BIOLOGICAL PROBLEMS IN WEST MALESIAN TROPICS: REMARKS FOR THE 1987–1988 SUMATRA RESEARCH

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Introduction

Since 1980 we have carried out field research to analyze the interactions between the human life and the Sumatran natural environment, such as primates, insects and plants, with the cooperation of many Japanese and Indonesian investigators, mainly organized by the staff of Andalas University, under the leaderships of Dr. S. Kawamura (Japanese side) and Dr. Amsir Baker (Indonesian side). Part of this Sumatra Nature Study Project, the Forest Ecology and Botany group (hereafter "Botany group") have established and maintained six forest ecological plots to study forest dynamics in detail, i. e., growth, death, innovation of forest trees and so on, at the Gunung (Mount) Gadut area of West Sumatra Province, and have investigated many ecological and botanical phenomena at the plot and its adjacent areas (Hotta, ed., 1984, 1986b).

We assume that the phenomenon of species richness in the tropics is a natural consequence of explosive variation among the intraspecific populations or complexities of interspecific relationships, and is a response to mosaic structures of divergent environments (Hotta 1986a). From the above points of view, the ecological and botanical studies were carried out beside the field surveys of forest ecological studies, and fruitful results have been already published in part (e. g. Hotta *et al.*, 1985; Okada and Hotta, 1987).

The West Sumatra Province, the region of our main activities, has been noted as a very interesting area for floristic studies since 19th century. For example, the botanical expeditions by P. W. Korthals (1833-34) and by J. E. Teysmann (1855-56) were undertaken in West Sumatra, and Miquel (1862) published a book introducing the flora of Sumatra based on early great mass of herbarium specimens. Many materials were collected from highlands over 1000 m in the Barisan Range. This area is the most frequently undertaken the herbarium collections among the Sumatra Island (van Steenis, 1950). Gunung Kerinci (3805 m alt.) has been repeatedly investigated for flora, because it is the highest mountain in Sumatra Island, by such teams as the Netherland's expeditions (1877-79), C. B.

Kloss' team (1914) (see Ridley, 1917). Although a large amount of material has been gathered from this area, many plants are still little known taxonomically. Our collections are kept at the Faculty of Science, Kyoto University (KYO), Faculty of Science, Kagoshima University (KAGS), Faculty of Science, Andalas University (AND), Herbarium Bogoriense (BO) and some European herbaria. Further studies of these should contribute to the understanding of the flora of West Sumatra. Fundamental collections and long-term and continuous studies are necessary to complete a reliable floristic study of West Sumatra.

Many species described by Miquel based on the materials of Korthals and Teysmann had not been collected again until our survey. We found and collected these 'missing' species, such as *Pentastemona egregia* (Stemonaceae) (Meijer and Bogner, 1983) and *Monophyllaea hirtella* (Gesneriaceae) (Kohyama and Hotta, 1986) in areas lower than 1000 m in West Sumatra. An aroid belonging to the genus *Homalomena* (Araceae) distributed commonly on lower hill areas around Padang is identified as an undescribed species with a peculiar male flower of only one stamen, but no herbarium specimens are deposited in the Herbaria of Bogor, Singapore nor Leiden, the research centers of the flora of the Malesian tropics, in spite of its conspicuous character (Hotta, unpubl.). Such delays in nomenclature and taxonomy hold back ecological and biosystematic studies.

The expedition team of 1987-88 was composed of both Japanese and Indonesian scientists from different specialities. Japanese researchers were M. Hotta, Dr. Sc. (Plant Taxonomy), H. Okada, Dr. Sc. (Plant Cytology), T. Kohyama, Dr. Sc. (Plant Ecology), T. Ichino, M. Agr. (Ecology of Insect) and M. Kato, Dr. Agr. (Ecology of Insect). The Indonesian researchers were Syahbuddin, M. Agr. (Forest Ecology), Idrus Abbas, Dr. Agr. (Entomology), Rusjdi Tamin, Drs. (Plant Taxonomy) and Erizal Mukutar, Drs. (Forest Ecology).

We aimed primarily to maintain and measure six forest ecological plots and to continuously observe the population dynamics such as the growth, death and renewal of trees. We also aimed to observe the coevolutionary relationships between plants and animals in the Malesian wet tropics and analyze how the relationships affect the speciation and the species richness of the areas.

I. Pollination Ecology - Problems Concerning the Coevolution of Plants and Animals

The relationships between pollen vectors and plants in the neotropics have been investigated frequently since Bawa (1974) and Bawa and Opler (1975) worked on the breeding systems of tree species in the tropical rain forests of Central and South America. In the Malesian tropics, however, few studies of pollination have been made. As the first step, we studied the dependence of species diversification upon the effects of pollinators of the certain taxa (Kato *et al.* in this report, p. 15).

(1) The principles on which plants were chosen for this survey

In the temperate zone, where the biota is well known and species are easily identified, it is possible to establish common viewpoints to describe analyze detailed relationships among organisms within the local biota. As a result, it is possible to understand the independent factors of pollination systems as elements of the structure and dynamics of local biomes, not as special cases. However, it is very difficult to analyze the detailed interspecific relationships in regions such West Sumatra which have no reliable floristic and faunistic studies. It is also very difficult to survey what happens at emergent tree canopies over 60 meters height. Irregularity of anthesis in the tropics is another disadvantage for analysis of the phenomena of pollination ecology.

The choice of materials is important for good results under severe conditions. We were only able to spend three months on field surveys, because of a restricted budget. There are various flora and fauna in the Malesian tropics, many of which are still uncertain. Interesting organisms sometimes have confused nomenclature or none at all. Fortunately, much fundamental information concerning flora and insect fauna is deposited in the SNS group, especially concerning bees, some of which act as important pollen vectors. So, we were able to choose the study materials by following certain criteria. We decided to restrict our field of study to the following: 1) taxa that are composed of multiple species and had taxonomical examination, 2) taxa that flower the whole year round and do not have a restricted flowering season, 3) taxa that do not contain any emergent and/or big tree species, and 4) taxa native to Malesia.

Almost all weeds growing around urban areas or by the road side were rejected despite their easiness of approach and of getting detailed data from whole year blooming, because most are exotic and not native. The recently established interrelationships between those exotic plants and insects offered no attraction for the analyses of natural systems in Malesian tropics.

The materials to which we paid our special attention were such genera as *Musa* (Musaceae), *Impatiens* (Balsaminaceae), *Macaranga* (Euphorbiaceae), *Monophyllaea* (Gesneriaceae). The studies on *Macaranga*, however, could not be carried out, because of the difficulties of approach to flowers. Beside routine surveys for these genera, we also searched for pollinators of the flowering plants we could find in the field.

(2) Pollinators of two wild bananas, Musa acuminata *subsp.* halabanensis *and* M. salaccensis

In the genus *Musa*, pollen grain transfer within the same inflorescence never occurs because of the inflorescence structures. The flowers align linearly on inflorescences with female flowers at a basal part, and male at the apical part. The anthesis proceeds from basal to apical flowers linearly within the inflorescence. Therefore, flower timing of each sex is different within the inflorescence. The effective outbreeding systems among different inflorescences are necessary. Judging from the rather high ratio of fruit sets and seed sets per inflorescence in almost all wild bananas, effective pollination must be taking place.

There are two wild bananas in West Sumatra, *Musa acuminata* and *M. salaccensis*. *M. acuminata* is composed of three subspecies, subsp. *halabanensis* (= *M. halabanensis*), subsp. *malaccensis* (= *M. sumatrana*), subsp. *rubrobracteata* (cf. identification list by Hotta in this report, p. 67). These two species have different basic chromosome numbers and belong to different groups: sect. *Musa* and sect. *Callimusa*, respectively. A report concerning the pollinators of wild bananas in Malay is published by Holttum (1954). According to Holttum, *M. acuminata* commonly has dark crimson bracts, pendulous inflorescences and nocturnal flowers and are pollinated by bats, while *M. violascens* has brilliant and bright bracts, erect inflorescences and diurnal flowers and are visited by honey-eating birds. In our survey, it appeared that *M. acuminata* subsp. *halabanensis* has nocturnal flowers and may be primarily pollinated by small-sized bats (Pteropodidae-*Macroglossus sobrinus*), while *M. salaccensis* has diurnal flowers and is visited by two species of honey-eating birds (Nectariniidae-*Arachnothera longirostra* and *Aethopyga siparaja*). Both bananas supply great quantities of nectar. In addition to bats and honey-eating birds, many insects, such as stingless bees, ants and etc., foraged both bananas. They were not, however, recognized as effective pollinators (Ichino, Kato and Hotta, in preparation). A fruit-eating tupai (*Sundasciurus* sp.) also sometimes foraged banana flowers and was possibly an effective pollen vector. It is an interesting phenomenon that fruit-eating bats act as primary pollinators for bananas. The flower structure of Musaceae is recognized to have somewhat specialized characteristics, such as ovary inferior, advance of perianth cohesion and reduction of anther number. These features suggest that the relationship between bananas and bats was established after the specialization of flower structure, but does not suggest primitive flower-animal relationships. Common ancestor of bat of the family Pteropodidae has diverged into two types, one of which has specialized to forage nectar of bananas and become a small-sized bats; the other has enlarged and specialized in foraging fruits.

It is not yet clear whether sect. *Musa* or sect. *Callimusa* is more primitive phylogenetically. Taxa belonging to *Callimusa* have diverged in the West Malesian area. Most are rather small and grow on the forest floor or at the edge of forests. Most have erect inflorescences, brilliant bracts and diurnal green flowers. In contrast, *Musa* have diverged into several species in continental area of South East Asia. Exceptionally, two species of *M. acuminata* and *M. balubisiana*, the mother species of cultivated bananas, are distributed throughout the West Malesian area. They have glaucous dark crimson bracts and nocturnal flowers.

Although mixed populations of both sections are sometimes found in West Malesian area, no natural hybrid between sections has yet been observed (Hotta, 1987). The phenomenon of no hybrid formation may not be connected with the diversity of pollen vectors. Rather, it seems that the phylogenetic difference represented by the different basic chromosome numbers forms an effective barrier for reproductive isolation. The following evolutionary process is presumed to have taken place. First, the relationship between bananas with diurnal flowers and honey-eating birds was established, and as a result bananas began to secrete a greater volume of low concentration nectar. Fruit-eating bats attracted by this great volume of nectar then foraged and pollinated the banana flowers with high volume nectar, and the nocturnal flowers diverged from diurnal ones.

(3) Impatiens *spp., speciation and pollinators*

Certain groups of *Impatiens* have diversiform speciations from Thailand through Malay Peninsula (Shimizu, 1987). Many species have diverged mainly in West Sumatra. Sixteen listed species of *Impatiens* including nine new species (see identification list by Hotta in this report, p. 59) are distributed in West Sumatra. These eight of sixteen belong to the yellow flowered *I. albo-flava* group, and demonstrate conspicuous speciation processes. This group includes *I. diepenhorstii*, which is a tetraploid, and diverged as a rheophyte at rapid stream banks, *I. gadutensis* (sp. nov.), which is a diploid and is found only on the forest floor of the montane oak forest at the summit of Gunung Gadut, and *I. delectans*, *I. paralleloneura* (sp. nov.), and *I. microserrata* (sp. nov.), which are endemic to the young volcano Gunung Kerinci. *I. albo-flava* is a common diploid species found in the understory of wet forests ranging from 200 to 1450 meter.

Two to four species of *I. albo-flava* group sometimes cohabit sympatrically. For instance, we can find four species in the same area around the river Batang Barus on the west slope of Gunung Talang. *I. dipenhorstii* (4x), a rheophytic species, grows on rock walls at the water fall, *I. pyrrhotricha* grows on relatively xeric slopes or hill ridges, and *I. albo-flava* (2x) and *I. talangensis* sp. nov. (8x), the biggest plants in this group, grow at wet places along the stream. At the other ravine several km southward from Batang Barus, *I. albo-flava*, *I. talangensis* and *I. eubotrya* (4x), which has many flowers on raceme infloresces and belongs to a different group from *I. albo-flava*, are distributed sympatrically (see Okada in this report, p. 11).

The main purpose of this survey of *Impatiens* was to analyze its interspecific relationships and to find its pollinators. We also studied how pollinators are connected with the speciation within *I. albo-flava* group (a detailed report by Kato, Ichino, Hotta and Okada is in preparation).

I. platypetala has pink and/or white flowers differing from *I. albo-flava* group and behaves like a weed growing rapidly in open areas. We could not detect any pollinators, in spite of long-term observation of many flowers. The only example of a flower visitor was a hawkmoth (*Macroglossum corythus*). This hawkmoth acted as an effective pollen vector. Fauna which have poor pollinators in spite of the attractive flower color, sunny location and large population size present an interesting problem. The species does not show self-incompatibility. The fact that it has the characteristics of weeds could have encouraged the development of self-compatibility and the establishment of a reproductive system without pollinators.

Impatiens albo-flava group and *I. eubotrya* attracted solitary bees and bamble bees (assumption). The yellow flowers were conspicuous in the dark understory of dense forest. Bees visited them somewhat frequently. The different flower shape between *I. albo-flava* group and *I. eubotrya* requires different foraging behaviour, therefore pollen flow between the two does not occur except accidentally. The observations at ravines along Airsirah Pass and Batang Barus indicate that similar apparent solitary bees pollinated *I. albo-flava* groups. In the case of *I. gadutensis*, the pollinator was presumed to be bumble bees. The endemic species to Gunung Kerinci were probably pollinated by certain bumble bees. We could not find, however, any evidence that each species of *I. albo-flava* group depended for fertilization on its own pollinators, nor prove that the division of pollinators induced the speciation of *I. albo-flava* group. It is clear from cytotaxonomic evidence that these sympatric species exhibited polyploid changes (Okada, this report, p.11). The evidence that diploid level speciation occurred in allopatric species of *I. gadutensis* and *I. albo-flava*, while polyploid changes occurred in sympatric species suggests that the speciation of sympatric species might originate in polyploidization, or that after polyploidization they could inhabit sympatrically.

II. *Nepenthes*, Relationships between Carnivorous Plants and Animals

Our field survey and taxonomical studies of herbarium materials have clarified that Sumatra Island possesses more than fifteen species of the genus *Nepenthes* (Tamin and Hotta, 1986), and twelve of these fifteen species are found in West Sumatra. Three species are endemic to West Sumatra, and *N. albo-marginata* and *N. bongso* are almost entirely restricted to West Sumatra.

The carnivorous plant, *Nepenthes*, has developed pitchers as effective traps of insects. Some species have developed heteromorphy between basal and upper stem pitchers, e.g. *N. rafflesiana*, *N. singalana*, *N. spinosa* etc. Some species [e. g., *N. ampullaria* and *N. rosulata* (= *N. caruncu-lata* Dans., p. p., excl. fig. 1)] have only developed rosette pitchers on the ground and seem to catch only crawling animals. These pitchers offer living spaces to the larvae of some flies and mosquitoes, and also to spiders (Beaver, 1979). However, comparative studies among multiple species with different habitats and different morphology of pitchers have not yet been carried out. In this study we observed the relationships between these *Nepenthes* plants and their victims or inhabitants.

(1) Typification of distribution patterns

Nepenthes in West Sumatra can be categorized into three groups on the basis of altitudinal distribution patterns.

(i) Lowland group - species distributed from lower hill to montane areas up to 1000 meters altitude: *N. ampullaria*, *N. gracilis*, *N. reinwardtiana*, *N. mirabilis*, *N. rafflesiana* etc. All species are also found in the Malay Peninsula and Borneo.

(ii) Montane group - species mainly found at montane areas of approximately 1000 meters altitude: *N. adonata* (restricted to Payakumbuh, West Sumatra), *N. alata* (in North and West Sumatra, Malay Peninsula and Philippine), *N. albo-marginata* (found from one place in North Sumatra, three places in West Sumatra, in the Malay Peninsula and West Sarawak).

(iii) Highland group - found in highland areas higher than 1500 meters altitude: *N. bongso*, *N. singalana*, *N. spinosa*, *N. rosulata*. All endemic to Sumatra.

Highland type *Nepenthes* include many endemic species to Sumatra, and seem to be restricted to Sumatra Island.

(2) Fauna captured by pitchers

The fauna in the pitchers of lowland *Nepenthes* consisted mainly of ants. Usually the pitcher was unable to digest the head part of the ant. The residues indicated clearly how many ants were captured. 300 to 400 individuals were sometimes found in a pitcher. The pitcher may act to supply nitrogen and phosphorus to *Nepenthes*. Many other kinds of animals were also found in pitchers, such as moths, flies, small beetles, bees, millipedes, slugs and so on.

The pitchers of highland *Nepenthes* contained ants rather less frequently the lowland species. The mossy forests in the highlands were too moist throughout the year to offer a good habitat for ants. It is not yet clear whether the low frequency of ant individuals in highland mossy forests gives rise to the low number of ants in pitchers of the highland species or whether other factors must be taken into account.

(3) Pitchers as residences

The pitchers of *Nepenthes* form interesting micro-ecosystems. Water in the pitchers is a good habitats for aquatics, such as the larvae of flies and mosquitoes. It offers not only a safe place from attack, but also supply feeds to them. Except for *N. bongso*, almost all old pitchers are occupied by many kinds of animals. For instance, we very frequently observed larvae of flies and mosquitoes in pitchers. Two kinds of spider were found in pitchers, one net-making and the other not, but they were always an individual of the same species in a pitche. The lack of living space and resources in the pitcher may limit the number of inhabiting carnivores.

These inhabitants are all carnivores. Some say that these carnivores are symbionts because they crunch their captives into small pieces and assist quick digestion by the plant. Contrary to this opinion, the bacterial flora in the pitcher, not the carnivorous inhabitants, may contribute to the digestion of the captures. The carnivorous inhabitants usually live in old pitchers which have little capacity to secrete digestive enzymes. But the enzyme activities of the old pitchers suddenly became higher when insects were captured. This arises from the activity of the digestive enzyme of certain bacteria, not from the pitcher's own enzyme (S. Higashi, pers. comm.).

(4) Pollinators unknown

In the genus *Nepenthes*, genetical isolation mechanisms between species do not seem to be completely established. There are some reports on natural hybrids, and we have observed interspecific natural hybrids in the field. Dioecious flowers of *Nepenthes* and the formation of mixed population with multiple species of the genes indicate the possibility of interspecific hybrids in nature.

The pollination system of the genus, however, is not yet known. Flower color (dark brownish-crimson) suggests that flies act as a pollen vector. But we failed to find any evidence that insects visited the flowers of *Nepenthes*. It is not easy to imagine that their tetrad pollen grains adapt to wind pollination. The evidence that populations with both female and male individuals showing large numbers of fertile fruit suggests the establishment of certain effective pollination systems. Some mixed populations produce good fruit in appearance, but the fruit rarely contain fertile seeds. This phenomenon may arise from the independent mechanisms of fruit development and fertilization. Fruit may develop by chemical substances contained in the incompatible pollen grains, such as gibberellin.

III. Tropical Rain Forest; Systems and Dynamics

Gunung Gadut is covered by a well developed and little disturbed forest which represents a typical tropical rain forests at the highest temperature and humidity on earth. It is thought that the forest has more than 7000 mm precipitation per year (Hotta, ed. 1984). Relatively dry seasons are recognized to occur twice a year, but even the dry seasons have more than 300 mm precipitation per month, which is more than the most monthly precipitation of Medan, North Sumatra, or Jakarta, Java.

Since 1980, when the SNS project started, we have established six permanent plots for the study of forest ecology in this highly humid area, namely Pinang Pinang, Pinang Pinang Bawah, Pinang Pinang Atas Transect, Gajabuih, Airsirah and G. Gadut. Measurements of dbh (trunk diameter at breast height) of ca. 3000 trees in these plots have been carried out continuously. These plots have been used for analysis of the spatial distribution pattern of certain species and the dynamics of understory herbaceous species (Hotta, 1984, 1986b; Hotta *et al.* 1985, Okada in this report, p. 49).

From 1987 to 1988, we measured the dbh of all trees in the plots as a fundamental and continuous study of forest dynamics. At the same time, identification of tree species was carried out, and the hitherto unidentified tree species which had the biggest dbh in the Gajabuih plot was determined as *Deplanchea bancana* (Bignoniaceae). This tree species is very rare in our study areas. We have found only three individuals in the Ulu Gadut Valley so far. Large areas of the Gajabuih Plot were destroyed by high winds on August, 1986, and forest renewal is now proceeding rapidly. Analysis of the process of renewal in this forest may contribute to the understanding of the dynamics of higher humid tropical forests. The branching architecture and allometry of saplings were also studied from the viewpoint of forest dynamics by Dr. Kohyama. The huge quantity of data from our continuous measurements must await future analysis. The article by Kohyama, Hotta, Ogino, Syahbuddin and Mukhtar in this report (p. 33) is merely a complication of the most fundamental data.

The forests of Gunung Gadut have several distinguishing characteristics from Malesian tropical forests in Malay Peninsula and/or Borneo (see Fox, 1973; Manokaran and Kochummen, 1987). The foothill Dipterocarp forest of Gunung Gadut, i.e. Pinang Pinang and Gajabuih had a rather low density of Dipterocarpaceae, and in contrast to other areas, *Swintonia schwenckii* dominates the emergent layer more than 50 meters high. The first layer, ca. 30-40 meter high, consists of many kinds of tree species, but in family level trees of Fagaceae, such as *Lithocarpus* spp., *Castanopsis* spp, *Quercus gemelliflora*, dominate. Rich flora and individuals of herbaceous plants in the understory were characteristic. Aroids, *Homalomena* and *Schismatoglottis*, grow particularly frequently from stream side to hill ridge. These distinguishing characteristics may arise from extremely wet environmental conditions.

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