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Inter- and intra-specific variation in prey assemblages and inhabitant communities in *Nepenthes* pitchers in Sumatra

M. KATO [1], M. HOTTA [2], R. TAMIN [3] and T. ITINO [4]

[1] *Biological Laboratory, Yoshida College, Kyoto University, Kyoto 606, Japan*
[2] *Department of Biology, Faculty of Science, Kagoshima University, Kagoshima 890, Japan*
[3] *Department of Botany, Faculty of Science, Andalas University, Padang, Sumatera Barat, Indonesia*
[4] *Laboratory of Applied Entomology, Faculty of Agriculture, Kagawa University, Kita-gun, Kagawa 761-07, Japan*

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Prey assemblages and inhabitant communities in pitchers were compared among 10 *Nepenthes* Linnaeus 1753 species with various pitcher morphologies in West Sumatra, Indonesia. There were significant differences in the number of prey organisms trapped per pitcher among *Nepenthes* species and among pitcher ages but no significant differences among localities nor between the vertical positions of pitchers. Prey assemblages of eight *Nepenthes* species were predominated by ants. *Nepenthes bongso* Korthals 1839 and *N. albomarginata* Lobb 1849 had prey assemblages characterized by high frequencies of midges and termites, respectively. Pitchers captured prey organisms not by random trapping but by attracting specific groups of organisms.

Inhabitant fauna was largely similar among *Nepenthes* species except for *N. bongso* which fostered no inhabitants. The typical inhabitant community was composed of *Toxorhynchites* Theobald 1901 larvae as aquatic predators, culicid larvae as filter feeders and ceratopogonid larvae as detritus feeders. There were significant differences in the number of inhabitants per pitcher both among *Nepenthes* species and among pitcher ages, but not among localities nor between the vertical positions of pitchers. An ecological role of inhabitants in accelerating nutrient cycling in a pitcher ecosystem and the mutual relationship between *Nepenthes* species and their inhabitants were discussed.

KEY WORDS: *Nepenthes*, community structure, pitcher ecosystem, prey trapping, Sumatra.

INTRODUCTION

Pitchers, that is highly modified reservoir-like leaves, have evolved as a means of prey trapping at least four times independently: Nepenthaceae in the Old World, Sarraceniaceae and Bromeliaceae in the New World and Cephalotaceae in Australia (JUNIPER et al. 1989). Southeast Asia is the diversification centre of Nepenthaceae, which is the largest family of pitcher plants (MIQUEL 1862, MACFARLANE 1908, DANSER 1928). The *Nepenthes* species exhibit a great diversity in pitcher morphology, although their reproductive organs are rather similar (DANSER 1928). An object of this paper is to detect the significance of the diversification in pitcher morphology.

A *Nepenthes* pitcher has three functions: (1) trapping prey, (2) decomposing prey organisms and digesting them into amino acids and inorganic nutrients, and (3) absorbing them (THIENEMANN 1932, 1935; LLOYD 1942). Pitcher morphologies are thought to be related with prey capture rates and prey assemblages. These functions are usually disturbed or supported by other organisms which have a tolerance to hydrolytic enzymes and can inhabit the pitcher fluid. Trapped prey organisms are degraded and decomposed by these macroorganisms (BEAVER 1979) and digested by enzymes secreted by pitcher itself (NAKAYAMA & AMAGASE 1968, AMAGASE et al. 1969, TÖKES 1974) and/or by microorganisms (JUNIPER et al. 1989).

For pitcher plants to enhance the rate of nutrient absorption, there are three strategies: (1) to maximize the rate of nutrient input into pitchers, (2) to maximize the rate of decomposition and digestion of prey, and (3) to minimize loss of nutrient. The first strategy involves effective prey trapping, and the second and third strategies involve managing the food web structure in a pitcher. Nutrient cycling in a pitcher can be estimated by investigating both the prey trapping and food web structure. Thus, to detect the evolutionary pattern of nutrient cycling in *Nepenthes* pitchers, we analyzed inter- and intra-specific variation in prey assemblages and inhabitant communities in pitchers in Sumatra, an evolutionary centre of the genus.

MATERIALS AND METHODS

We sampled 160 pitchers of 10 *Nepenthes* Linnaeus 1753 species at seven localities in mountain forests and meadows in West Sumatra, Indonesia (Fig. 1) from 19 Dec. 1987 to 26 Jan. 1988. Hereafter, we call the *Nepenthes* species by the code names N1-N10 as shown in Table 1. Generally a few *Nepenthes* species coexisted in a habitat (Table 2). Ten *Nepenthes* species which we found had distinct morphological characteristics of pitchers, e.g., shape of pitcher, posture of lid, morphology of nectary and volume of pitcher (Table 1, Fig. 2). N1, N2, N3, N6 and N8 had slender pitchers, while N7, N9 and N10 had large saccate pitchers, N4 had ovoid and N5 had funnel-like pitcher. The latter two species had pitchers with inverted lids, which admitted rain into their pitchers, whereas other species had lids covering the pitcher's mouth to prevent rain falling into the pitchers. All species had nectaries on pitcher rim although nectaries of N3, N5 and N6 were vestigial. N8 had pitchers very similar to N6, but was distinguished from the latter by the presence of two nectaries on the inner wall of the upper part of the pitcher. The volumes of pitchers of grown plants varied between species. N10 had the largest and N5 had the smallest pitchers.

We sampled ≥ 5 pitchers for each species at each site and recorded vertical position (terrestrial or arboreal) and age of each pitcher (young, intermediate and old) by checking leaf order and conditions of the pitcher itself and pitcher fluid. All living organisms and fragments of dead organisms in each pitcher (we call the former inhabitant and the latter prey) were filtered through a nylon net and collected with forceps, and preserved in 70% ethanol separately for each pitcher. The

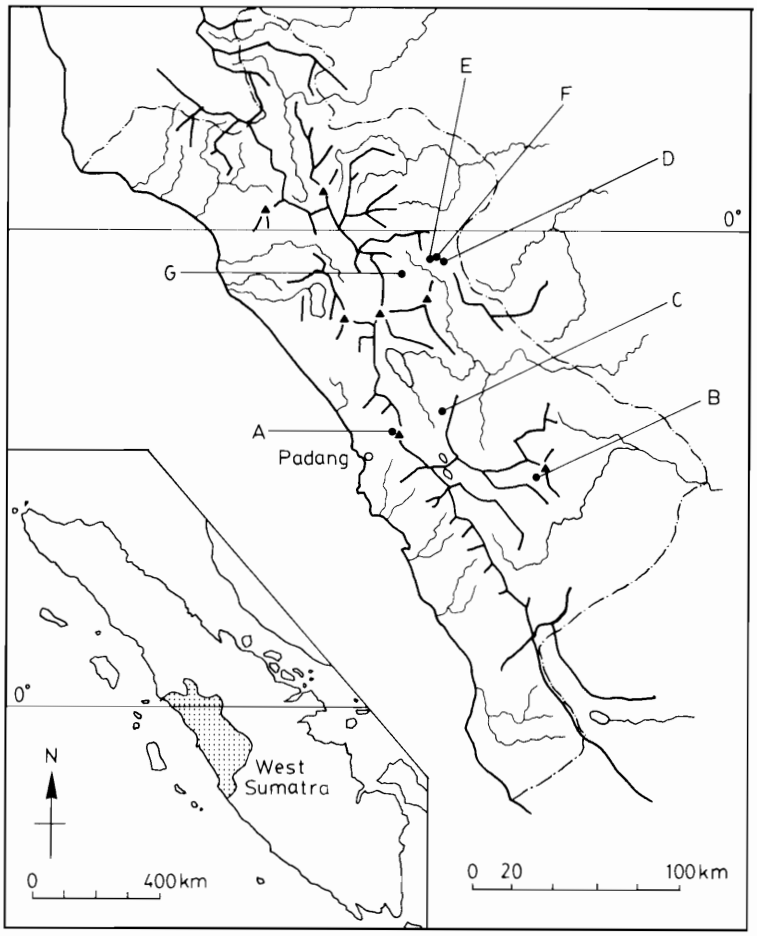

Fig. 1. — Map showing the main ridges of the Barisan Range, the river systems and the study sites in West Sumatra. A, Gunung Gadut; B, Bukit Gadang; C, Payung Sukaki; D, Kelok Sembilan; E, Air Putih; F, Harau; G, Andalas Andalas.

majority of the prey organisms had been more or less browsed and decomposed into pieces, and the degree of decomposition was recorded for each prey. All specimens of inhabitants and prey organisms were identified to genera and families, respectively.

Inhabitants in pitchers were classified into five feeding types: terrestrial predator, aquatic predator, filter feeder, detritus feeder and visitor (Fig. 3). The feeding type, carrion feeder recognized by BEAVER (1985) was included in detritus feeder, because there were no clear-cut differences between the two feeding types. We treated all mosquito larvae except for *Toxorhynchites* Theobald 1901 as filter feeders in this paper, though the feeding types of mosquito larvae were classified, using functional morphology of the mandibles, into filter feeder, browser and predator by SURTEES (1959), or into plankton feeder, surface feeder, bottom feeder and scavenger by HARBACH (1977).

To discriminate among the prey assemblages of 10 *Nepenthes* species, we used cluster analysis and canonical discriminant analysis (SAS 1985). Ratios and mean numbers of prey organisms

Table 1.
Some morphological features of pitchers of 10 *Nepenthes* species studied in West Sumatra.

Code	*Nepenthes* species	Shape of pitcher	Posture of lid	Nectary		Volume of pitcher (ml)*
				Pitcher rim	Inner wall	
N1	sp. A	slender	covering	+	−	10-50
N2	*alata* Blanco 1837	slender	covering	+	−	80-170
N3	*albomarginata* Lobb 1849	slender	covering	+	−	50-100
N4	*ampullaria* Jackson 1835	ovoid	inverted	+	−	50-80
N5	*bongso* Korthals 1834	funnel-like	inverted	+	−	10-30
N6	*gracilis* Korthals 1839	slender	covering	+	−	70-140
N7	*mirabilis* Druce 1916	saccate	covering	+	−	100-160
N8	*reinwardtiana* Miquel 1852	slender	covering	+	+	70-140
N9	sp. B	saccate	covering	+	−	100-220
N10	*spathulata* Danser 1935	saccate	covering	+	−	220-300

* Volume of content of pitcher, not of fluid secreted by pitcher; +, present; −, absent.

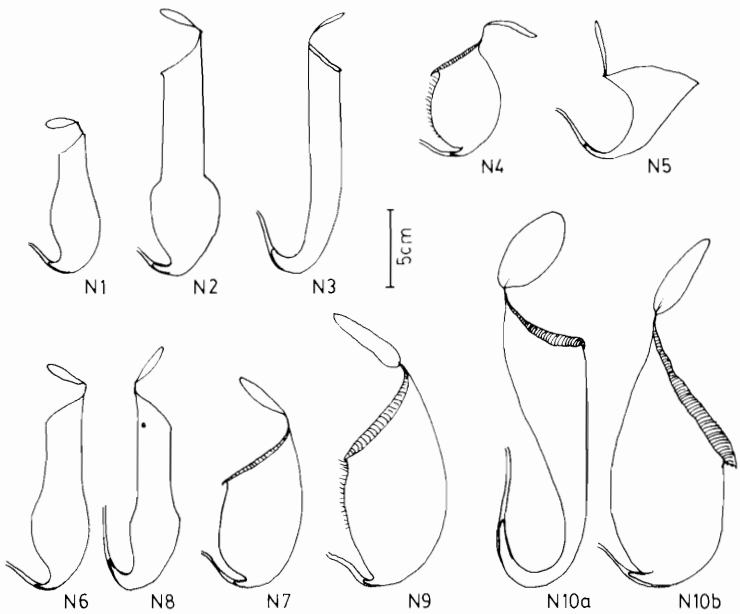

Fig. 2. — Cross sections of the 10 *Nepenthes* pitchers studied. The code numbers (N1-N10) refer to those in Table 1. N10a and N10b denote arboreal and terrestrial pitchers of *N. spathulata*, respectively.

Table 2.
Localities and dates of sampling of *Nepenthes* pitchers and numbers of pitchers sampled at each locality.

Code	Locality	Altitude (m)	Date	*Nepenthes* species code									
				N1	N2	N3	N4	N5	N6	N7	N8	N9	N10
A	Gunung Gadut, Padang	1600-1800	1 Jan. 1988	–	–	–	–	21	–	–	–	24	13
B	Bukit Gadan, Alahanpanjang	1100-1200	24 Jan. 1988	–	–	–	–	+	–	–	–	+	6
C	Payung Sukaki, Solok	700-1000	26 Jan. 1988	–	+	–	–	–	–	5	+	–	–
D	Kelok Sembilan, Payakumbuh	700-1000	20 Dec. 1987	7	18	–	13	–	7	–	+	–	–
E	Air Putih, Payakumbuh	600-700	20 Dec. 1987	–	5	9	–	–	+	–	–	–	–
F	Harau, Payakumbuh	550-600	19 Dec. 1987	–	–	–	9	–	14	–	–	–	–
G	Andalas Andalas, Payakumbuh	550-600	21 Dec. 1987	–	–	–	–	–	–	–	9	–	–

+, present but not sampled; –, absent.

trapped per pitcher were variables used in these respective analyses. To detect some patterns in the inhabitant communities of *Nepenthes* species, we used primary component analysis (SAS 1985). Variables used in this analysis were the mean numbers of five feeding types of inhabitants and the total number of prey organisms.

RESULTS

Prey assemblages

The number of prey organisms trapped per pitcher varied greatly among pitchers of the same species (Fig. 4). This large intraspecific variation was due partly to differences of pitcher age. The mean number of trapped prey organisms per pitcher was largest in N1 and smallest in N4. Mean number of prey organisms for each

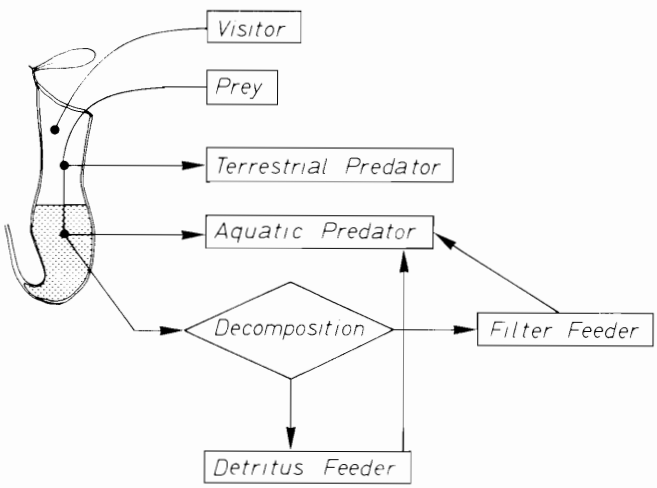

Fig. 3. — A schematic food web in a *Nepenthes* pitcher.

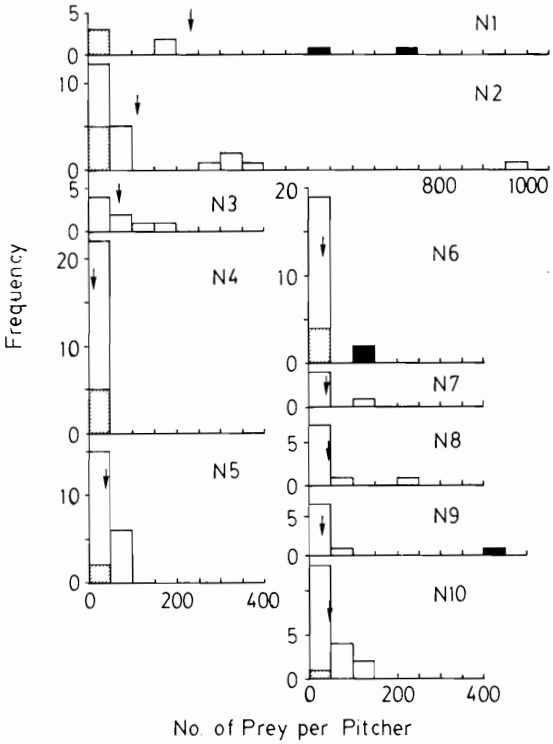

Fig. 4. — Frequency distributions of the numbers of prey organisms trapped per pitcher. Arrows indicate mean numbers. Shaded, open and solid columns denote young, intermediate and old pitchers.

Nepenthes species was not correlated with the mean volume of a pitcher ($y = -0.31x + 96.1$; $r = -0.318$, $P = 0.371$). By ANOVA, there were significant differences in the number of prey organisms per pitcher among *Nepenthes* species and among pitcher ages, but no significant differences among the localities nor between the vertical positions of pitchers (Table 3).

Prey organisms trapped in pitchers belonged to two phyla, six classes including 14 insect orders, and were classified into 37 groups (P1-P37: the lowest rank of taxon was superfamily, Table 4). The mean numbers of prey organisms trapped per pitcher are shown in Appendix 1. The most abundant prey organisms of *Nepenthes* species other than N3 and N5 were ants (P33, Fig. 5). The prey assemblages of N1, N2, N6, N7, N8 and N9 were highly dominated by ants. The percentages of ants in the prey assemblages were 99.9, 97.2, 95.0, 90.2, 90.2 and 90.0%, respectively. The prey assemblage of N4 was also dominated by ants (71.1%), but had many other taxa.

As for the prey assemblage of N10, ants was the most abundant (56.5%), in decreasing order are Mycetophiloidea (22.1%), Coleoptera (2.8%), Blattariae (2.2%), Phalangida (2.1%), Nematocera (excluding Tipuloidea and Mycetophiloidea, 2.1%)

Table 3.
Results of analyses of variance (ANOVA) of numbers of inhabitants and prey organisms per pitcher.

Source of variation	df	Dependent variable					
		Number of prey organisms		Number of filter feeders		Number of detritus feeders	
		F	*P*	F	*P*	F	*P*
Species	9	4.88	0.0001	3.54	0.0005	6.15	0.0001
Locality	6	0.16	0.8484	0.10	0.9030	1.62	0.2024
Vertical position	1	0.00	0.9539	0.01	0.9383	1.01	0.3174
Age	2	27.12	0.0001	7.68	0.0007	1.08	0.3408

Table 4.
Taxa of prey organisms trapped in *Nepenthes* species.

Phylum	Class	Order	Suborder	Superfamily	Code
Mollusca	Gastropoda	Stylommatophora			P1
Arthropoda	Arachnida	Pseudoscorpionida			P2
		Phalangida			P3
		Acarina			P4
		Araneida			P5
	Crustacea	Isopoda			P6
		Amphipoda			P7
	Chilopoda	Geophilomorpha			P8
	Diplopoda				P9
	Insecta	Blattariae			P10
		Dermaptera			P11
		Orthoptera			P12
		Isoptera (winged)			P13
		Isoptera (apterous)			P14
		Embioptera			P15
		Psocoptera			P16
		Thysanoptera			P17
		Hemiptera	Heteroptera		P18
			Homoptera		P19
		Neuroptera			P20
		Trichoptera			P21
		Lepidoptera			P22
		Diptera	Nematocera	Tipuloidea	P23
				Mycetophiloidea	P24
				others	P25
			Brachycera	Platypezoidea	P26
				others	P27
		Coleoptera			P28
		Hymenoptera	Apocrita	Ichneumonoidea	P29
				Cynipoidea	P30
				Chalcidoidea	P31
				Proctotrupoidea	P32
				Formicoidea	P33
				Pompiloidea	P34
				Sphecoidea	P35
				Vespoidea	P36
				Apoidea	P37

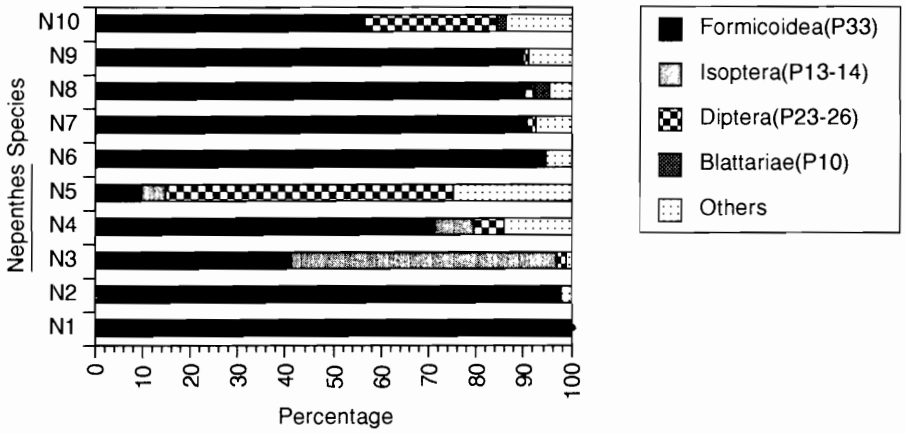

Fig. 5. — A comparison of prey assemblages in pitchers among *Nepenthes* species. Prey organisms are classified into five groups: 1, Formicoidea (P33); 2, Isoptera (P13-14); 3, Diptera (P23-26); 4, Blattariae (P10); 5, others.

and Platypezoidea (1.7%). Blattariae and Phalangida, irrespective of the low densities, seemed to be important for nutrient input due to their large sizes. As seen in Fig. 1, N10 showed clear dimorphism in pitcher shape according to the vertical positions of pitchers. The numbers of prey organisms per pitcher were similar between terrestrial and arboreal pitchers (41.5 ± 35.7 and 56.3 ± 69.9, mean ± SD, respectively), whereas the percentage of ants for the former (51.3%) was lower than that of the latter (76.9%).

The most abundant prey organisms in N3 pitchers were apterous termites (56.7%), followed by ants (40.9%). Most of the termites were workers of Rhinotermitidae. The prey assemblages of N5 were distinguished from those of other *Nepenthes* species by the fact that Mycetophiloidea was the most abundant (40.4%), then in decreasing order are Nematocera (excluding Tipuloidea and Mycetophiloidea, 17.8%), Formicoidea (9.7%), Ichneumonoidea (6.5%), apterous Isoptera (5.3%), Chalcidoidea (3.1%) and Tipuloidea (3.0%).

Further analyses of prey assemblages showed some interesting patterns. Many adults of Mycetophiloidea (especially Scialidae) and of Platypezoidea (especially Phoridae) were trapped in pitchers, while few adults of Culicidae and Ceratopogonidae whose larvae are typical inhabitants of *Nepenthes* pitchers were trapped in pitchers. As for Apoidea, *Nomia* sp. (Halictidae) and *Apis dorsata* Fabricius 1804 (Apidae) were found in N7 and N10 pitchers, respectively, the former had two conspicuous nectaries on inner wall of its pitcher. Two individuals of Mollusca, *Lamprocystis* sp. and *Microparmarion strubelli* Simroth 1893 (both Helicarionidae), were trapped in terrestrial pitchers of N4 and N9, respectively.

We clustered *Nepenthes* species by the composition of trapped prey organisms using Word's method (SAS 1985, Fig. 6). Six *Nepenthes* species were clustered well because their prey organisms were highly dominated by ants. Other *Nepenthes* species, i.e., N3, N4, N5 and N10, had more specific prey assemblages.

Fig. 7 shows the result of canonical discriminant analysis of the prey assemblages

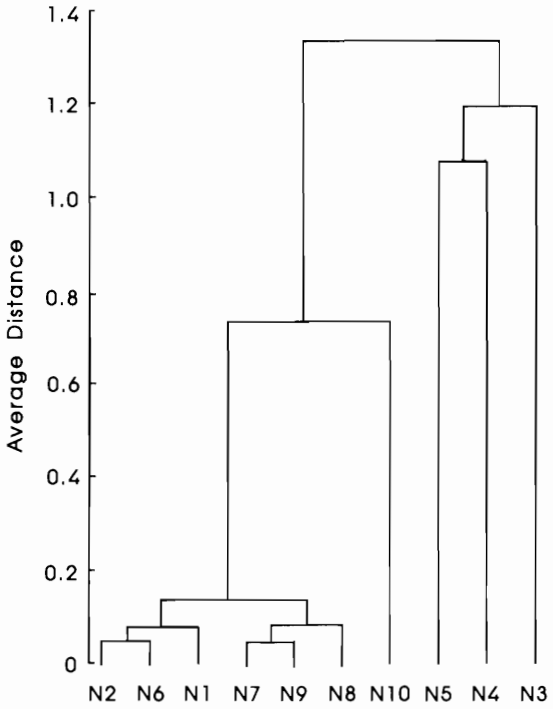

Fig. 6. — Cluster analysis of composition rates of prey organisms trapped per pitcher among *Nepenthes* species.

among 10 *Nepenthes* species. The 1st canonical variable was positively correlated with the numbers of Phalangida, Blattariae, Orthoptera, Vespoidea and Apoidea, and negatively correlated with those of Trichoptera, Nematocera (excluding Tipuloidea and Mycetophiloidea), and Cynipoidea. The 2nd canonical variable was positively correlated with the numbers of Araneida, Homoptera, Trichoptera, Tipuloidea, Mycetophiloidea, Nematocera (excluding Tipuloidea and Mycetophiloidea), Brachycera (excluding Platypezoidea), Ichneumonoidea, Chalcidoidea and Proctotrupoidea but because ants were commonly the predominant prey, it did not characterize specific prey assemblages. Most *Nepenthes* species had largely similar prey assemblages, whereas N5 and N10 had prey assemblages distinct from other species.

Finally, we compared the prey assemblages in pitchers with the arthropod community sampled from Bornean lowland rain forest trees by insecticide fogging (STORK 1987). Table 5 suggests that prey assemblages are significantly different from the arthropod community in the forest canopy, and that prey organisms were not randomly trapped. Generally, the prey assemblage was characterized by the higher proportion of ants and the lower proportion of herbivores (chewers and suckers) and predators than the arthropod community of the forest canopy.

Inhabitant community

All the inhabitants in pitchers except for terrestrial predators (Araneida Thomisidae) were dipterous insects: aquatic predators, *Toxorhynchites* larvae (Culicidae); filter

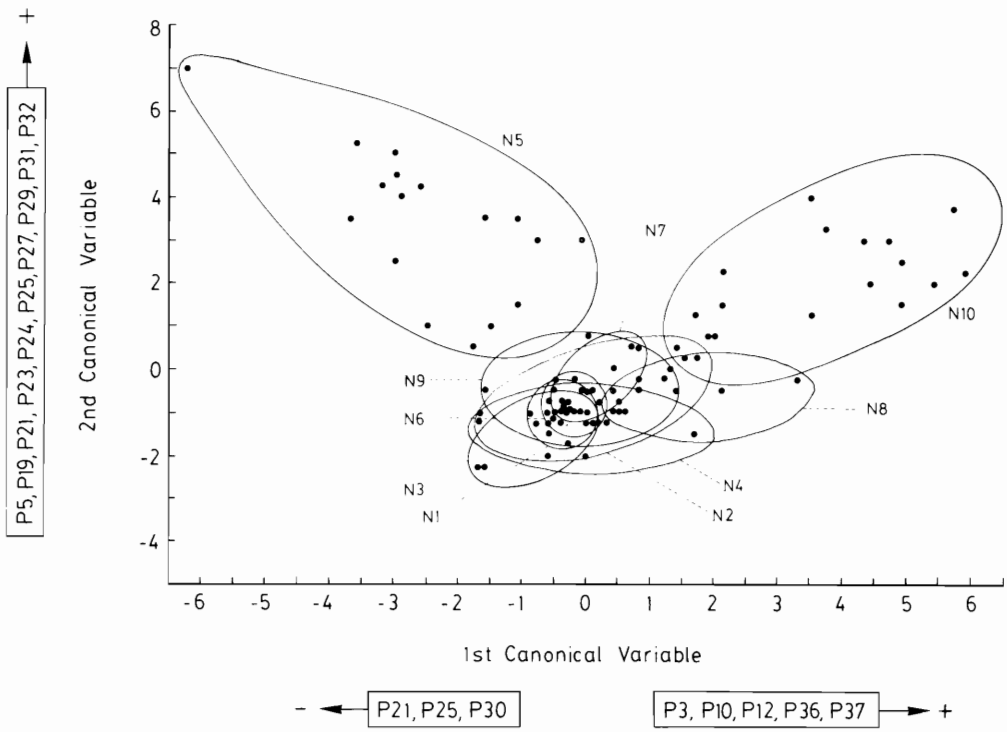

Fig. 7. — Result of canonical discriminant analysis on interspecific variation in prey assemblages in pitchers. Factors affecting the 1st and the 2nd components are shown along each axis.

Table 5.
Percentages of arthropods in *Nepenthes* pitchers and those collected by fogging from Bornean rain forest trees by STORK (1987).

Guilds	*Nepenthes* species code										STORK's tree fauna
	N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	
Chewers	–	0.12	0.18	1.51	0.40	0.24	0.98	0.50	0.67	1.31	13.64
Suckers	0.05	–	0.18	–	1.85	0.24	1.47	0.75	2.75	1.90	11.95
Epiphyte grazers	–	0.07	56.33	1.68	5.29	–	–	0.25	0.16	0.11	7.23
Scavengers	–	0.32	–	7.54	2.02	0.24	–	3.51	2.43	5.61	13.31
Insect predators	–	0.64	–	0.84	1.17	–	0.49	0.50	0.31	2.65	6.37
Other predators	–	0.04	–	–	0.68	0.49	–	–	–	0.72	5.41
Parasitoids	–	0.32	–	3.85	12.55	2.84	3.43	1.27	0.16	0.95	8.36
Ants	99.88	97.38	40.92	71.52	9.73	95.01	90.20	90.20	89.95	56.06	18.41
Tourists	0.06	1.10	2.40	13.06	66.31	0.93	3.43	3.02	3.57	30.69	15.33

feeders, culicid larvae other than *Toxorhynchites;* detritus feeders, ceratopogonid, phorid and syrphid larvae. There was a clear habitat segregation between filter feeders and detritus feeders; the former were swimming in pitcher fluid and the latter were aggregating among prey debris in a narrow, deep hollow at the base of a pitcher. Visitors were phorid flies, which stayed inside the upper part of pitchers probably to mate and/or to oviposit. In addition, we found some herbivores, e.g., unidentified gracillariid moth larvae mining in the parenchyma of pitchers and leaf-like petioles of N2, N5 and N9.

Fig. 8 shows the mean numbers of terrestrial predators, aquatic predators, filter feeders, detritus feeders, visitors and prey organisms per pitcher for 10 *Nepenthes* species. The numbers of terrestrial and aquatic predators per pitcher were usually either 0 or 1 probably through cannibalism. The mean numbers of inhabitants were high in N7, N9 and N10, which had large pitchers. N5 lacked an inhabitant fauna in its pitchers.

The result of principal component analysis on the numbers of inhabitants and prey organisms in pitchers is shown in Fig. 9. The major inter-pitcher trend involved variation in the number of prey organisms trapped per pitcher (1st principal component, 97.3%). The second factor was mainly related to variation in the number of detritus feeders per pitcher (2nd principal component, 2.2%). The aggregation of points in the lower left in Fig. 9 refers to the low density of inhabitants of young pitchers. In N1 and N2, high prey density and low inhabitant density were shown, whereas in N9 and N10 low prey density and high inhabitant density was shown.

By ANOVA, there were significant differences in the number of filter feeders per pitcher among *Nepenthes* species and among pitcher ages, and in the number of detritus feeders per pitcher among *Nepenthes* species (Table 3). Among inhabitants with different feeding types, there was a significant positive correlationship between filter feeders and detritus feeders ($n = 158$, $P < 0.001$). The number of aquatic

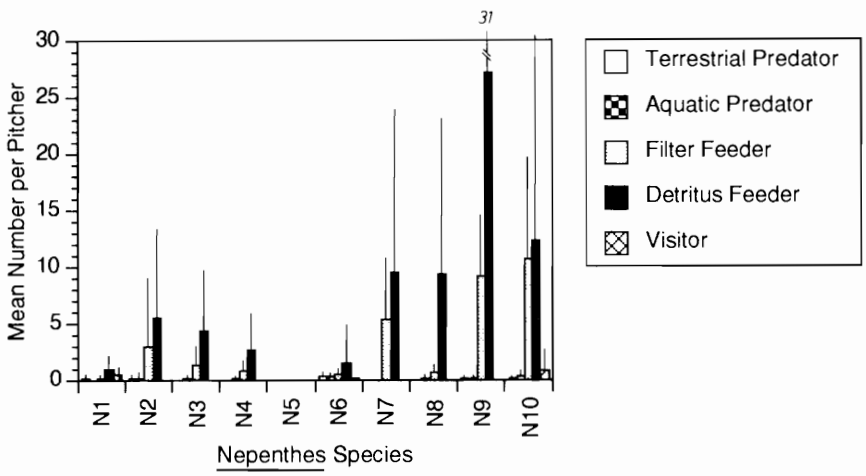

Fig. 8. — Mean number of inhabitants per pitcher for 10 *Nepenthes* species. Vertical bars denote one standard deviation.

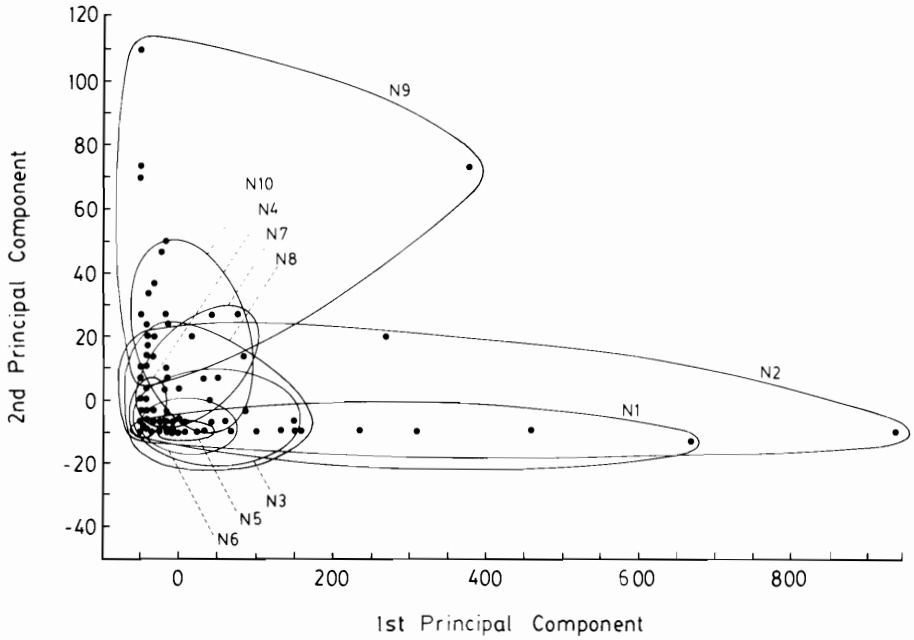

Fig. 9. — Result of principal component analysis on interspecific variation in the numbers of inhabitants and prey organisms in *Nepenthes* pitchers. The 1st and the 2nd principal components were mainly related to variation in the numbers of prey and that of detritus feeders, respectively.

predators was negatively correlated with that of detritus feeders ($P<0.05$) but not with that of filter feeders ($P>0.1$).

DISCUSSION

Because pitcher morphology of *Nepenthes* species is much more diverse than their reproductive and vegetative organs (DANSER 1928), nutrient cycling in a pitcher may be a key process for the evolution of pitcher plants. We discuss some common characteristics and interspecific differences of nutrient cycling from the following three aspects: (1) nutrient inflow, (2) decomposition and digestion and (3) nutrient outflow.

Nutrient inflow

Prey trapping by pitchers is the only process of nutrient inflow in a pitcher. Most pitchers except N5 trapped predominantly ants (Fig. 5) probably attracting them by nectar secreted from nectaries on pitcher rims. Aggregated distribution of ants trapped among conspecific pitchers (Fig. 4) may suggest that some chemicals, e.g., trail pheromone of ants which collected the nectar successfully and returned to its nest, may be participating in the process of prey attraction. Trapping is generally accidental and nectar is regarded as a reward by ants which are rarely sacrificed (JOEL 1988), but recurrent trapping may sometimes have a severe influence on some ant colonies.

Is there any attraction of prey other than ants? N3 caught many apterous termites as well as ants. As termites are not attracted by nectar, the pitchers are thought to adopt some ways to attract foraging termites. However, it is still unknown whether this termite trapping was due to a real attraction of foraging termites or only an accidental event. Large pitchers of N10 often trapped larger individuals of Phalangida and Blattariae. The older pitcher fluid releasing the odour of putrefaction may attract such saprophagous arthropods. The broad peristome of the pitcher rim was dark brown and might mimic some rotten substances.

The prey trapping of N5 was very unique. N5 trapped few ants and many small midges, some of which were adults of potential pitcher inhabitants. The fluid in the pitcher was sticky and contained no living inhabitants. These facts may suggest that the pitcher may attract adults of phytotelmata inhabitants and trap them. The funnel-like pitcher without covering lid can keep a constant volume and possibly constant concentration of enzyme by pouring out surplus water even if rain falls into the pitcher. Although detailed information is lacking, the pitcher fluid may be toxic to all inhabitants, and digest prey trapped in pitchers only by enzymes secreted by itself. Digestion is thought to be possible because the majority of the prey organisms are not ants but adult midges such as Mycetophiloidea which have soft bodies.

Is there any competition for prey among coexisting *Nepenthes* species? Three sympatric *Nepenthes* species in montane forests at Gunung Gadut had different prey assemblages (N5, N9 and N10 in Fig. 7). The availability of prey is thought to be largely similar among the three species because their microhabitats were largely similar. This suggests that the differences between prey assemblages is due to different prey trapping patterns. It is still unknown whether the niche segregation in prey trapping results from competition among the pitchers.

Decomposition and digestion

Prey organisms trapped in a pitcher are decomposed by aquatic inhabitants and digested by enzymes secreted by the pitcher itself and by microorganisms in the pitcher fluid (JUNIPER et al. 1989). Accordingly, the inhabitant community structure must affect the process of decomposition and digestion in a pitcher. *Nepenthes* species other than N5 had a largely similar composition of inhabitants (Fig. 8). Browsing of prey by filter feeders and detritus feeders will accelerate prey decomposition on the whole. Filtration by filter feeders, however, may reduce the density and diversity of microorganism such as bacteria, protozoans and rotifers (ADDICOTT 1974). To detect the relationship between the inhabitant community structure and nutrient cycling in a pitcher, we need analytical and experimental approaches.

BEAVER (1985) reported that food webs in pitchers were more complex in the centre of diversification of *Nepenthes* than in the periphery of its range. In this study in Sumatra where *Nepenthes* has well diversified, the food webs were not always complex. For example, N5 pitchers fostered no inhabitants.

Nutrient outflows

Nutrient outflows from pitcher fluid are the nutrients absorbed by pitchers and the adult emergence of aquatic inhabitants. Inorganic nutrients such as PO_4^{3-} and SO_4^{2-} and organic nutrients such as amino-acids are absorbed by *Nepenthes* pitchers

(LÜTTGE 1965, JUNIPER et al. 1989). Inhabitants in pitchers have been believed to be parasites of pitcher plants because the adult of the inhabitants flies away from pitchers together with nutrients (BEAVER 1979). However, is the nutrient outflow through adult emergence of inhabitants so large? About 8-26% of pitchers of eight *Nepenthes* species fostered *Toxorhynchites* larvae, which were effective predators of other aquatic inhabitants (STEFFAN & EVENHUIS 1981). The presence of a *Toxorhinchites* larva in a pitcher must result in a reduction of the adult emergence rates of aquatic inhabitants. A significant negative correlation was found between the number of *Toxorhinchites* larvae and that of detritus feeders but not between the number of *Toxorhinchites* larvae and that of filter feeders.

The nutrient outflow rate reduced by the food web structure and the putative role of inhabitants in accelerating prey decomposition support the view that some inhabitants may be mutualists of pitcher plants. To detect what kinds of inhabitant communities benefit pitcher plants, an experimental study of nutrient cycling is necessary. Whether natural selection has favored the pitchers which foster inhabitant communities which accelerate nutrient cycling and maximize the pitcher's intake rate of nutrients is a fascinating problem.

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Appendix 1.
Mean numbers of prey organisms trapped per pitcher in 10 *Nepenthes*.

Prey code	*Nepenthes* species code									
	N1	N2	N3	N4	N5	N6	N7	N8	N9	N10
P1	–	–	–	0.05	–	–	–	–	0.04	–
P2	–	–	–	–	–	0.05	–	–	–	–
P3	–	0.04	–	0.18	–	–	–	–	0.33	0.89
P4	0.14	–	–	–	–	–	–	–	0.08	–
P5	–	0.04	–	–	0.24	0.10	–	–	–	0.32
P6	–	0.09	–	0.09	–	–	–	–	–	0.11
P7	–	0.13	–	–	–	–	–	–	–	–
P8	–	0.09	–	0.18	–	–	–	0.11	–	0.53
P9	–	–	–	–	0.19	–	–	0.11	0.04	–
P10	–	–	–	–	–	–	–	1.33	0.17	0.95
P11	–	–	–	–	–	–	–	–	0.08	–
P12	–	0.13	0.13	–	0.14	0.05	0.40	0.22	0.17	0.58
P13	–	0.04	–	0.36	0.29	0.14	–	0.11	0.08	–
P14	–	0.04	41.00	0.05	1.86	–	–	–	–	0.05
P15	–	–	–	–	0.52	–	–	–	–	–
P16	–	–	0.13	–	–	0.05	–	0.11	–	–
P17	–	0.04	–	–	–	–	–	–	–	–
P18	–	–	–	–	–	–	0.20	0.22	0.58	0.16
P19	–	–	0.13	0.05	0.67	0.05	0.40	0.11	0.04	0.68
P20	–	0.04	–	–	0.05	–	–	–	–	–
P21	–	–	–	–	0.29	–	–	–	–	–
P22	–	0.26	–	0.18	0.14	–	–	–	0.04	0.32
P23	–	0.04	–	–	1.05	–	–	–	0.08	0.26
P24	–	0.26	–	–	14.29	–	0.20	0.22	0.13	9.68
P25	–	0.04	–	0.05	6.19	0.05	–	0.11	–	0.89
P26	–	0.13	–	0.14	0.19	–	–	–	–	0.74
P27	–	0.08	1.75	–	0.48	–	0.20	0.56	–	0.21
P28	–	0.30	–	0.14	0.33	0.14	1.00	0.22	0.58	1.21
P29	–	0.17	–	0.23	2.29	0.24	0.20	0.56	0.04	0.42
P30	–	0.09	–	–	0.43	–	1.00	–	–	–
P31	–	–	–	–	1.10	0.10	–	–	–	–
P32	–	0.09	–	–	0.39	0.10	–	–	–	0.11
P33	234.57	105.34	29.88	4.27	3.42	19.42	36.80	39.78	22.92	24.79
P34	–	0.65	–	–	0.28	–	–	–	0.04	0.53
P35	–	–	–	0.05	0.04	–	–	0.11	0.04	0.11
P36	–	0.04	–	–	0.09	–	0.20	0.11	–	0.53
P37	–	–	–	–	–	–	–	0.11	–	0.26