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REPRODUCTIVE BIOLOGY OF BORNEAN *NEPENTHES* (NEPENTHACEAE) SPECIES

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ADAM, J.H. 1998. Reproductive biology of Bornean *Nepenthes* (Nepenthaceae) species. A study on the reproductive biology of Bornean *Nepenthes* species showed *Nepenthes* to exhibit reproductive syndromes that suggest insect pollination. A pollen trapping experiment in *N. villosa* showed that wind played no part in pollination. The presence of nectar-licking insects and the absence of nectar-sucking insects such as butterflies is correlated with the morphological nature of sepal nectar glands. Diptera is the main visitor group in *N. rajah*, *N. kinabaluensis* and *N. villosa;* Hymenoptera and Diptera are the main visitors in *N. curtisii* ssp. *zakriana* and *N. reinwardtiana.* The absence of ants in *N. villosa* and *N. kinabaluensis* may be due to the high altitude habitat of the plants which is unsuitable for ants, or the presence of ant-repellent nectar. Insect activity around the inflorescence is influenced by local weather conditions and the stage of development of the inflorescence. *Nepenthes* flowers are clustered into long inflorescence and are positioned well above the surrounding vegetation or grow into the canopy of tall trees in disturbed forests. This conspicuous appearance not only attracts potential pollinators but also separates them from the pitcher traps thus reducing the competition between them.

Key words: *Nepenthes* - Borneo - Kinabalu Park - pollination - pollen - nectar glands - Hymenoptera - Diptera - Formicidae - altitude - SEM - prey spectra

ADAM, J.H. 1998. Biologi pembiakan spesies *Nepenthes* (Nepenthaceae) di Borneo. Kajian dijalankan mengenai biologi pembiakan spesies *Nepenthes* di Borneo menunjukkan bahawa *Nepenthes* mempunyai tanda-tanda pembiakan yang mengesyorkan pendebungaan serangga. Kajian perangkap serangga dalam *N. villosa* menunjukkan bahawa angin tidak memainkan peranan dalam pendebungaan. Kehadiran serangga jenis menjilat madu dan ketidakhadiran serangga jenis menghisap madu seperti kupu-kupu mempunyai korelasi dengan sifat semula jadi kelenjar madu pada permukaan sepal. Diptera didapati merupakan pelawat utama bunga *N. rajah, N. kinabaluensis* dan *N. villosa*; Hymenoptera dan Diptera pula adalah pelawat utama bunga *N. curtisii* ssp. *zakriana* dan *N. reinwardtiana.* Semut yang tidak dicerap menghampiri bunga *N. villosa* dan *N. kinabaluensis* mungkin disebabkan oleh habitat yang dihuni oleh dua spesies *Nepenthes* tersebut terletak pada paras altitud yang tinggi, jadi habitat ini tidak sesuai untuk semut, atau berkemungkinan disebabkan oleh kehadiran madu penghalau semut. Kegiatan serangga di kawasan jejambak bunga dipengaruhi oleh iklim setempat dan peringkat perkembangan jejambak. Bunga *Nepenthes* terletak pada paksi jejambak yang panjang dan berada di atas daripada aras vegetasi atau kanopi hutan yang tinggi. Ketrampilan yang ketara bukan sahaja menarik perhatian agen-agen pendebungaan tetapi juga mengasingkan bunga daripada perangkap periuk yang mengurangkan persaingan di antara kedua-duanya.

Introduction

A few studies have been reported on the pollination of *Nepenthes* in Borneo. It has been suggested that these dioecious plants species are pollinated by either wind or insects. Veitch (1897) suggested wind pollination. According to him, the structure of the flower favours this mode of pollination since the male flowers are produced in larger numbers than the female flowers, male flowers produce enormous numbers of pollen grains thereby compensating for the pollen lost during transfer, and the female flowers have viscid stigmas that are fully exposed. Hotta (1989) suggested a fly as a pollen vector, but failed to find any evidence that insects visited the flowers of *Nepenthes.* He argued against wind pollination, saying that it is not easy to imagine the tetrad pollen being suited to wind pollination. Macfarlane (1908) suggested both insect and wind pollination. Green (1967) observed bees visiting the flower of *Nepenthes,* sucking nectar while straddling the stamina column. Pallot (in Green 1967), suggested wind pollination, thus going against the opinion of Hotta.

Pallot pointed out that the pollen tetrads are small enough to be carried by wind. Kaul (1982) suggested insect pollination in two Bornean species, *N. lowii* and *N. villosa,* based on proximity and synchrony of anthesis of both sexes at a time when insects are present, equality of reward, and attractiveness of both sexes to potential pollinators. Som (1988) favoured insect pollination. She observed insects crawling over the flowers and the presence of nectar-secreting and odour-emitting glands on the inner surface of the sepal. The spiny pollen of *Nepenthes* can easily adhere to the body and appendages of the insects. In addition, the inflorescence is positioned above the undergrowth or canopy making it conspicuous to insects. Adam *et al.* (1989) showed that Diptera are the most abundant visitors in *N. villosa, N. kinabaluensis* and *N. rajah.* They also found that Hymenoptera are abundant in *N. reinwardtiana* and *N.* aff. *fusca* .

The role of ants as pollinators of angiosperm flowers has been said to be insignificant (Beattie 1982). It has been argued by many researchers that pollens do not usually adhere to ants, but in fact many ant species are hairy, are covered with bristles or are heavily sculptured. Such species are capable of carrying pollens (Cole 1940, Sparks 1941, Wyatt 1981 cited in Beattie *et al.* 1984), and there are some examples of adaptation to pollen dispersal by ants (Percival 1965, Pijl & Dodson 1966, Kugler 1970 cited in Beattie 1982). However, ants are likely to be inefficient pollinators because ants groom their bodies frequently (Beattie *et al.* 1984); worker ants do not fly and have a limited foraging areas (Beattie *et al.* 1984). Thus, ants are generally regarded as "nectar thieves" removing floral rewards without effecting pollination.

This is further supported by the recent finding that myrmicacin, a substance isolated from secretions of south American leaf-cutting ants (Schildenknecht & Koob 1971, Iwanami 1978 cited in Nakamura & Miki -Hirosige 1982), inhibits pollen germination, pollen tube elongation and mitotic progression even after metaphase, which are not inhibited by other known inhibitors. Nakamura and Miki-Hirosige (1982) also demonstrated that myrmicacin (50-100 ppm) stops germination of pollen tube growth of *Camellia japonica.* Iwanami and Iwadare (1978) found that pollens of *C. japonioca, Hyacinthus orientalis,* and *Lilium speciosum* were inhibited by synthetic dl-myrmicacin. Beattie *et al.* (1984) showed that pollens exposed to ants for brief periods exhibit reduced pollen tube elongation. Despite numerous studies done on the effect of myrmicacin on pollen germination, no work has been done on this aspect on the species of *Nepenthes.* Since the male flowers on *Nepenthes,* particularly the lowland species, are frequently visited by ants, the latter's role in inhibiting pollen germination cannot be ruled out and should be investigated in detail.

Janzen (1977) hypothesised that "floral nectar in general contains chemicals that are powerfully repugnant, indigestible, or toxic to ants." The hypothesis has been disputed by some authors. Rico-Gray (1980), and Schubart and Anderson (1978) found that ants readily visited flowers and will eagerly consume floral nectars. On the other hand, Feisenger and Swarm (1978) bioassayed several nectars and found that ants do avoid some species.

Materials and methods

The study of the reproductive structures of Bornean *Nepenthes* species is based on the field observation and the examination of the dried herbarium specimens from major herbaria in Southeast Asia, [Herbarium Bogoriense (BO); Herbarium, Department of Biology, Faculty of Science and Natural Resources, Universiti Kebangsaan Malaysia (UKMS); Singapore Botanic Gardens Herbarium (SING); Sabah National Park Herbarium (SNP); Sabah Forest Department Herbarium, Sandakan (SAN); Sarawak Forest Department Herbarium, Kuching (SAR)], Europe [Royal Botanic Gardens Herbarium (K); Rijksherbarium, Leiden (L); Royal Botanic Garden, Edinburgh (E); Herbarium Botanische Staatssamlung, München (M); Botanische Garten und Botanisches Museum, Berlin-Dahlem (B)] and Australia [Queensland Herbarium (BRI)].

Pollination studies were carried out in Kinabalu National Park area at three different localities. These localities were: 1) along the summit trail above Carson's Camp [2600-3000 m above sea-level (asl)], involving *N. kinabaluensis* and *N. villosa;* 2) at East Mesilau Valley (1950 m asl) involving *N. rajah;* 3) at Mamut Copper Mine area (1400 m asl) involving *N. curtisii* ssp. *zakriana* and *N. reinwardtiana.* The study involved daily observations of flower visitor behaviour, i.e. recording the movement of visitors and recording actual time spent on the flowers. The observations were carried from 0800 to 1700 h for periods between one to thirteen days per species. The majority of the visitors were caught manually using net, numbered individually and pickled in 70% alcohol. Visitors which escaped were noted and identified by local name and order if known. The specimens pickled in 70% alcohol were examined under microscope the following night for the presence of the pollen tetrads stuck on the insect's body or left in the medium. The preserved samples were also identified initially according to order and some of the samples were identified according to the family level, particularly of Diptera using Unwin's key (1981). Representatives samples were sent to the Sarawak Forest Department, Entomological Section for identification and confirmation.

Pollen trapping experiment was carried out for *N. villosa.* Slides smeared with vaseline were arranged in slide holders placed on a specially made frame placed about 1.5 m from the ground. The frames positioned at about right angles were placed around the inflorescence facing towards and away from male and female inflorescences respectively, at a distance of about 2 m. The frames were left from 0800 to 1700 h and the slides were, at the end of the day, collected and examined under the microscope for the presence of pollen tetrads. This experiment was repeated daily for a period of thirteen days. Daily weather conditions were also recorded.

The pollen grains of *N. villosa, N. reinwardtiana* and *N. kinabaluensis* were taken from dried herbarium specimens of my own collection from Kinabalu Park Area in Sabah. The pollen samples for SEM study were acetolysed following the treatment of Walker and Doyle (1975). The pollens were placed in corked centrifuge tubes in acetolysis fluid of nine parts of acetic anhydride to one part of concentrated sulphuric acid in an oven at 50 °C overnight. They were then washed once with glacial acetic acid and three times with water. Pollens for examination under SEM were air dried on filter paper, then transferred on to double adhesive tape, stuck on to metal stub and then coated with gold. These samples were viewed under a SEM Cambridge Stereoscan 3000.

Specimens used in the study of sepal nectar glands were obtained from my own collections from Sabah and Sarawak. Species used in this study included *N. villosa* and *N. kinabaluensis* collected from Kinabalu Park Area, *N. gracilis* from Bukit Padang in Kota Kinabalu, *N. macrovulgaris* from Mt. Silam in Lahad Datu, *N. veitchii* from Bukit Tawai in Telupid, all in Sabah; and two species from Sarawak, i.e. *N. northiana* and *N. hirsuta.* One sepal of the flower was stuck using double sided adhesive tape onto the metal stub. These samples were coated with gold before viewing under a SEM Cambridge Stereocsan 3000.

Formulas from Brower and Zar (1977) were used to determine the mean number of visitors per day, standard error and 95% confidence interval for the mean (μ) to both male and female flowers of *N. villosa, N. kinabaluensis, N. rajah, N. curtisii* ssp. *zakriana* and *N. reinwardtiana.*

Results

Reproductive biology

Studies on the reproductive structures of many Bornean *Nepenthes* plant species show that the male and female reproductive organs are morphologically similar. The flowers are unisexual and relatively small up to about 20 mm diameter and are arranged along the elongated axis called inflorescence. Nepenthaceae are dioecious, i.e. staminate inflorescences as illustrated by *N. villosa* (Figure 1.2) and *N. kinabaluensis* (Figure 1.3), and pistillate inflorescences as illustrated by *N. villosa* (Figure 1.1) and *N. kinabaluensis* (Figure 1.4) are borne on separate plants.

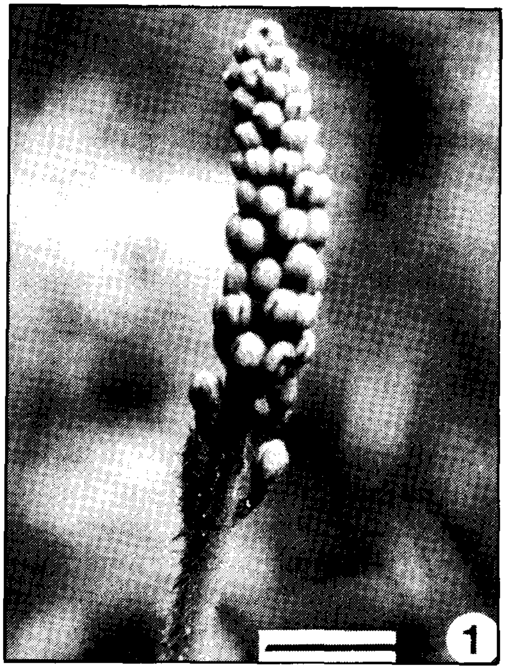


Figure 1.1. Pistillate racemose inflorescence of *N. villosa*. Scale bar 5 cm.

Figure 1.2. Staminate racemose inflorescence of *N. villosa*. Scale bar 5 cm.

Figure 1.3. Staminate racemose inflorescence of *N. kinabaluensis*. Scale bar 6 cm.

Figure 1.4. Pistillate racemose inflorescence of *N. kinabaluensis*. Scale bar 6 cm.

In the majority of Bornean *Nepenthes* species, the inflorescence is racemose (Figures 1.1 - 1.4). The number of both male and female flowers per inflorescence varies from as few as 6 flowers per inflorescence in *N. muluensis* to as many as 700 flowers in *N. rajah*. The length of both the male and female inflorescences varies within and between species, ranging from 6 cm in *N. muluensis* to about 140 cm in *N. rajah*.

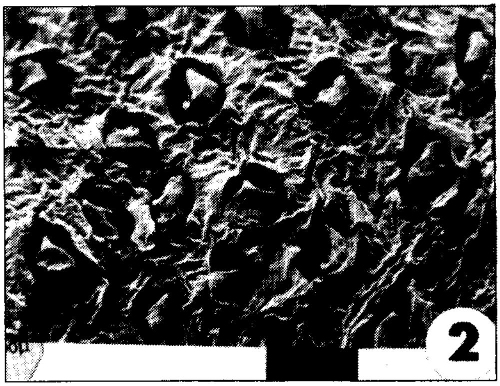
Initially, the inflorescence of the *Nepenthes* species is apical, but it becomes displaced laterally later. The inflorescence protrudes above the vegetation, thus making it visible to potential insect visitors and pollinators. The habit of the plants and the timing of flowering are seemingly correlated with the type of habitat: in *N. ampullaria,* for example, the plant is a shrub or a creeper in open places, and produces flowers when the plant length or height reaches about 1 m; in bushy vegetation, the plant is a climber and produces flowers when it has reached a height of about 3 m; in disturbed mixed lowland dipterocarp forests, the same species is a very tall climber climbing up to about 30 m and it only flowers when it has successfully reached the canopy. *Nepenthes* species can occur as terrestrial or epiphytic plants; *N. curtisii* is normally terrestrial, but may also occur as an epiphyte in the montane mossy forests.

The male and female plants of a single species commonly grow side by side as to ensure pollination; in *N. villosa,* for example, both male and female plants sometimes can be seen growing at about 0.3 m apart. Different species of *Nepenthes* may often be seen growing together: for example, *N. villosa* and *N. kinabaluensis* on the summit trail of Kinabalu, *N. burbidgeae* and *N. rajah* on Pig Hill on the foot of Mt. Kinabalu, *N. rafflesiana* and *N. gracilis* in Bukit Padang, *N. rafflesiana, N. albomarginata* and *N. ampullaria* in Weston, *N. gracilis, N. mirabilis* and *N. hookeriana* in Telupid, *N. lowii* and *N. edwardsiana* on Mt. Trusmadi, all in Sabah; and *N. tentaculata* and *N. muluensis* on Mt. Mulu in Sarawak. Sympatric species may hybridise forming an intermediate morphological form.

In all species examined, the individual male and female flowers are pale with glistening greenish colour later turning maroon or dark red. In the male flowers, the anther head may either be red (e.g. in *N. curtisii* ssp. *zakriana*) or yellow (e.g. in *N. reinwardtiana* and *N. rafflesiana*). In the female flowers, the stigmatic surface is pale green for about two weeks and then turns black. These distinctive colours exhibited by male and female flowers may also aid as an attractant to potential pollinators.

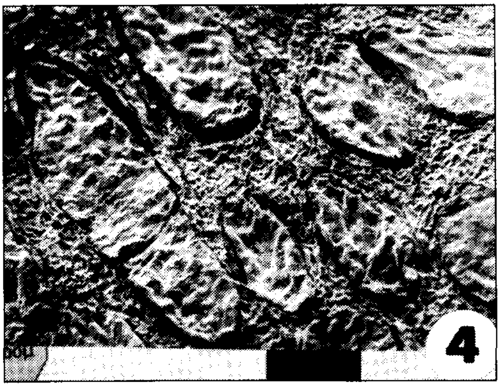
The inflorescences of most species produce a weak, foetid smell. In *N. veitchii,* however, the nectar from the inflorescence emits a strong odour and can be detected from a considerable distance. SEM studies on the glands of all *Nepenthes* plant species from Borneo show that the upper surface of the sepal is densely covered with sessile, nectar glands seated in very shallow epidermal cavities. The results are selectively illustrated by *N. northiana* (Figure 2.1), *N. villosa* (Figure 2.2), *N. macrovulgaris* (Figure 2.3), *N. hirsuta* (Figure 2.4), *N. kinabaluensis* (Figures 2.5 & 2.6), *N. gracilis* (Figure 2.7) and *N. veitchii* (Figure 2.8).

Figures 2.1. Sepal nectar glands of *N. northiana* (200 µm)

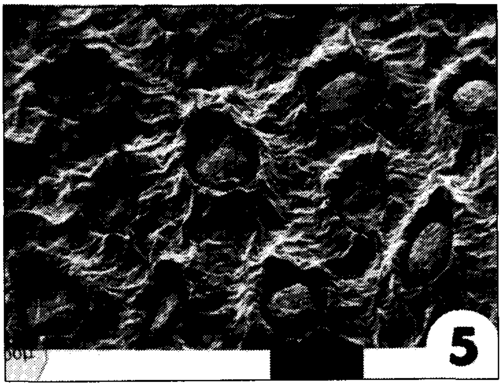


Figures 2.2. Sepal nectar glands of *N. villosa* (200 µm)

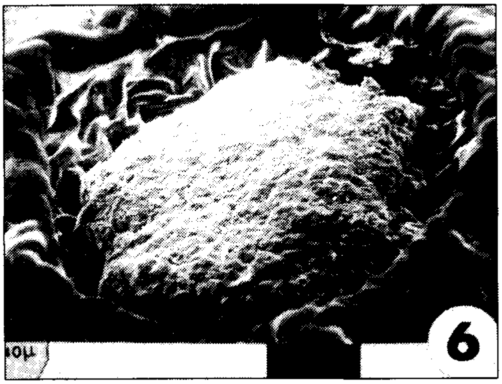
Figures 2.3. Sepal nectar glands of *N. macrovulgaris* (200 µm)



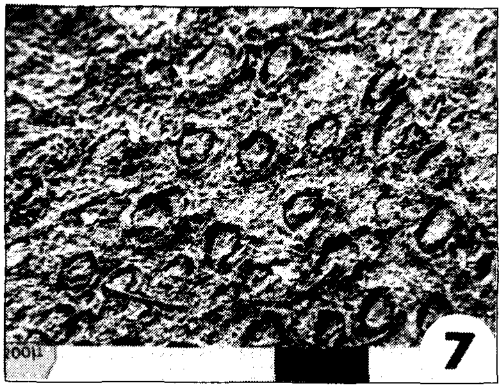
Figures 2.4. Sepal nectar glands of *N. hirsuta* (200 µm)



Figures 2.5. Sepal nectar glands of *N. kinabaluensis* (200 µm)



Figures 2.6. Sepal nectar glands of *N. kinabaluensis* (40 µm)



Figures 2.7. Sepal nectar glands of *N. gracilis* (200 µm)

Figures 2.8. Sepal nectar glands of *N. veitchii* (20 µm)

Macfarlane (1908) reported the irregular blooming period of some *Nepenthes* species in the wild, but flowering is generally common from March to September. Observations on *N. villosa* at Mt. Kinabalu Park showed that the male and female plants flowered continuously during the observation period, which spanned from July 1987 to January 1988. In some species, for example *N. mirabilis* in Kampong Bawang Matu in Sarawak, I have seen male and female plants flowering synchronously, producing hundreds of inflorescences on a small tree top. Other species which flower synchronously but to a lesser degree are *N. reinwardtiana* in Mamut and on Mt. Alab in Sabah, and *N. muluensis* and *N. lowii* on Mt. Mulu in Sarawak. The blooming period of the male inflorescences, depending on the number of flowers in the inflorescence, may last up to three months; for example, my field observations of *N. villosa, N. kinabaluensis* and *N. rajah* from Mt. Kinabalu showed that each inflorescence consists of up to 700 flowers, and may last up to three months. In each inflorescence, 0 to 6 flowers open each day. In the female inflorescence, the young fruits of *N. villosa, N. kinabaluensis, N. rajah, N. curtisii* ssp. *zakriana* and *N. reinwardtiana* increase in size dramatically after pollination. The matured capsules of *Nepenthes* species dehisce longitudinally into 4 locules, partially exposing numerous filiform seeds. The seeds are light and dispersed over a short distance by wind; my field observations on species such as *N. mirabilis* from Telupid and Entilebon in Sabah show that the seeds are also dispersed by water over a short distance.

Pollination study

Observations of visitors to male and female inflorescences of *Nepenthes* are summarised in Table 1. Diptera were the most frequent visitors in *N. villosa, N. kinabaluensis* and *N. rajah,* while Hymenoptera and Diptera were equally abundant visitors in *N. curtisii* ssp. *zakriana.* The abundance of visitors, particularly Diptera and Hymenoptera, may explain the presence of arachnid webs on the inflorescences of these four *Nepenthes* species. Very few visitors were observed at *N. reinwardtiana.* Ants were frequent visitors to *N. curtisii* ssp. *zakriana* compared to *N. rajah* and *N. reinwardtiana.*

Table 1. Visitors to male and female inflorescences of five *Nepenthes* species from Kinabalu Park Area in Sabah State of Malaysia

Species		*N. villosa*		*N. kinabaluensis*		*N. rajah*		*N. curtisii* ssp. *zakriana*		*N. reinwardtiana*	
Altitude (m)		2600-3000		2790-2850		1950		1400		1400	
Locality		Summit Trail		Summit Trail		E. Mesilau		Mamut		Mamut	
Sex		M	F	M	F	M	F	M	F	M	F
Diptera	1*	48	32	23	10	15	23	19	0	2	4
	2	7830	2175	4470	1377	1560	2520	2460	0	-	-
	3	163	68	194	138	104	110	130	0	-	-
	4	65	39	197	363	53	48	64	0	-	-
Hymenoptera	1	1	0	0	1	1	4	28	7	2	2
	2	120	0	0	90	120	480	660	1860	-	-
	3	120	0	0	90	120	120	24	266	-	-
	4	0	0	0	0	0	270	121	263	-	-
Formicidae	1	0	0	0	0	2	3	12	4	1	1
	2	0	0	0	0	540	600	5760	3000	-	-
	3	0	0	0	0	270	200	480	750	-	-
	4	0	0	0	0	762	455	438	548	-	-
Lepidoptera	1	4	2	0	0	1	1	0	0	0	0
	2	720	540	0	0	60	60	0	0	0	0
	3	180	270	0	0	60	60	0	0	0	0
	4	156	162	0	0	1	1	0	0	0	0
Coleoptera	1	1	0	2	1	0	0	0	0	0	0
	2	240	0	110	120	0	0	0	0	0	0
	3	240	0	55	120	0	0	0	0	0	0
	4	0	0	127	0	0	0	0	0	0	0
Unknown	1	2	0	0	0	0	0	0	0	0	0
	2	65	0	0	0	0	0	0	0	0	0
	3	33	0	0	0	0	0	0	0	0	0
	4	709	0	0	0	0	0	0	0	0	0
Duration (days)		13	11	5	3	1	2	4	2	2	2
Duration (h)		119	97.5	40.5	27	9	18	36	18	18	18
No. visits		56	34	25	11	22	32	59	11	5	7
μ per day		4.31	3.10	5.00	3.67	22.00	16.00	14.75	5.50	2.50	3.50
Standard error		1.28	0.91	3.05	0.88	0	11.00	1.80	0.50	0.50	3.46
95% confidence interval for μ		2.79	2.03	8.48	3.89	0	140	5.73	6.36	6.36	44.50

*: 1:	Total number of visits	M :	Male
2:	Total time of visits (s)	F :	Female
3:	μ Mean time of visits (s)	- :	No data
4:	95% confidence interval for μ		

The sizes of the visitors were generally small, ranging from 3 to 10 mm long. In addition, the behaviour patterns of these visitors were fairly similar. The small visitors (<4 mm long) normally alighted on the upper surface of the sepal while sipping nectar from the glands, and occasionally moved around from flower to flower, sometimes landing on an anther before moving to the sepal. The larger visitors (>4 mm long) had similar behaviour, but in most cases, they rested the abdominal part of their bodies on the staminal column of the male flower or the ovary, and the stigmatic surface of the female flower. It was observed that female flowers of the five species of *Nepenthes* studied open only partially such that visitors, especially the larger ones, had to alight on to the stigma while sucking nectar from the sepal.

I found that the mean number of visitors per day was higher for the male inflorescences compared to that for the female inflorescences, except for *N. reinwardtiana*. In addition, *Nepenthes rajah* and *N. curtisii* ssp. *zakriana* growing at lower altitudes (1000 - 2000 m) had more visitors compared to *N. kinabaluensis* and *N. villosa* growing at higher altitudes (2600 - 3000 m) (Table 1). The mean (μ) numbers of visitors per day visiting the male and female flowers were 4.31±1.28 (SE) and 3.10 ± 0.91 respectively for *N. villosa*, 5.00 ± 3.05 and 3.67 ± 0.88 respectively for *N. kinabaluensis*, 22.00 ± 0.00 (day of observation, n =1) and 16.00 ± 11.00 respectively for *N. rajah*, 14.75 ± 1.80 and 5.50 ± 0.50 respectively for *N. curtisii* ssp. *zakriana*, and 2.50 ± 0.5 and 3.50 ± 3.46 respectively for *N. reinwardtiana* (Table 1). The foraging activity of the insects is influenced by local weather conditions and the stage of the inflorescence development. Few or no visitors were recorded visiting flowers of *N. villosa* and *N. kinabaluensis* during the rainy days or on cloudy and cold days with an air temperature of about 12 °C or below. Insect activity was generally greater during the sunny parts of the day when the temperature was about 16 °C. Insect activity declined around male inflorescences toward the end of the flowering stage.

SEM study on the pollen grains showed that all *Nepenthes* species from Borneo have spinose pollen tetrads with diameters ranging from 20 to 40 µm. The results of this study are selectively illustrated by *N. villosa* (Figures 3.1 & 3.2), *N. reinwardtiana* (Figures 3.3 & 3.4) and *N. kinabaluensis* (Figures 3.5 & 3.6). The spines may help the pollen stick to the hairy bodies of the pollinators.

The examination of the medium of the preserved specimens studied under a light microscope showed the presence of pollen tetrads. In *N. curtisii* ssp. *zakriana*, 6 out of 10 dipteran and 4 out of 7 hymenopteran specimens observed visiting both the male and female flowers showed the presence of pollen tetrads. The filtrate of ant specimens which visited the staminate flowers and pistillate flowers of the same species also contained pollen tetrads. Some dipterans that had visited male and female flowers in *N. rajah*, *N. kinabaluensis* and *N. villosa* still had pollen tetrads attached. Examination of these visitors, particularly Dipterans and Hymenopterans, showed their bodies to be covered with hairs or bristles. The above results suggest that the flowers of *Nepenthes* in Borneo are insect pollinated. The role of ants as potential pollinators in *Nepenthes* has to be investigated further for the presence of myrmicacin, and if positive, to further study the effect of this substance on the pollen germination of *Nepenthes* species.

In my study of flower visitors to *Nepenthes* species on Mt. Kinabalu, I found ants visiting the flowers of *N. rajah*, *N. curtisii* ssp. *zakriana* and *N. reinwardtiana* (growing at lower altitudes). No ants were observed visiting the male and female inflorescences of *N. villosa* and *N. kinabaluensis* in a sample plot at Mt. Kinabalu at an altitude of *c.* 2600-3000 m. The absence of ants may be attributed to the high altitude and the associated cold weather. Janzen (1977) mentioned that many of the tropical habitats above *c.* 2200 m elevation are free of ants. In addition, Hotta (1989) suggested that the mossy forests are too moist throughout the year to offer a good habitat for ants, and that flies are possible pollinators of *Nepenthes* species.

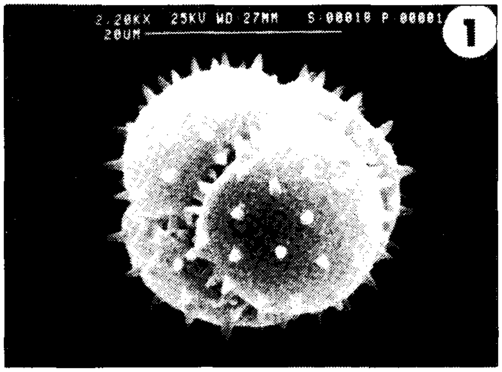


Figure 3.1. Pollen grain of *N. villosa* (20 μm)

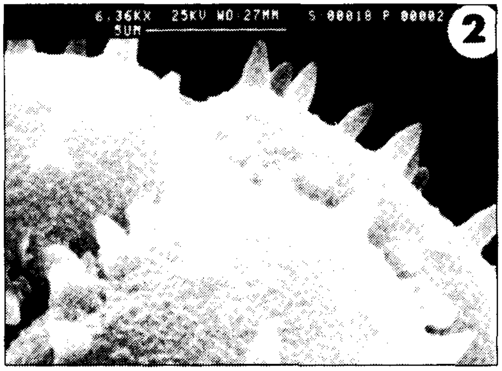


Figure 3.2. Pollen grain of *N. villosa* (5 μm)

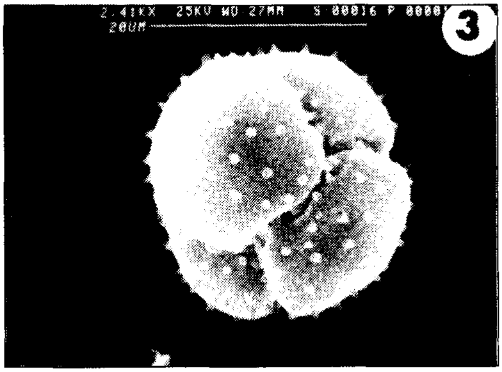


Figure 3.3. Pollen grain of *N. reinwardtiana* (20 μm)

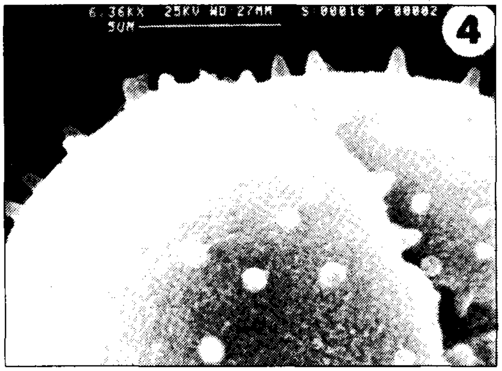


Figure 3.4. Pollen grain of *N. reinwardtiana* (5 μm)

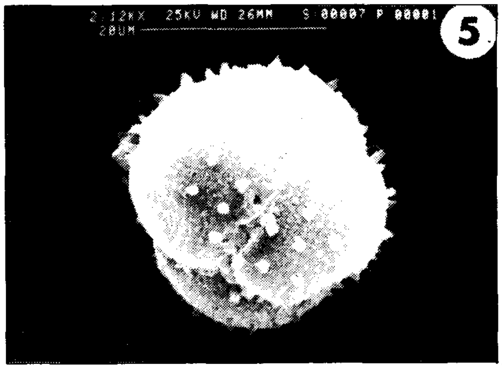


Figure 3.5. Pollen grain of *N. kinabaluensis* (20 μm)

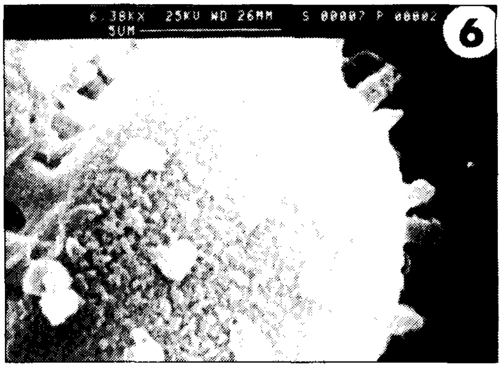


Figure 3.6. Pollen grain of *N. kinabaluensis* (5 μm)

The absence of ants visiting the flowers of these two species may possibly be due to the presence of ant-repellant nectars, but this has to be tested. Ants were observed visiting flowers of the lower altitude species, but with relatively higher frequency in *N. curtisii* ssp. *zakriana* (1400 m asl) than in *N. rajah* (1950 m asl) and *N. reinwardtiana* (1400 m asl). The presence of ants may reflect the fact that these habitats, at lower altitude, have abundance of ants. The local weather at this altitudes is warmer, and rain is less frequent in the afternoon than at the Summit Trail above Carson's Camp (above 2600 m).

My observation on ants agrees with that of Rico-Gray (1980); the ants moved actively on the stem, on the inflorescence axis, on to the upper surface of the sepal, sipping nectars for several minutes (mean period of 5-6 min in *N. rajah* and 8-12 min in N. *curtisii* ssp. *zakriana*). The ants were not seen to move to or stay around the bright yellow pollens, which are a potential alternative source of food. Though contradicting my earlier finding on pollen presence in the preserve medium of ants, the behavioural pattern suggests that ants play a very minor role on pollen transfer, acting primarily as "nectar thieves", as suggested by Rico-Gray (1980).

Analysis of flower visitors

Comparative data in pitcher prey spectra (Adam 1997) and flower visitors in *Nepenthes* species from Kinabalu Park Area are summarised in Table 2. The data show that the pitchers attract a broad spectrum of prey whereas the flowers attracted limited fauna taxa. The decomposed bodies of pitcher prey attract carrion feeders including Diptera, Dictyoptera, Coleoptera; detritus and larvae inhabitants attract other fauna group such as Chilopoda and Diplopoda. The enormous food source in the pitcher may account for some differences in fauna composition of flower visitors and prey spectra of the pitcher.

The data, however, show an overlap between the main prey groups and the flower visitors in all the species studied. For example, Diptera and Hymenoptera are common both as prey and as flower visitors in these species. In *N. rajah, N. curtisii,* and *N. reinwardtiana,* Formicidae, the commonest prey in pitchers, are also flower visitors in these species.

This overlapping may be attributed to the fact that both flowers and pitchers of these *Nepenthes* produce nectars attractive to ants. Diptera, flighted Hymenoptera, Lepidoptera and Coleoptera on the flowers of *N. kinabaluensis* and/or *N. villosa* may be attracted to pollen, an alternative source of food for the visitors.

Pollen trapping experiment in N. villosa

In this experiment, no pollen tetrads were trapped, suggesting that the pollen of *N. villosa* is not dispersed by wind.

Table 2. Prey spectra vs. flower visitors in five *Nepenthes* species from Kinabalu Park Area in Ranau, Sabah

Species	Site	Structure	1	2	3	4	5	6	7	8	9	10	11
N. villosa	Summit Trail, Mt. Kinabalu	Pitcher	+	+	+	+	+	+	-	+	+	+	-
		Flower	-	+	-	-	-	+	-	-	-	+	-
N. kinabaluensis	Summit Trail, Mt. Kinabalu	Pitcher	+	+	-	+	+	+	-	-	-	+	+
		Flower	-	+	-	-	-	+	-	-	-	+	-
N. rajah	East Mesilau, Mt. Kinabalu	Pitcher	-	+	+	+	-	+	+	-	+	-	-
		Flower	-	-	-	-	-	+	+	-	-	+	-
N. reinwardtiana	Mamut, Ranau	Pitcher	-	+	+	+	-	+	+	+	+	+	-
		Flower	-	-	-	-	-	+	+	-	-	+	-
N. curtisii ssp. *zakriana*	Mamut, Ranau	Pitcher	-	+	+	+	-	+	+	+	+	+	-
		Flower	-	-	-	-	-	+	+	-	-	+	-

Key:
1 Chilopoda*
2 Coleoptera
3 Dermaptera
4 Dictyoptera*
5 Diplopoda*
6 Diptera
7 Formicidae*
8 Homoptera
9 Heteroptera
10 Hymenoptera
11 Orthoptera
\+ Present
\- Absent
* Creeping fauna

Discussion

The evidence from this study shows that the flowers of *N. villosa, N. kinabaluensis, N. reinwardtiana* and *N. curtisii* ssp. *zakriana* are insect pollinated, thus supporting other authors' observations (Macfarlane 1908, Gibbs 1913, Holttum 1954, Kaul 1982, Hotta & Tamin 1986, Som 1988).

The reproductive structures of these species are characterised by relatively small flowers clustered or arranged on the inflorescences; the upper surface of the sepal of each flower is brightly coloured, i.e. glistening green and maroon; male inflorescences are brightly coloured with red or yellow anther head, held in a position well above the vegetation. These inflorescence characters are easily visible to the potential visitors such as Diptera and Hymenoptera. The male and female inflorescences are positioned well above the vegetation cover as compared to the pitchers, particularly the ground pitchers. This may reduce the competition for insect visitors. The flowers emit a foetid smell; the smell may be very weak or strong, and thus aids in attracting potential insect visitors. It has been reported that all *Nepenthes* species which produce nectar do not seem to produce any attractive scent at all (Juniper *et al.* 1989), but Som (1988) found that *Nepenthes* flowers produce a faint odour; Macfarlane (1893, 1908) found *Nepenthes* flowers to produce a heavy foetid odour similar to but fainter than that of *Ailanthus* flower.

The glands on the upper surface of the sepal secrete nectar, and this secretion gives the sepal a glistening colour thus acting as an additional attractant to the visitors. Juniper *et al.* (1989) reported that "in some flowers, the watery exudate of stigmatic papillae provides a glistening attractant for dipterous visitors and it is well known that many insects, in particular Diptera, are attracted by the glistening drops." Nectar drops secreted by glands on the upper surface of the flower sepal may help in explaining the presence of dipterous group of visitors in all of the five *Nepenthes* species studied .

The insect visitors attracted to the flowers are rewarded with nectar; according to Vogel (1983) (cited in Juniper *et al.* 1989), nectar is one of the main floral rewards in the plant kingdom and insects suck or lick it for its nourishment and water supply. In some *Nepenthes* species, for example in *N. bicalcarata, N. gracilis, N. mirabilis* and *N. rafflesiana*, a few nectar glands are found on the stem and on the lower surface of the lamina, the petiole, the inflorescence axis, the pedicels and the lower surface of the sepal, and several on the upper surface of the sepal. These glands which secrete nectar attract crawling insects on the ground level leading to the sepal of the flower. Macfarlane (1908) reported numerous small nectar glands on the pedicels of *N. pervileii,* an endemic species of the Seychelles. SEM study showed that pitcher plants have their sepal nectar glands seated in a very shallow cavity (Adam & Wilcock 1995). This may explain the presence of Diptera and Hymenoptera and the absence of insects such butterflies among visitors to the *Nepenthes* flowers.

In this study, insect visitors were attracted to both male and female inflorescences; they were shown to be capable of carrying pollen tetrads that stick to their hairy bodies and, thus the insects may affect pollination.

All the five species studied showed both male and female inflorescences produced at more or less at the same time; both flower sexes also open more or less at the same period of time, and show equality of attractiveness and reward between sexes.

Though there has been suggestions that flowers of *Nepenthes* species may be wind pollinated (Veitch 1897, Macfarlane 1908), most authors seem to favour insect pollination (Macfarlane 1908, Holttum 1954, Kaul 1982, Hotta & Tamin 1986, Som 1988). The pollen trapping experiment under natural conditions of *N. villosa* failed to trap any pollen tetrads from male inflorescences or any incoming pollen tetrads at female inflorescences. This together with the sticky nature of the pollen tetrads further suggests that they are insect pollinated rather than wind pollinated.

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