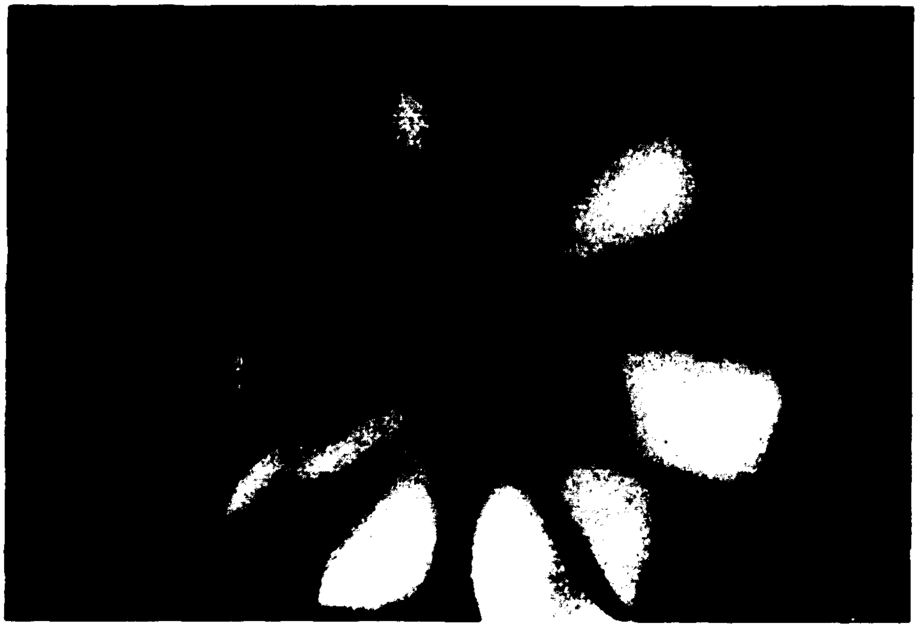


Fig. 8. Flower of *Blakea gracilis*.

The flowers are large (∼4.5 cm. wide), the buds deep pink and the mature fruit red. The zygomorphic flowers (Fig. 8) are usually white, but sometimes pink, with deep pink stripes alternating with white on the underside of the petals. The filaments are white, anthers yellow and stigma white. The style is either white or pink. Open flowers have a light sweet pleasing scent.

Blakea grandiflora Hemsley

This species is restricted to the cloud forest. The flowers (Fig. 9) and bracts are similar to those of *B. gracilis* but slightly larger (∼5.5 cm. wide). Like the zygomorphic flowers of *B. gracilis* the petals are white, with alternating white and pink stripes on the underside of the petals. The anthers are yellow and the pistil is white. The leaves differ from those of *B. gracilis* in being larger and more coriaceous and except for lacking the small flaps at the base, are similar in size and texture to those of *B. chlorantha*.

Blakea tuberculata Donn. Smith

Blakea tuberculata grows in the lower section of the cloud forest. The flowers are large (∼7 cm. wide) and distinctive (Fig. 10). The petals are deep pink becoming whitish toward the center and thick and leathery. They anthers are yellow and the pistil is white with many small glandular hairs along the sides.

These flowers are actinomorphic. The stamens remain in a circle around the pistil throughout the life of the flower. When

Fig. 9. Flower of Blakea grandiflora.

Fig. 10. Flower of Blakea tuberculata.

picked the flowers quickly lose their color and turn a drab beige-brown. The scent is heavy and differs from that of the other Blakeas in this study. The flowering period is brief. New buds are formed immediately. These become quite large and remain on the plant 9 to 10 months before opening, giving *B. tuberculata* the appearance of being ready to bloom throughout most of the year. The leaves are pubescent and much larger than the leaves of the other species of *Blakea* in Monteverde.

Blakea chlorantha Almeda

The floral morphology of *B. chlorantha* differs considerably from that of the other species in Monteverde. The stigma protrudes from the closed bud as much as three to four days before the flower opens. The actinomorphic flowers are campanulate rather than dish-shaped; the petals and sepals are green and the anthers are purple (Fig. 11). The corolla diameter is approximately 14 mm. in first day flowers and 17 mm. in second day flowers. *B. chlorantha* is unique among the species studied, in that it produces copious nectar and lacks any scent discernable to humans. Both nectar availability and pollen presentation occur at dusk, with nectar being produced throughout the night.

The leaves are similar in size, shape and texture to those of *B. grandiflora* with the addition of two small flaps at the base.

B. chlorantha grows in the elfin forest, along the continental divide and in the upper canopy of the cloud forest. These are the harshest environments in the Reserve.

Fig. 11. Flowers of Blakea chlorantha.

Fig. 12. Flower of Topobea durandiana.

Topobea durandiana Cogn.

Topobea durandiana was not included in this study until February, 1980 when it was located growing in the lower part of the Quaker community (elevation 1320 meters) along the Rio Guacimal. Two plants were found, of which only one was low enough to work with.

This species has large leaves and large showy flowers (Fig. 12) about 4 cm. wide. The petals are light pink, anthers maroon and filaments white. The pistil curves to one side and then back again toward the center of the flower, rather than toward the front as in the other zygomorphic species.

Topobea brenesii Standl.

This species is common in the middle and upper canopy of the cloud forest and in cut-over areas which are transition zones between the cloud forest and wet montane forest.

The pink flowers are approximately 3.5 cm. wide (Fig. 13). The anthers are yellow and the filaments white. The pistil is white and the flowers have a pleasant sweet scent. The bracts and sepals curve backwards making this species easy to identify. The mature fruits are bright red.

Topobea pittieri Cogn.

Topobea pittieri is rare in the Monteverde area. I found four plants, only one of which was large enough to produce flowers regularly. It is possible that this species is in the process of becoming established. On the other hand, the only plants large

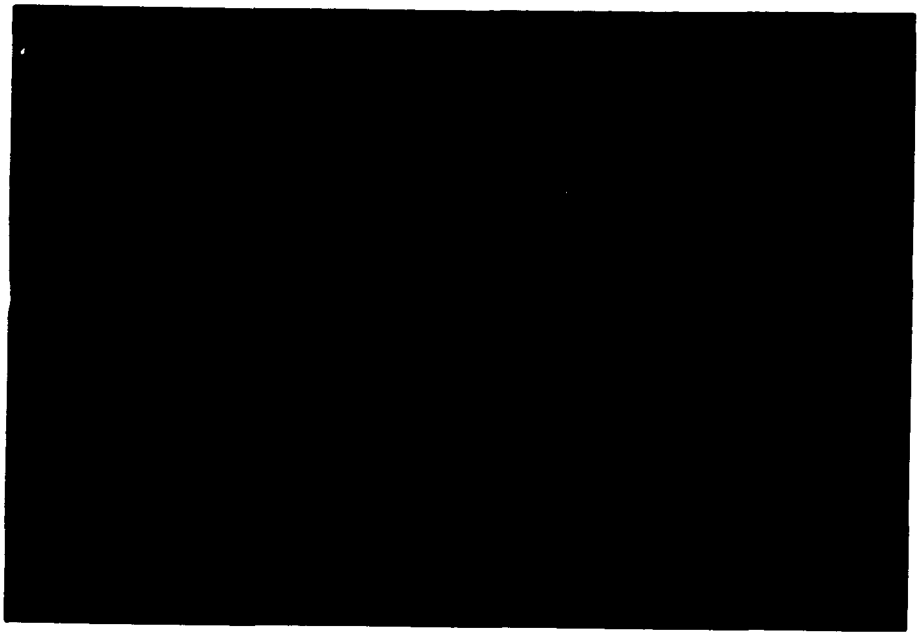


Fig. 13. Flower of Topobea brenesii.

Fig. 14. Flower of Topobea pittieri.

enough to have flowers were growing along the trail on the continental divide where they were being overgrown and shaded out by weedy species, especially *Smilax sp*.

Although it too is a hemi-epiphyte, growing on trees and fallen logs, its aspect is between that of a shrub and a vine, whereas the other species were all shrubby or tree-like.

The flowers are relatively small for the genus and casually resemble species of *Solanum* (Fig. 14). The white reflexed petals are approximately 1 cm. long. The anthers are yellow and the pistil and stigma white. As the fruits mature they turn upwards and become purplish-pink. The leaves make this an easy species to identify, even in its vegetative state. On the underside of the leaf, toward the base, there are two domatia, one on each side of the mid-vein. Mites were observed in several of these. *T. pittieri* does not have a scent detectable to humans.

MATERIALS AND METHODS

Floral and Vegetative Phenology

Data were collected monthly for 15 months. In some cases records do not cover the entire period but begin at the time the plant was first located. For all species studied, an effort was made to include plants from different habitats to insure as complete a representation as possible.

The plants were often too large to count individual flowers, fruits or buds, and these were not evenly distributed. Therefore, I used the methods of Frankie et al (1974) with some modifications. I observed the plant closely and after taking into consideration its size, I scored the number of flowers, buds, mature and immature fruits on a scale of 0 to 5. Vegetative growth was scored in a similar manner, noting old and new leaves. Other information, such as unusual herbivory, visitors and weather were also noted.

The number of plants per species used in gathering these data were: _Blakea_ _anomala_ 8, _B_. _chlorantha_ 7, _B_. _gracilis_ 7, _B_. _grandiflora_ 9, _B_. _tuberculata_ 6, _Topobea_ _brenesii_ 8, _T_. _durandiana_ 2 and _T_. _pittieri_ 4.

Observations of Floral Behavior and Visitors

For all species, ten to fifteen mature buds per species were tagged and observed to determine time of flower opening, pollen presentation, scent production and the life span of individual flowers.

All species were closely monitored for floral behavior and visitors over a 15 month period. *Blakea anomala*, *B. tuberculata*, *B. grandiflora*, *Topobea pittieri* and *T. durandiana* were each observed for more than 50 hours and *B. chlorantha*, *B. gracilis* and *T. brenesii* each for more than 100 hours. Hours of observation for all species began at 4:00 a.m. (CST) and ended at 6:00 p.m. (with an approximate 15 minute variation, daylight lasted 12 hours, from 6:00 a.m. to 6:00 p.m.). In addition, *B. chlorantha* was monitored for more than 50 hours from 5:00 p.m. to 8:00 a.m. The evening observations were limited to three plants, the first and third of which were about 750 meters apart. A red filter was placed over a white light for evening observations. Since this species produces nectar during the night, nectar volume was measured with capillary tubes every hour through one night from 5:00 p.m. to 8:00 a.m. from 15 bagged flowers on two plants. Nectar was also collected on filter paper and sent to I. Baker for chemical analysis to determine sugar, amino acid and starch content.

I made additional observations when collecting phenological data, while walking through an area, when checking the results of breeding tests and while photographing flowers and collecting visitors. An attempt was made to monitor all species throughout their flowering seasons, as well as throughout the day, and to observe different plants of the same species.

In an effort to learn which bees were effective in cross pollination, mark and recapture studies were performed on several occasions. Bees captured visiting *B. gracilis* were marked with Testor enamel paint on the dorsal side of the thorax and then released. This was done twice with the help of a field assistant on two plants approximately 100 meters apart. Captured bees from one plant were marked with green paint and those captured on the second plant were marked with red paint.

On another occasion, members of the Monteverde community assisted in monitoring a larger number of plants. People were stationed at five individuals of _B. gracilis_. Their job was to capture the bees, note any paint marks and then release the bees. My field assistant and I, stationed at two other plants, caught and marked bees as described above.

During one mark and recapture session, fluorescent powder was placed on open flowers of three plants. Different colors were used for each plant. Captured bees were then checked for fluorescent powder as well as for paint marks.

Bees visiting the flowers were collected and placed in killing jars containing ethyl acetate, then pinned and dried over the plant dryer. Bees were identified by Drs. R. Dressler, G. Eickwort, W. Haber, D. Roubik and A. Wille. Rodent visitors to _B. chlorantha_ were trapped in Sherman live traps, killed and preserved in alcohol. The trapped rodents and photographs were identified by Drs. A. Gardner and G. Musser. All animal vouchers were deposited at the American Museum of Natural History, New York City. Plants collected as voucher specimens were identified by Dr. J. J. Wurdack and deposited at the Museo Nacional, San Jose, and The New York Botanical Garden, New York City.

Breeding Systems

Tests were conducted for apomixis, self-compatibility (with a vector), autogamy (selfing without a vector) and self-incompatibility. Whenever possible, about 20 buds per plant on five plants per species were used for each test. The methods used were as follows:

1. To prevent animal interference pollen tector bags from the Carpenter Paper Co. were placed over mature buds. When necessary the bags were removed for hand manipulations, replaced and left for two weeks. Mature buds are those expected to open the next day.
   a. Apomixis: The anthers were removed from mature buds before covering with pollen tector bags.
   b. Autogamy: Mature buds were covered and left for two weeks.
   c. Self-compatibility: Pollen from the same flower or a flower on the same branch was placed on the stigma of the flower being tested.
   d. Self-incompatibility: The anthers were removed from mature buds. The following day pllen from another plant of the same species was placed on the stigma.
2. Individual buds were tagged with marked aluminum strips and flagging tape was tied to branches to indicate the location of the manipulated flowers. This enabled me to follow the fate of the fruits for many months.
3. Because the unfertilized ovary often remains on the plant

for three to four weeks, two months were allowed before an individual fruit was scored.

4. In those cases in which I wanted to germinate seeds, fine mesh was placed around branches with immature fruits. This did not seem to interfere with normal maturation and enabled me to collect the mature fruits before they fell or were eaten by birds.

The number of plants and flowers used were:

Blakea gracilis: On five plants 86 flowers were tested for self-compatibility, 103 for apomixis, 95 for autogamy and 103 were out-crossed.

Blakea anomala: Five plants were originally picked for these tests, but only two produced enough flowers for all tests. Therefore, 44 flowers on five plants were tested for self-compatibility, but only two plants were used for the other tests. On these 34 flowers were out-crossed, 44 tested for apomixis and 39 for autogamy.

Blakea grandiflora: Due to extreme weather conditions and vandalism in September, 1979 tests on this species were carried out during two seasons.

1979: On four plants 34 flowers were tested for self-compatibility, 93 flowers on five plants for apomixis and 59 flowers on three plants for autogamy. Tests for out-crossing were not performed.

1980: Seventy-four flowers on five plants were tested for self-compatibility.

Blakea tuberculata: Tests were conducted in two flowering seasons on the one reachable plant.

1979: Nine flowers were tested for autogamy, 7 for apomixis.

1980: Twenty-three flowers were tested for self-compatibility, but these were destroyed by vandals before the data could be collected.

Blakea chlorantha: Vandalism by humans and rodents, as well as extreme weather conditions prevented adequate tests on this species.

Topobea durandiana: On one plant 20 flowers were tested for apomixis and 16 for self-compatibility.

Topobea pittieri: Twenty-six flowers were used to test for autogamy and 39 for apomixis on two plants.

Topobea brenesii: Because of the high rate of self-compatibility and the large number of emasculated flowers which produced fruits, tests were conducted twice:

1979: On three plants 66 flowers were tested for autogamy, 28 for apomixis and 58 for self-compatibility.

1980: On five plants, 77 flowers were tested for autogamy, 107 for apomixis, 58 for self-compatibility and 60 were out-crossed.

Seed-Ovule Ratios and Seed Germination

Ten mature fruits were randonly collected from each plant on which breeding tests had been conducted. The number of ovules was estimated by counting the total number in one locule and multiplying by the number of locules (usually six). Seeds were counted individually in all locules, since they were not evenly distributed.

Mature fruits which resulted from the breeding tests were collected and their seeds and aborted ovules were counted in the same way. The data were analyzed using Analysis of Variance (Sokol & Rohlf, 1969).

Most mature fruits contained seeds and aborted ovules. The seeds and/or ovules were removed from mature fruits and separated by size. They were then soaked 15 to 18 hours in water, rinsed and placed on napkins in petri dishes. This was done for ten randomly chosen fruits per species that had been pollinated naturally, and for many of the mature fruits which resulted from the breeding tests.

UV Patterns and Other Photographs

UV photographs of the flowers of all species were taken using a Kodak 18A Wratten filter. Except for *B. chlorantha*, whose flowers opened over a period of two to three days, photographs were taken of the flowers of all species as they opened at dawn. Additional photographs were taken later in the day of flowers, fruits, buds and pollinators.

Photographs of rodent visitors to *B. chlorantha* were taken by focusing a red-filtered light and camera on one or two flowers and waiting for the rodents to appear. A 6 meter cable release was used to trigger the camera.

Pollen

Pollen was collected from all species and sent to I. Baker for chemical analysis and D. Carmichael for acetolysis. When bees were collected their pollen loads were removed and set aside to identify in New York. This was done to discover whether or not the bees were flower constant. The pollen was examined and photographed under SEM by A. Remec at The New York Botanical Garden, and measured under the light microscope.

Since the rodents had been trapped using live traps, they groomed themselves before they could be tested for pollen loads. Therefore, with the help of B. burns and D. Carmichael of New York University, the guts were removed and put through acetolysis to check for the presence of pollen.

Pollen was counted for pollen/ovule (P/O) ratios using a Coulter Counter at Memorial Sloan-Kettering Cancer Center. Ten flowers per species were used. One anther per flower was macerated, then rinsed and put through a 25 micron filter to remove debris. Four counts per anther were performed and the average was multiplied by 12 to give the average number of pollen grains per flower. Counts were verified with a haemocytometer for one anther per species.

BLAKEA

Results

Phenology

All species are evergreen. New leaves are produced and old leaves shed throughout the year.

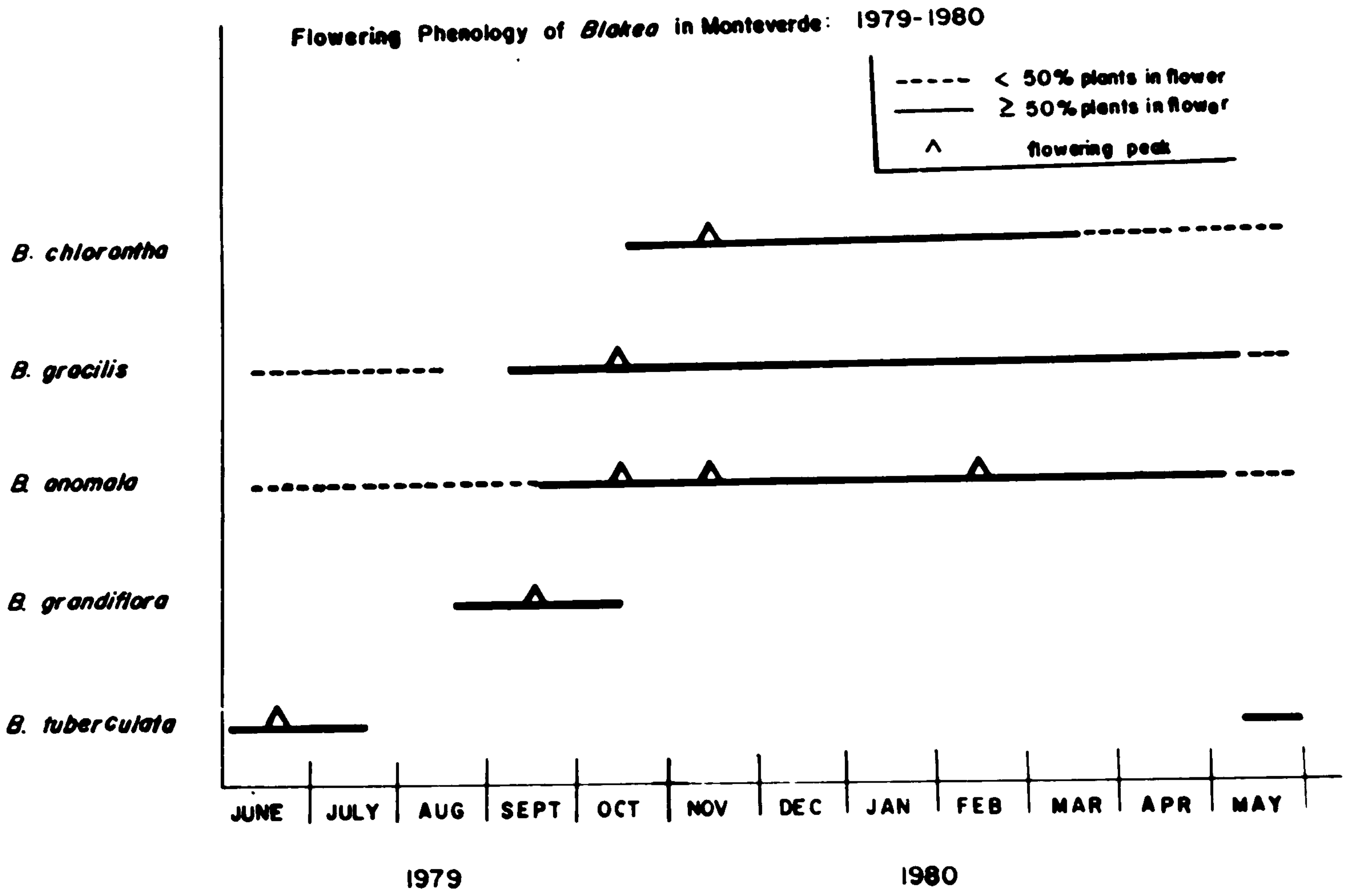
Two types of flowering patterns were observed (Fig. 15). Blakea grandiflora and B. tuberculata have short synchronized blooming periods lasting 4 to 6 weeks with a massive floral display, whereas B. anomala and B. gracilis have extended unsynchronized flowering cycles. Blakea anomala flowered throughout the year, but November, 1979 was the only month when all observed individuals were in bloom while in June, July and August, 1979 only one of the 5 observed plants flowered. Individuals of B. gracilis flowered for ten months. I was unable to correlate either altitude or exposure with the asynchrony for either species. Plants of the same species, growing side by side, had different flowering peaks.

Blakea chlorantha also blooms asynchronously, but for a shorter period. Flowers are produced from late October through May, and different plants peak in different months.

Immediately after flowering B. tuberculata produces large buds which remain on the plant for approximately ten months before opening, giving it the appearance of imminent flowering most of the year. This can be deceptive when viewing herbarium specimens.

In February and again in March, 1979 I collected branches with mature buds from a large individual of B. grandiflora. However,

Fig. 15. Floral phenology of *Blakea* species at Monteverde.


Flowering Phenology of *Blakea* in Monteverde: 1979-1980
----- < 50% plants in flower
—— ≥ 50% plants in flower
^ flowering peak
B. chlorantha
B. gracilis
B. anomala
B. grandiflora
B. tuberculata
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
1979
1980

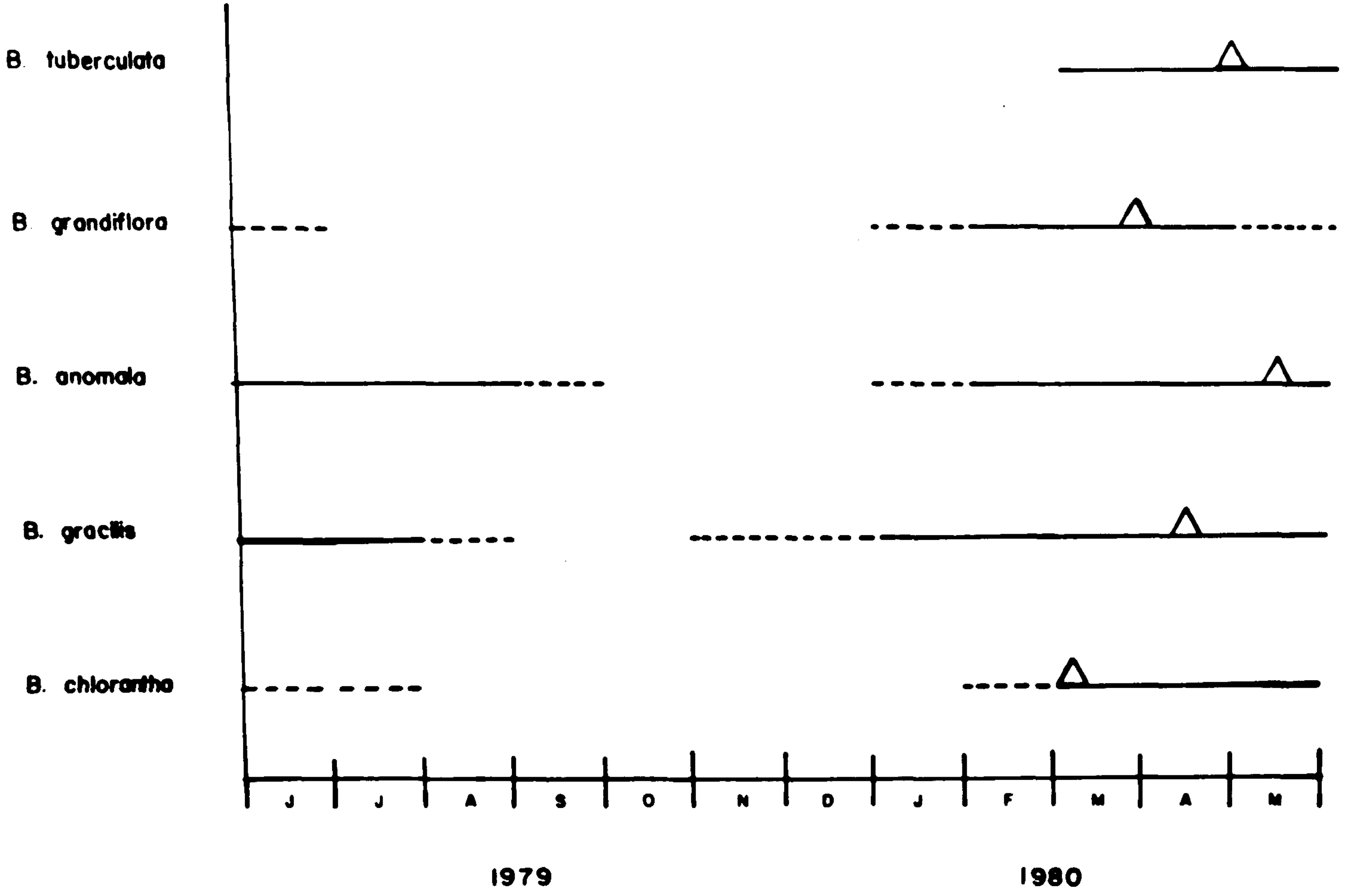
neither this nor any other individual of B. grandiflora flowered until the following September. These large buds eventually dropped and must have been 'left-overs' from the preceeding October. This is another example where herbarium specimens can be misleading.

The phenological patterns for mature fruits closely followed that of the flowers (Fig. 16). Blakea gracilis and B. anomala both bear mature fruits during a large part of the year, whereas B. tuberculata and B. grandiflora have mature fruits for only a few months. Blakea chlorantha is intermediate. All five species bear mature fruits between January and the end of May, the dry season in Monteverde.

Floral Visitors

Bee pollinated species: A wide variety of pollen collecting bees visit and pollinate the flowers of Blakea (Table 3). Blakea gracilis received the largest number of visitors ranging from the large Xylocopa frontalis to tiny halictid species. The bees collect pollen by the buzz method. They land on the anthers and vibrate their indirect flight muscles which causes pollen to shoot out of the anthers and dust the bees ventrally (Buchmann, 1974; Michener, 1962; Wille, 1963). The bees then clean themselves, usually while hovering in front of the flower, but sometimes while hanging on to a leaf by their mandibles. The larger bees (Xylocopa frontalis, Euleama polychroma, E. seabrai, E. cingulata, Epicharis spp. and the queens of Bombus ephippiatus and B. volucelloides) visited four to ten flowers per visit to a plant, spending from three to fifteen

Fig. 16. Mature fruit phenology of *Blakea* species at Monteverde. Solid lines indicate 50% or more observed plants carried mature fruit. Dashed lines indicate less than 50% of observed plants carried mature fruit. Triangles show peak fruiting periods.


B. tuberculata
B. grandiflora
B. anomala
B. gracilis
B. chlorantha
J
J
A
S
O
N
D
J
F
M
A
M
1979
1980

seconds on a flower. The body of these large bees covers the stigma and all or most of the anthers. The smaller bees (*Melipona fasciata*, *B*. *ephippiatus* and *B*. *volucelloides* workers, halictid and *Trigona* species) visit many flowers per visit to a plant, often returning again and again to the same flower. Exceptions were *Trigona grandipennis* which gleaned pollen left on the petals by the activity of other bees, and *T*. *fulviventris*, which bored a hole in the stamens and removed the pollen with its proboscis. Neither of these species were pollinators and both were rare visitors.

Eight bee species were seen collecting pollen from the flowers of *B*. *anomala* of which five were regular visitors. These bees were also recorded on flowers of *B*. *gracilis* (Table 3, Fig. 17). The bees foraged in the same manner as at *B*. *gracilis*, the larger bees stopping at fewer flowers for a shorter time and the smaller bees spending an extended time on the plant, returning to the same flowers more than once.

Only four species were recorded at the flowers of *B*. *tuberculata*. These were the large *Xylocopa frontalis*, *Euleama seabrai*, *Bombus volucelloides* queen and the relatively small worker bee *B*. *ephippiatus*. Hummingbirds were observed on the flowers of one plant at 6:00 a.m.

The queen of *Bombus volucelloides* was the only large bee seen visiting *Blakea grandiflora* and this was a single observation. The major visitors were the *Bombus ephippiatus* worker, *Melipona fasciata* and two halictid species.

Table 3

Hymenoptera Visitors to *Blakea* at Monteverde

	Blakea anomala	Blakea gracilis	Blakea tuberculata	Blakea grandiflora
LARGE BEES				
Bombus ephippiatus Q	+	+	-	-
B. volucelloides Q	+	+	+	R
Euleama seabrai	+	+	+	-
E. polychroma	-	+	-	-
E. cingulata	-	+	-	-
Xylocopa frontalis	-	+	+	-
Epicharis sp.	+	+	-	-
MEDIUM BEES				
Bombus ephippiatus	+	+	+	+
B. volucelloides	-	+	-	-
Ptiloglossa ducalis	-	+	-	-
Melipona fasciata	+	+	-	+
M. flavipennis	R	-	-	-
SMALL BEES				
Neocorymura rupa	+	-	-	R
Coeraugochlora sp.	-	-	-	R
Trigona fulventris	-	+NP	-	-
T. grandipennis	-	+NP	-	+NP
Examolopsis sp.	-	+?	-	-

R = Rare
NP = Not pollinator

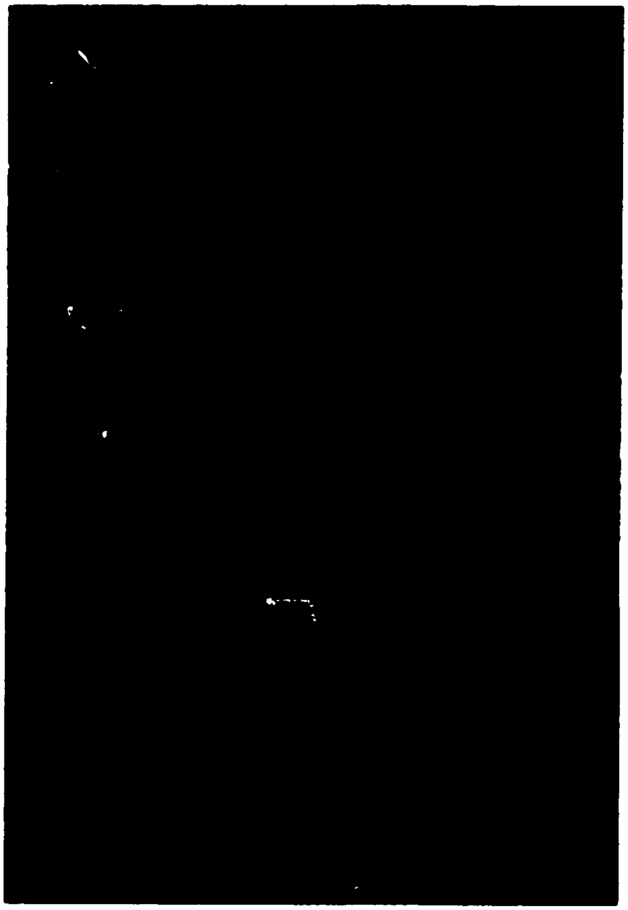


Fig. 17. Hymenoptera recorded on Blakea anomala and Blakea gracilis.

The mark and recapture studies performed on bees visiting Blakea gracilis were not highly successful. Marked bees immediately cleaned themselves of paint while sitting on the grass or hanging on to a leaf by their mandibles.

However, on one occasion when both fluorescent powder and paint were used, the following results were obtained:

An individual of Euleama seabrai was captured carrying pink fluorescent powder from another plant. It was marked with red paint and released. Within a few minutes it was recaptured on the first plant still marked with fluorescent powder plus red paint. Another individual of E. seabrai was recaptured returning to the same plant and one individual of Epicharis sp. was captured, marked and recaptured on another plant.

On the day that member of the Monteverde community assisted with these experiments, only one bee, Epicharis sp., was captured with paint marks indicating a previous visit to another monitored plant. However, a number of individuals of Euleama seabrai, Epicharis sp. and Melipona fasciata were recaptured on revisits to the same plant.

The number of species and the number of individuals per species, visiting different plants of Blakea gracilis during the same hours on the same day varied (Table 4). For instance, of five plants monitored, Epicharis sp. was recorded 17 times on one individual, 8 times on another, once on two other plants and not at all on the fifth.

Table 4

Bees captured during mark and recapture sessions on *Blakea gracilis*

	PLANTS				
Bees	#1	#2	#3	#4	#5
Epicharis sp.	>17	8	1	-	1
Bombus volucelloides Q	2	1	1	-	-
Euleama seabrai	4	2	2	1	6
B. ephippiatus	-	-	-	-	2
Xylocopa frontalis	-	3	-	-	1
Melipona fasciata	-	>5	-	-	-

Rodent pollinated species: The important visitors to Blakea chlorantha were three species of rodents, Peromyscus mexicanus Huckaby (= P. nudipes J. P. Allen) (Fig. 18). Oryzomus devius Bangs (Fig. 19) and an unidentified rodent (Fig. 20). Nocturnal observations yielded 22 sightings of rodents visiting flowers. Trapping netted two species: Oryzomus devius and Peromyscus mexicanus.

Diurnal visitors were infrequent. The bumblebee Bombus ephippiatus was seen twice on one plant, and two species of hummingbirds were recorded three times on two of the seven observed plants.

The stamens of Blakea chlorantha form a complete ring around the style, which is exserted 3 to 4 mm beyond the stamens. Pollen is released explosively without vibration, by pressure on the outside of the petals or by slight pressure at the base of the staminal filaments. This can be demonstrated by placing a dissecting needle at the base of the filaments. When the rodents grasp the flowers in their front paws they put pressure on the outside of the petals which causes a cloud of pollen to be released (Figs. 18-20). Pressure at the base of the filaments, in the area where nectar is produced, occurs when the rodents probe with their tongue for nectar. Nectar volume varies from 27 to 161 microliters per flower per night for both first and second day flowers. Analysis of the nectar by I. Baker indicates that it is sucrose rich

$\left(\frac{\text{Sucrose}}{\text{Glucose + Fructose}} = \frac{.431}{.295 + .274} = .759\right).$

Fig. 18 - 20. Rodents visiting flowers of *Blakea chlorantha*.

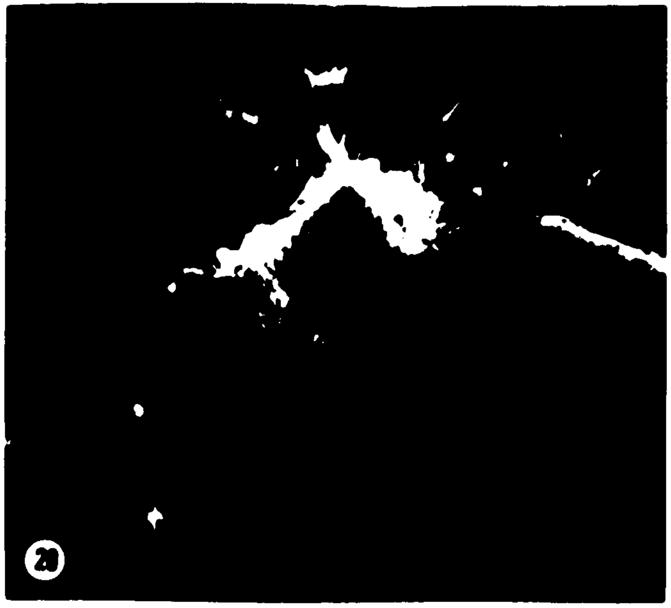
Fig. 18. *Peromyscus mexicanus*.

Fig. 19. *Oryzomus devius*.

Fig. 20. Unidentified rodent. Note exserted tongue.


⑱


⑲


⑳

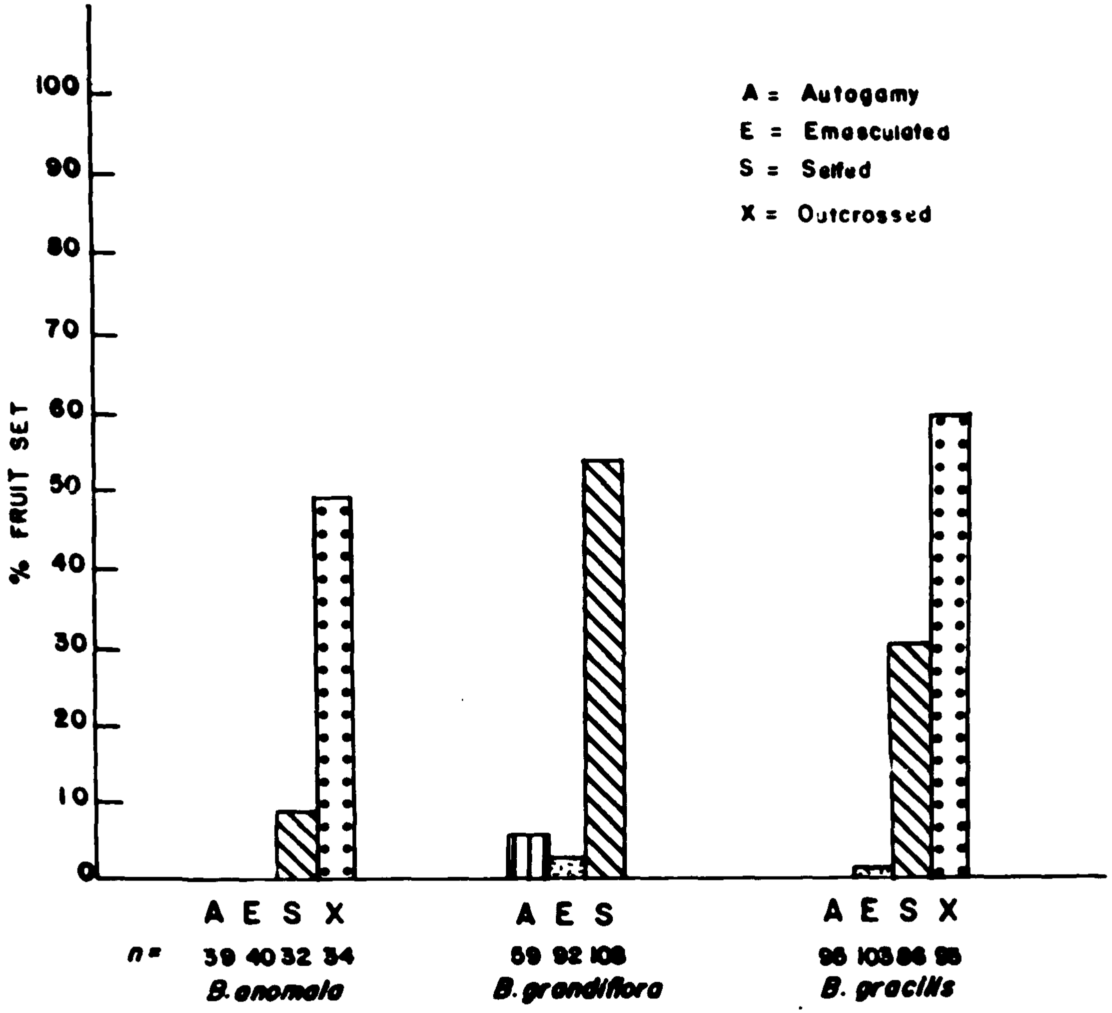
Breeding Systems

The results of the breeding system experiments for *Blakea anomala*, *B. gracilis* and *B. grandiflora* are shown in Fig. 21. The three species are self-compatible with a vector, although to varying degrees. Self-pollinations resulted in 54.6% fruit set for *B. grandiflora*, 31.4% for *B. gracilis* and 9.4% for *B. anomala*. *Blakea grandiflora* was the only species capable of autogamy with 6.8% of unmanipulated flowers setting fruit. *Blakea gracilis* and *B. grandiflora* both produced a small number of mature fruits without seeds from emasculated flowers (*B. gracilis* 1.9%; *B. grandiflora* 3.3%).

Unfortunately, the data for *B. chlorantha* and *B. tuberculata* could not be quantified. Although I hand pollinated for self-compatibility and noted tagged fruits about seven weeks later, vandals destroyed the data before it could be recorded. Therefore, although I lack precise figures, I consider these species to be self-compatible. Neither species was autogamous or apomictic.
All five species produce adventitious roots and are presumed to be capable of vegetative reproduction.

Germination experiments confirm that many ovules are aborted (Fig. 22). Seeds of all species germinated within four to seven days. The seed to ovule ratios are shown in Table 5. Analysis of variance indicates a lack of statistical correlation between the number of ovules and the number of seeds per fruit for any of the species. In addition, for *B. gracilis* there was no significant difference in percent seed-set between fruits from flowers I had

Fig. 21. Breeding systems of _Blakea_ species at Monteverde.


A = Autogamy
E = Emasculated
S = Selfed
X = Outcrossed
% FRUIT SET
100
90
80
70
60
50
40
30
20
10
0
A E S X
n= 39 40 32 34
B. anomala
A E S
59 92 108
B. grandiflora
A E S X
96 103 86 95
B. gracilis

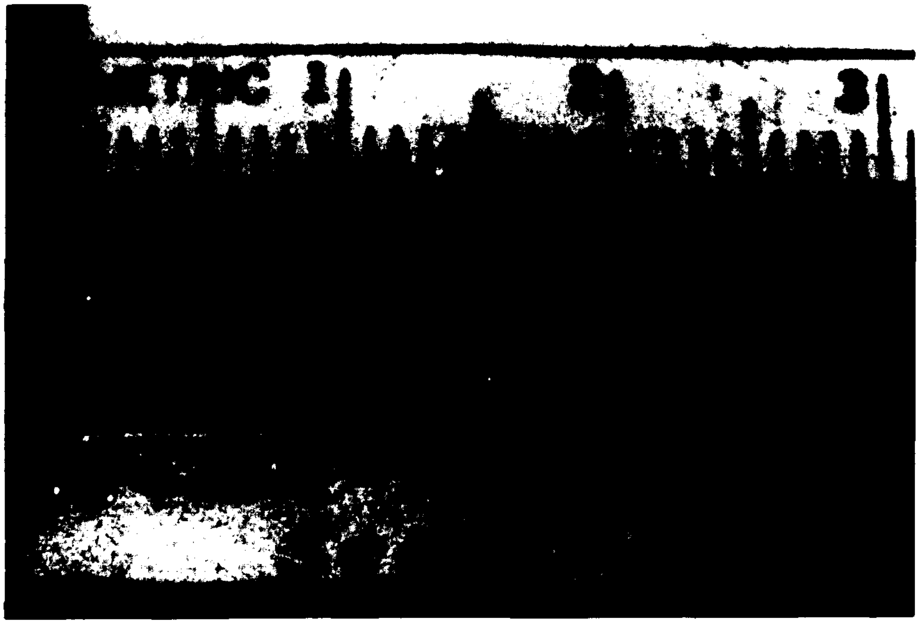


Fig. 22. Seeds and undeveloped ovules of Blakea tuberculata.

Table 5

Seed-Ovule Ratios of *Blakea*

BLAKEA ANOMALA	OPEN	OUTCROSSED	SELFED	F	P	S/NS
n	20	8	3	.068	.946	NS
$\bar{x}$ ovules	1072	1318	1412			
$\bar{x}$ seeds	94.1	108.1	113.6			
% seeds	8.8	8.2	8.1			
BLAKEA GRACILIS						
n	17	6	13	.125	.899	NS
$\bar{x}$ ovules	1877.1	1814.3	1428.3			
$\bar{x}$ seeds	282	266.5	212.5			
% seeds	15	14.7	14.9			
BLAKEA GRANDIFLORA						
n	19		14	.190	.674	NS
$\bar{x}$ ovules	2831.8		2322.9			
$\bar{x}$ seeds	194.2		140.1			
% seeds	6.9		6.0			
BLAKEA TUBERCULATA						
n	18					
$\bar{x}$ ovules	4579.6					
$\bar{x}$ seeds	209.1					
% seeds	4.57					

out-crossed, from flowers I had self-pollinated and from randomly picked fruits (F=.125, P=.899). The same was true for B. anomala (F=.068, P=.946) and for the selfed and randomly picked fruits of B. grandiflora (F=.190, P=.674).

Absence of UV Patterns

Photographs taken with a UV filter did not reveal UV absorption patterns for any of the species.

Information from Photographs

Although I observed the rodents visiting the flowers of Blakea chlorantha, it was not practical to stand closer than about ten feet from the plant. Photographs of the rodent visits are important because they reveal the way the animals behave with the flowers. Three photographs were clear of rain and mist (Figs. 18-20). In these the rodents are holding the flower in their front paws. In one photograph, the sound of the cable release caused the rodent to move its head out of the flower, and the extended tongue is visible (Fig. 20).

Pollen of Blakea and Topobea

The pollen ranges from 11 to 21 microns in diameter (Table 6). They have very similar exines and are tricolporate (Figs. 23-29). With the exception of B. tuberculata, the pollen of the different species cannot be distinguished from one another by either size or exine sculpturing. Therefore, the pollen loads which I removed from the captured bees could not be used to determine whether the bees

Fig. 23 - 29. SEM of pollen grains of *Blakea* and *Topobea* species at Monteverde. All x3000.

Fig. 23. *B. anomala*.

Fig. 24. *B. chlorantha*.

Fig. 25. *B. gracilis*.

Fig. 26. *B. grandiflora*.

Fig. 27. *B. tuberculata*.

Fig. 28. *T. brenesii*

Fig. 29. *T. durandiana*

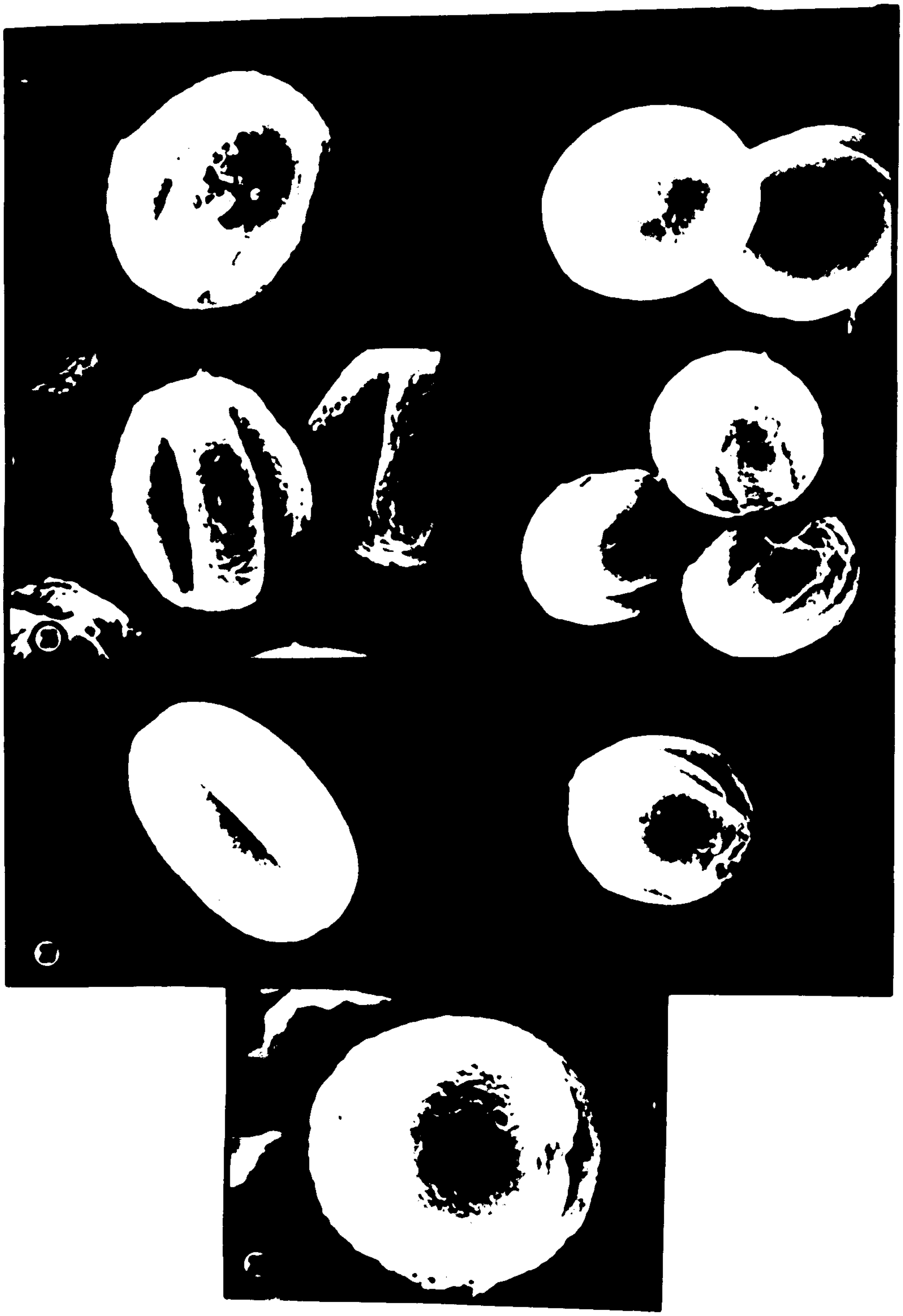


Table 6

Average Pollen Diameters of Blakea and Topobea

Blakea anomala	18 microns
B. gracilis	19 "
B. grandiflora	14 "
B. tuberculata	21 "
B. chlorantha	14 "
Topobea brenesii	14 "
T. pittieri	11 "

visited more than one species of Blakea or Topobea per trip. However, examination of the pollen loads did show very few pollen grains which were not from Blakea or Topobea.

Analysis of the guts of the three trapped rodents showed that the rodents had injested Blakea pollen, as well as the pollen of at least three other plant species.

Pollen-ovule ratios are high (Table 7). These ratios can be interpreted in many ways. For instance, weedy plants tend to have a high P/O and the P/O of self-compatible plants tends to be lower than the P/O of an obligate out-crosser in the same taxa (Cruden, 1976, 1977). However, we do not have the P/Os of enough species of Blakea and Topobea to make this kind of analysis. Nor do we have the P/Os for other melastomes or other species in Monteverde. The high P/O may in fact, be related to the method of pollen ejection. I plan to carry out work on the P/Os of buzz-pollinated plants.

Table 7

Pollen-Ovule Ratios of Blakea

	$\bar{x}$ Pollen Grains (P)	$\bar{x}$ Ovules (O)	P/O
B. anomala	4,528,800	1072.6	4222.26
B. gracilis	6,025,200	1877.1	3209.84
B. grandiflora	5,715,600	2831.75	2018.40
B. tuberculata	5,176,800	4420.5	1171.09
B. chlorantha	3,684,240	706.	5218.47

DISCUSSION

Many authors have discussed ways in which closely related plants avoid or lessen competition for pollinators (Gentry, 1974, 1976; Grant & Grant, 1965; Heinrich, 1975; Waser, 1978). The most obvious strategy is to have different pollinators. In this regard, the rodent-pollinated *Blakea chlorantha* is effectively removed from competition with its congeners.

However, the remaining four species of *Blakea*, three of which are sympatric, share many of the same pollinators. Since there is no evidence of hybridization, and seed-set is not pollinator limited, the staggered blooming periods of these species are probably an effort to minimize competition for pollinators in an environment in which pollinator activity is often unpredictable (Cruden, 1972).

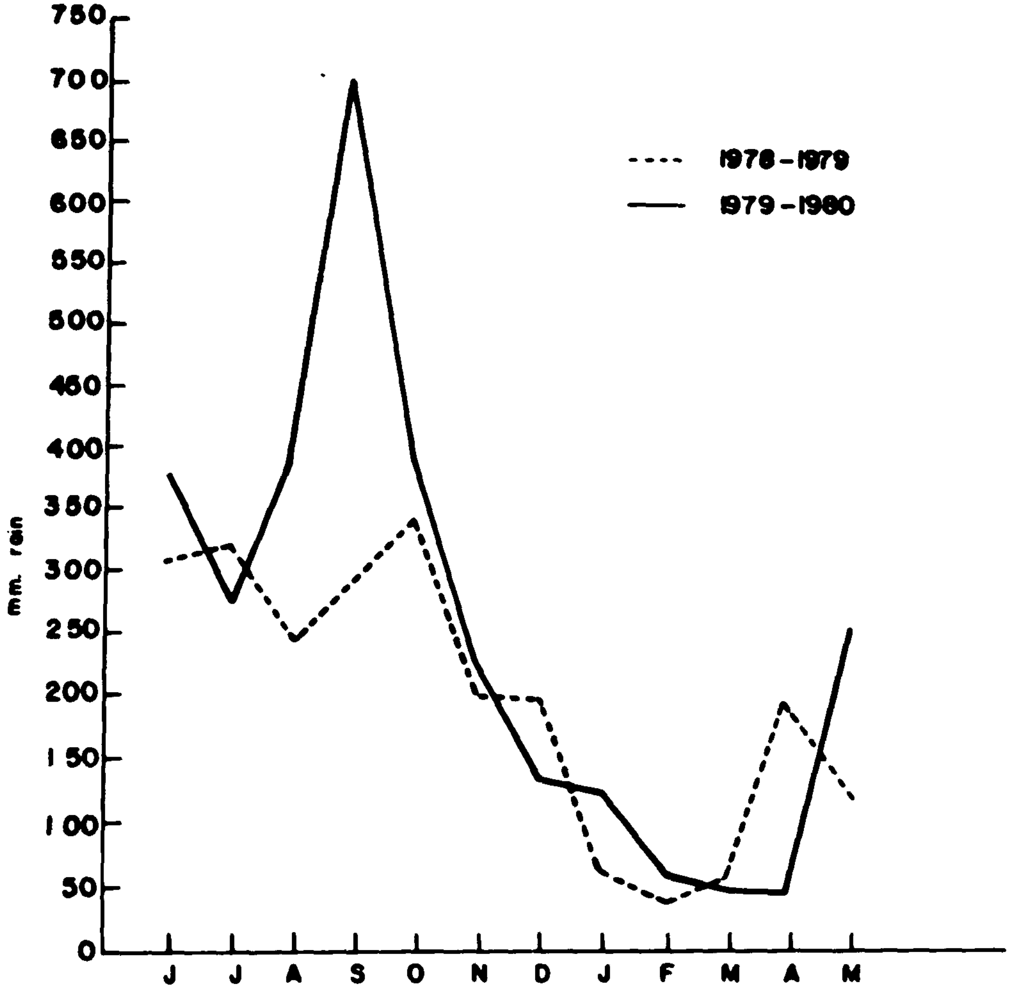
By flowering synchronously for brief periods and in different months, *B. grandiflora* and *B. tubercülta* avoid competition with each other (Fig. 15). The extended flowering period of *B. anomala* does overlap somewhat with that of these two species, but the overlap is at a time when few plants of *B. anomala* are in bloom, so that essentially the flowering periods of the three species are separate. For example, one tree contained a very large individual of *B. grandiflora* and a smaller individual of *B. anomala*. On this tree, *B. anomala* did not bloom until *B. grandiflora* was finished flowering.

Blakea gracilis occupys a different habitat, that of the wet montane forest below the cloud forest and therefore it is not in direct competition with the other species for pollinators. However, a number of large plants of B. gracilis and B. anomala grow in close proximity in a large pasture which can be considered a transition zone between cloud forest and wet montane forest. Probably their extended flowering periods, as well as their self-compatibility enables them to co-exist in this area.

Blakea gracilis is the only species found in the wet montane forest below the Reserve. The winds here are less harsh and the weather slightly more predictable than in the cloud forest. This is reflected in the greater number of bee species which were recorded at the flowers of B. gracilis. In contrast, the relatively fewer visitors to B. grandiflora may be the result of the weather, as well as its short flowering period. Rainfall in September, 1979 (Fig. 30) was >700 mm, while in September, 1978 it was <300 mm. It is possible that in other less climatically extreme years, the flowers of B. grandiflora are visited and pollinated by a greater number of bee species than I observed (Fig. 30).

One assumption at the start of this study was that the differences in floral size, texture and anther position among the bee-pollinated species would be correlated with differences in pollinator size and perhaps with mode of pollination. This has proved not to be the case. The four bee-pollinated species were pollinator generalists, receiving visits from the same species of large, medium and small bees. The very large flowers of B. grandiflora were visited, with only one exception, by the small to medium sized Bombus ephippiatus, Melipona fasciata and very small halictid

Fig. 30. Average monthly rainfall at Monteverde, 1978-1980.


750
700
650
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300
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200
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100
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mm. rain
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1978-1979
1979-1980

bees. Although B. tuberculata has the largest flowers with very thick, leathery petals, Bombus ephippiatus was a common visitor, along with larger bees. In this species, the stamens do not move toward one end of the flower, as in most blakeas, but remain in a circle around the pistil. This in no way affected the method and approach of the bees, who worked the flowers exactly as they did those of the other species.

Since the Blakea species in this study are self-compatible to varying degrees, large, medium and small bees are effective as pollinators. The smaller bees tend to remain a long time on one plant, going from flower to flower, often returning to the same flower more than once. Their role appears to be largely one of selfing. Larger bees, such as Xylocopa and Euleama, visit fewer flowers per plant. While these bees are probably involved in some amount of selfing, judging by their behavior they are likely to be effective agents of out-crossing.

The discovery that Blakea chlorantha is pollinated by rodents was unexpected and work on this topic should be pursued further. More information is needed both in regard to the distance rodents travel between plants and as to whether all rodent species which visit low plants also visit plants in the upper canopy. Additional trapping is needed before it can be decided whether the flowers of B. chlorantha are visited by more rodent species than the three we now know of. In addition, analysis of the rodent guts produced pollen from plants other than B. chlorantha. It appears that nectar may be an important part of the rodents' diet, but further information is needed on their ecology and feeding habits.

The information I have gathered to date indicates that rodents are the major pollinators of *B. chlorantha*. In the last few months I have received information that hummingbirds and tanagers also visit the flowers of *B. chlorantha* in a different part of the Reserve than where I worked (B. Busby, pers. comm.), and I observed hummingbirds three times on two plants. Since hummingbirds are known to be opportunistic feeders and unused nectar often remains in the flowers the next day, this is not unexpected. However, *B. chlorantha* with its cryptic flowers is clearly not adapted to bird pollination and visitation by birds is casual.

The bumblebee, *Bombus ephippiatus*, ignored the nectar and attempted to vibrate the anthers. While the bees were awkward, due to the shape of the flower, they did receive a dusting of pollen due to the explosive mechanism of pollen release and may occasionally be responsible for pollination, if the stigma is receptive at that time. I do not have information about stigma receptivity. However, these flowers last for two nights and pollen is available during the day following the first night. Therefore, it is probable that the stigma is receptive at that time. The fact that the bees ignore the nectar, as well as their rare occurrence and awkward handling of the flowers indicate that bees cannot be considered the major pollinators of this species.

The visits of opportunistic birds and bees in no way detracts from rodents being the major pollinators of *Blakea chlorantha*.

Since pollen presentation and nectar production occur at night it is clear that these flowers have evolved with a nocturnal pollinator. Very few plants have evolved such a tight fit with their pollinators that they exclude all other visitors (Baker & Hurd, 1966).

Little is known of the habits and movements of rodents in Central American cloud forests. At this time, photography and trapping indicate that three species of rodents visit *Blakea chlorantha*, but it is possible that other rodent species are also involved.

Preliminary data indicate that *Blakea chlorantha* is self-compatible, as are the other Blakea species at Monteverde. While my observations lead me to believe that the rodents do move from plant to plant and do effect cross-pollination, this has yet to be proved. It is clear, however, that the rodents are involved in the transfer of pollen from one flower to another on the same plant.

The animals are very fast, do not hesitate and do not stop at closed buds or old flowers. As part of the study to determine self-compatibility, flowers were covered with brown paper pollination bags. When all, or the majority of flowers on a plant were covered, the bags were found ripped open. Rodent teeth marks were on the ripped bags.

Although the flowers do not have an odor discernable to humans, it is possible that they have an odor detectable to rodents. Rodents are known to have an acute sense of olfaction (Dr. G. Musser, pers. comm.) and this appears to be the only possible signal by which they could have known the bags contained flowers.

The nectar of Blakea chlorantha is sucrose-rich, as is the nectar of the rodent-pollinated Proteaceae, whereas the nectar of bat-flowers is known to be hexose-rich (Dr. H. Baker, pers. comm.). This is compatible with the hypothesis that these flowers have evolved as rodent-flowers.

Sussman and Raven (1978) suggest that non-volant mammals may prove to be important pollinators in "areas where flower-bats are rare or absent and consequently do not compete for resources". Dr. H. Baker (pers. comm.) further suggests that the harsh,windy environment where B. chlorantha grows may indeed favor the tightly grasping rodents over bats. Because little is known of the bat population in the Monteverde Cloud Forest Reserve, it is not possible to say at this time if such a correlation exists.

The Monteverde Cloud Forest Reserve is an area of almost constant rain or mist, and variable often extreme wind. Bees are known to be unpredictable pollinators in such climates (Cruden, 1972; Heinrich & Raven, 1972). Therefore, it is not surprising to find that the four bee-pollinated species, as well as the rodent pollinated B. chlorantha have flexible reproductive modes. Three species have extended flowering periods. All five are pollinator generalists, self-compatible and presumed to be capable of vegetative reproduction. Blake grandiflora, which has the greatest degree of self-compatibility, was the only autogamous species. Since it blooms during the rainy season, its ability to be autogamous, as well as self-compatible may be a necessary adaptation to the extreme weather conditions. Blakea anomala, on the other hand, blooms all or most of the year and displayed the least amount of self-compatibility.

When tested for apomixis, both B. gracilis and B. grandiflora set a small number of fruits without seeds. These ovaries mature and look like normal fruit, but the ovules remain undeveloped. The ecological reasons for this remain obscure. Possibly this helps to assure dispersal by helping to attract the avian dispersers even in times of low fruit set of out-crossed and selfed flowers.

Blakea flowers produce numerous small seeds contained in an attractive fleshy fruit. The proportion of seeds to ovules is quite low, but the overall number of seeds per plant is high.

Seed-set was not pollinator limited since the number of seeds per fruit which resulted from controlled pollinations was not significantly different from that of fruits which developed from bee-pollinated flowers.

For Blakea gracilis and B. anomala the proportion of seeds to ovules was not influenced by whether the flower was out-crossed or selfed, and seeds produced from both types of pollinations germinated in the same amount of time.

TOPOBEA

Results

Of the three species of Topobea in the Monteverde area, only T. brenesii was studied in detail. I found four plants of T. pittieri, but only one was large enough to produce flowers regularly. This species had not been previously recorded in the Reserve and might be in the process of becoming established. On the other hand, three of the four individuals grow in cut-over areas on the continental divide where they are presently being overtaken by many other plants, especially Smilax sp., which I constantly cut back. The fourth plant was very small, grew in the shade on a tree in the cloud forest proper and never produced flowers.

Topobea durandiana was found in February, 1980 growing at the lower edge of the Monteverde community. Although this area was not originally included in my research I added the one accessible plant to this study.

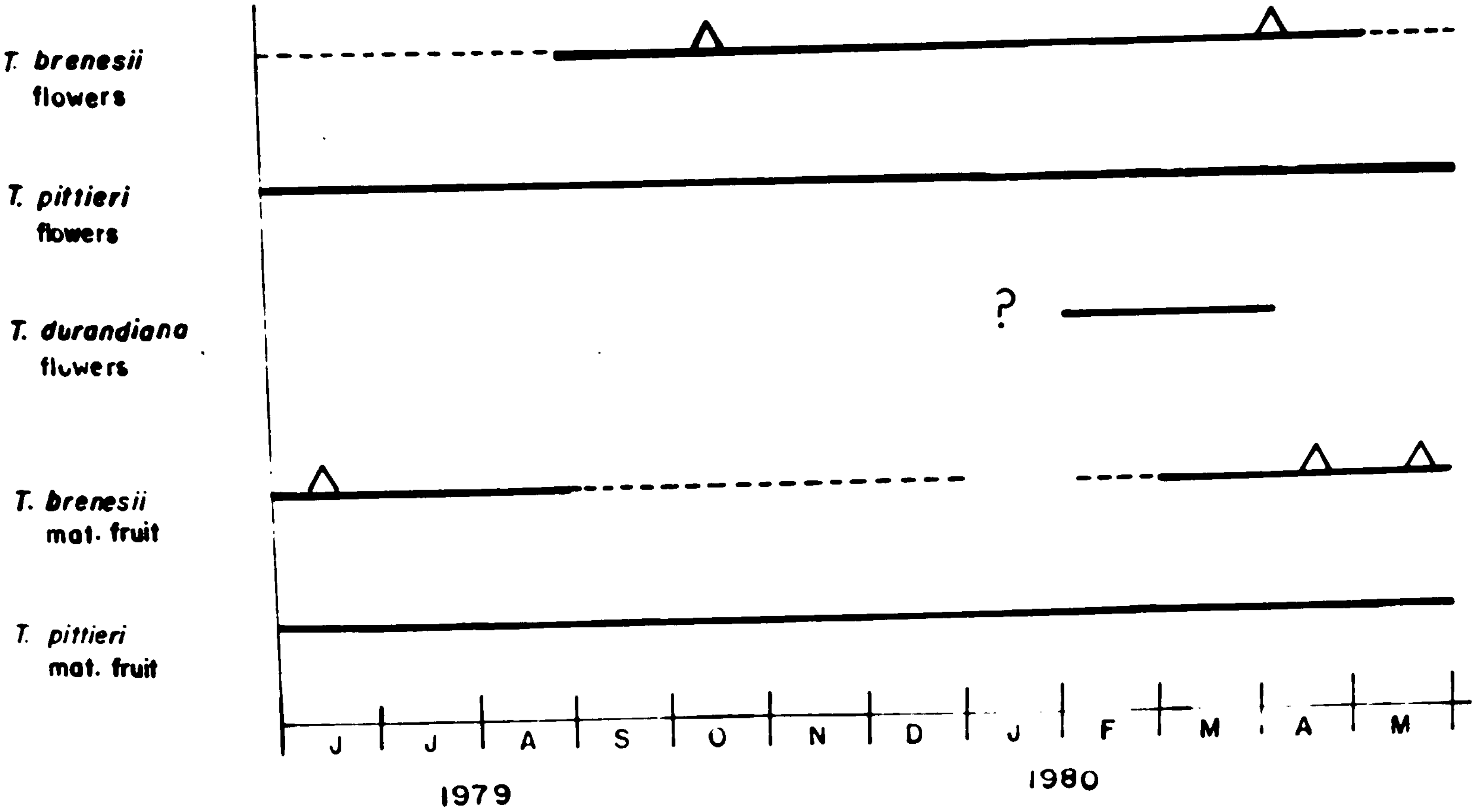
Phenology

As with Blakea, the plants are evergreen, shedding old leaves and producing new leaves throughout the year.

The one large plant of T. pittieri flowered throughout the year, producing a few flowers almost every day (Fig. 31).

Topobea durandiana was in flower when located in February, 1980 and finished flowering in April. I do not know when this species

Fig. 31. Floral and mature fruit phenology of _Topobea_ species at Monteverde.



T. brenesii flowers
T. pittieri flowers
T. durandiana flowers
?
T. brenesii mat. fruit
T. pittieri mat. fruit
J
J
A
S
O
N
D
J
F
M
A
M
1979
1980

began to flower, but I am inclined to believe that flowering was at its peak in February.

Topobea brenesii has an extended asynchronous flowering season similar to that of *Blakea anomala* and *B. gracilis*. There were individuals which flowered the entire year and others which flowered for five to six months. Flowering peaks occurred in April and October.

Fruiting phenology closely followed the flowering patterns (Fig. 31) for *T. pittieri* and *T. brenesii*. *Topobea pittieri* produced a small number of mature fruits daily. *Topobea brenesii* produced mature fruits most of the year with a peak from April to June. These data are not available for *T. durandiana*.

Floral Visitors

The same species of bees that visit and collect pollen from *Blakea* flowers were recorded at *T. brenesii* flowers (Table 8).

They approach and manipulate the anthers of *T. brenesii* exactly as they do those of *Blakea*. As with *Blakea*, large bees visited fewer flowers for a shorter time than smaller bees, and the number of visitors was greater during peak flowering times. Large bees were *Xylocopa frontalis*, *Eulaema polychroma*, *E. seabrai*, *Epicharis sp*. and the queens of *Bombus ephippiatus* and *B. volucelloides*. Other important visitors were the medium sized *B. ephippiatus*, *Melipona fasciata* and smaller *Trigona* and halictid species. Sometimes *T. grandipennis* gleaned pollen left on the petals by the activity of other bees, and at other times it

Table 8

Hymenoptera Visitors to Topobea brenesii

Bombus ephippiatus (queen and worker)

B. volucelloides (queen only)

Euleama polychroma

E. seabrai

Xylocopa frontalis

Epicharis sp.

Pseudaugochloropsis nigerrima

Trigona grandipenis

Crawfordopsis sp.

Melipona fasciata

vibrated the anthers to release the pollen. *Crawfordopsis sp.* was the only floral visitor to *T. brenesii* not seen on *Blakea* flowers.

Only the halictid, *Pseudaugochloropsis nigirima* and *Euglossa sp.* were collected from the flowers of *Topobea durandiana*. However, six other species were observed on this plant, but were too high to collect. These included *Xylocopa frontalis* and *Euleama seabrai*.

Although I spent many days in the vicinity of *T. pittieri* not one floral visitor was observed. In addition to the time set aside to observe this species, I passed the plants regularly during all months of the year, and always stopped in the hope of seeing a floral visitor, but unfortunately, I was never rewarded with a sighting.

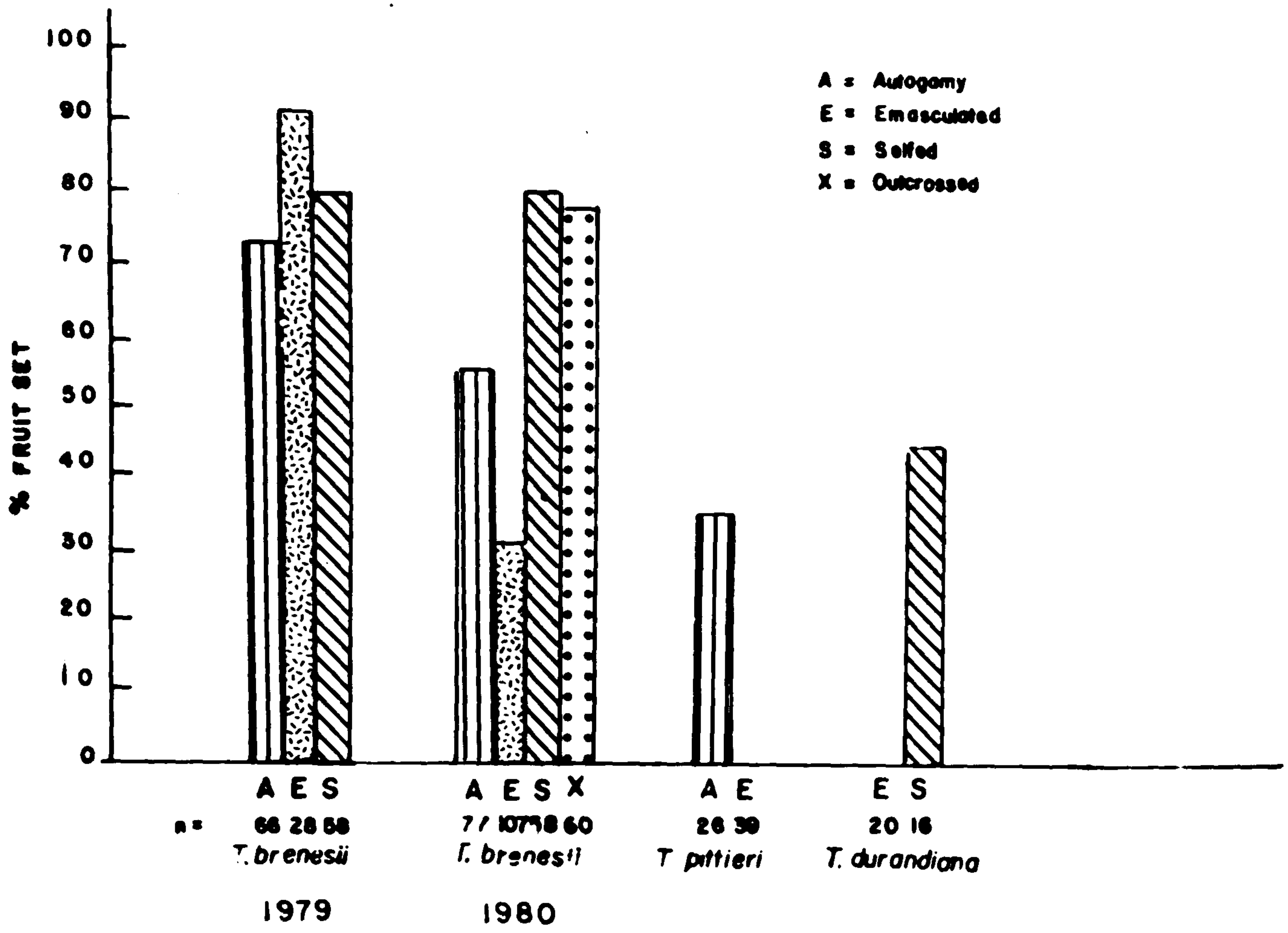
Breeding Systems

Topobea brenesii and *T. durandiana* are self-compatible (Fig. 32). Selfing experiments were not performed on *T. pittieri*, but 35% of unmanipulated bagged flowers produced mature fruits with seeds.

Topobea durandiana set seed in 44.8% of selfed flowers.

Topobea brenesii is capable of autogamy and is also able to produce mature fruits without seeds from emasculated flowers. I tested this species in April, 1979 and again in April, 1980. Both times 81% of selfed flowers set seed, but the percent of seed set for autogamy was higher in 1979 (74.2%) than in 1980 (55.8%), as was the percent of emasculated flowers which produced seedless fruits

Fig. 32. Breeding systems of *Topobea* species at Monteverde.


% FRUIT SET
100
90
80
70
60
50
40
30
20
10
0
A = Autogamy
E = Emasculated
S = Selfed
X = Outcrossed
A E S
n = 66 28 68
T. brenesii
1979
A E S X
71 107 98 60
T. brenesii
1980
A E
26 30
T pittieri
E S
20 16
T. durandiana

(1979, 92.9%; 1980 31.8%).

Seed-ovule ratios are shown in Table 9. There was no statistical correlation between the number of ovules and the number of seeds for these species. However, in the case of *T. brenesii* there was a strong correlation in seed set for fruits which developed from flowers I had selfed and randomly picked fruits (F=.0813, P=.781), as well as a correlation in seed set between fruits from flowers I had out-crossed and fruits which developed through autogamy (F=.0327, P=.854). Seeds germinated in 4 to 7 days.

Absence of UV Patterns

The results of UV photographs were the same for *Topobea* as for *Blakea*, i.e. there were no differences in floral patterns between the UV and normal photographs.

Pollen

The pollen diameters are shown in Table 6. They are similar to those of *Blakea* and cannot be distinguished from each other or from *Blakea* pollen. Examination of pollen loads collected from bees visiting *T. brenesii* showed that the bees did not carry more than a few grains other than that of *Topobea* and/or *Blakea* pollen. Table 10 shows P/O ratios for *Topobea*.

Table 9

Seed-Ovule Ratios of *Topobea*

TOPOBEA BRENESII

	OPEN(O)	OUT-CROSSED(X)	SELFED(S)	AUTOGAMOUS(A)
n	27	10	26	10
$\bar{x}$ ovules	1016.	952.	1119.9	1153.
$\bar{x}$ seeds	174.6	42	174.1	44.
% seeds	17.1	4.4	15.5	3.8

Analysis of Variance

	n	F	P	S/NS
X O	10 27	26.7	0	S
X S	10 26	28.4	0	S
X A	10 10	.033	.854	NS
S A	26 10	30.44	0	S
S O	26 27	.0813	.781	NS
A O	10 27	28.42	0	S

TOPOBEA PITTIERI

	OPEN
n	14
$\bar{x}$ ovules	1013.6
$\bar{x}$ seeds	64.3
% seeds	6.34

TOPOBEA DURANDIANA

	OPEN
n	10
$\bar{x}$ ovules	1973.6
$\bar{x}$ seeds	332.8
% seeds	16.9

Table 10

Pollen-Ovule Ratios of *Topobea*

	$\bar{x}$ Pollen Grains (P)	$\bar{x}$ Ovules (O)	P/O
T. brenesii	3,630,000	1057.80	3431.65
T. pittieri	2,778,000	1022.57	2716.68

Discussion

The three species of *Topobea* in the Monteverde area do not compete for pollinators. *Topobea durandiana* grows well below the other two species at an altitude of 1320 meters, and *T. pittieri* is rare. While I assume that there are more plants than the four I found, I would still consider it uncommon.

Topobea brenesii, on the other hand, grows throughout the Reserve, as well as in transition zones between the cloud forest and wet montane forest. Its range, as well as its floral and vegetative phenology are similar to that of *Blakea anomala*.

The reproductive biology of *Topobea brenesii* is the most flexible of all the species studied, displaying the greatest degree of self-compatibility and autogamy as well as producing the greatest number of seedless fruits. The results of statistical analysis of seed-ovule ratios indicate that most flowers in nature are selfed rather than out-crossed. This correlates well with my observations. Most floral visitors were medium to small bees who, for the most part, are responsible for selfing, rather than out-crossing. The pollen is easily released from the anther pores and autogamy may occur relatively frequently.

An interesting observation was that of occasionally finding viviparous seeds germinating while still in the fruit and on the plant (Fig. 33). I doubt that this is of ecological value. The seeds are dispersed by birds and a small seedling would probably be destroyed. Since the seeds I germinated all produced cotyledons

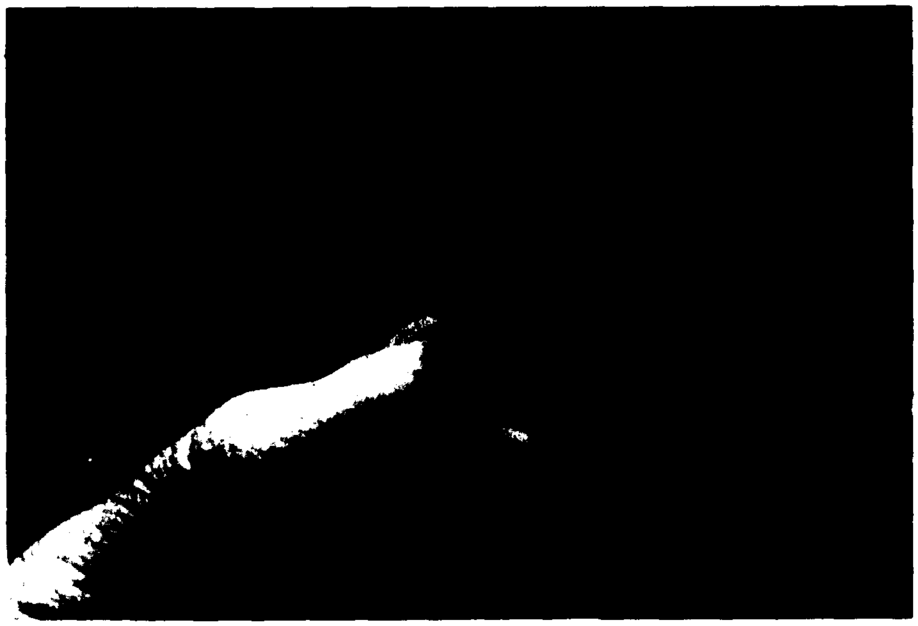


Fig. 33. Viviparous fruit of Topobea brenesii.

within 4 to 7 days, it is more likely that the seeds have a built-in time mechanism for germination and that the ovary provides the necessary moisture.

Topobea brenesii is visited by a large number of different birds which eat the fruit and disperse its seeds by wiping their beaks on nearby branches. In fact, except in peak fruiting periods, mature fruits were often not seen unless previously covered with mesh, because the birds usually arrived before me.

The large number of seedless fruits which resulted from emasculated flowers may, as with *Blakea grandiflora* and *B. gracilis*, be a method of assuring seed-dispersal even at times of low seed set.

CONCLUSION

It is clear that except for anther shape, the morphological and ecological differences within the species of *Blakea* studied are greater than the differences between *Topobea* and *Blakea*. In addition, in Monteverde the species in both genera have similar breeding systems.

On the other hand, *Blakea anomala* and *Topobea brenesii* have similar distribution and phenological patterns, as well as the same pollinators. If they belong to the same genus we might expect to find differences in these patterns which would lessen competition for pollinators. However, this is not uncommon for species in different genera.

However, we know nothing about the reproductive biology of these species in other areas or of other species in these genera, and very little about the reproductive biology of the Melastomataceae in general. Therefore, further studies are needed before information derived from the reproductive biology of these genera can be used in taxonomic decisions.

If we consider the bee-pollinated species of *Blakea* and *Topobea* it is easily seen that together they are a food source for pollinators throughout most of the year. In addition, as the phenological records indicate, the species combined produce mature fruits year round with the heaviest concentration occuring during the dry season, when all bear mature fruits. This period coincides with the nesting period of a large number of avian species in the area (Powell, 1977). Many different species of birds were observed eating the fruit and it is probable that *Blakea* and *Topobea* are an important food source for these animals, as well as for their pollinators.

So little is known about the reproductive biology and pollination ecology of cloud forest plants, as well as of other melastomes, that it is difficult to place the rodent-pollinated *B. chlorantha* in any context. At this time it stands alone as the only known rodent-pollinated species in the neotropics.

However, there are two other green-flowered species of *Blakea* in Costa Rica which occupy habitats similar to that of *B. chlorantha*. These are *B. austin-smithii* and *B. penduliflora*. Their floral morphology is similar to that of *B. chlorantha*. They too, have green flowers, purple anthers and produce nectar at night. In a brief field observation in May, 1980 I observed a rodent on an individual of *B. austin-smithii*. I believe that these species will prove to be pollinated by rodents.

At the present time there is no evidence of a bird or bat pollinated *Blakea*, which might help indicate the possible evolutionary pathway from bee to rodent-pollination. However, as mentioned previously, we lack adequate knowledge of the reproductive biology of the Blakeae and cannot be sure that such a species does not exist.

The flexible and opportunistic reproductive strategies of the species studied at Monteverde would seem to be a logical adaptation to the extreme and unpredictable environment. Arroyo (1979) and Sobrevila and Arroyo (1982) reported apomixis and self-compatibility in Venezuelan cloud forest plants, while Nevling (1971) noted almost a complete lack of sexual reproduction among plants in the elfin forest at Pico del Oeste. On the other hand, several species of *Inga* at Monteverde are obligate out-crossers (Koptur, pers. comm.) as are the species of *Monochaetum* (Almeda, 1978) and the melastome tree *Conostegia macrantha* (Lumer, unpub. data).

If the cloud forest environment is extreme and unpredictable, then the hemi-epiphytic habit might impose even greater strains upon a plant. Hemi-epiphytes must compete for light with their host, as well as with each other and other epiphytes. The species studied were able to root and grow in the shade, but needed open areas with full light to flower. Only further studies of the breeding systems of cloud forest plants, as well as studies of their lowland counterparts will indicate whether the flexibility seen in the reproductive biology of *Blakea* and *Topobea* at Monteverde is common to other hemi-epiphytes or peculiar to the Blakeae.

Appendix A

KEY TO THE SPECIES AT MONTEVERDE

Both Blakea and Topobea can be separated from other members of the Melastomataceae by their axillary 6-merous flowers, which are subtended by two pairs of decussate bracts.

1. Flowers green, anthers purple, nectar present.....*B. chlorantha*
1. Flowers white or pink, anthers yellow, nectar absent
    2. Stamens in circle around pistil, flowers deep pink, late May to early July.....*B. tuberculata*
    2. Stamens cupped at rear of flower, flowers white or pink
        3. Sepals and bracts curled, flowers pink.....*T. brenesii*
        3. Sepals and bracts not curled, bracts sometimes small and insignificant.
            4. Flowers pendant, white, petals reflexed, bracts small.....*T. pittieri*
            4. Flowers not pendant
                5. Pistil curved to one side, flowers pink, anthers maroon-red, below Reserve, alt 1320 m... ...*T. durandiana*
                5. Pistil curved to front, flowers white or pink, anthers yellow
                    6. Bracts very small, flowers white, anthers yellow, filaments pink.....*B. anomala*

6. Bracts large and showy, flowers white or pink, often with striped pattern on back
    7. Leaves coriaceous, cloud forest only, Sept. & Oct.......*B. grandiflora*
    7. Leaves not coriaceous, common along roadsides and pastures below cloud forest, Sept. to June........*B. gracilis*

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