REPRODUCTIVE ECOLOGY OF TROPICAL FOREST PLANTS
Research Insights and Management Implications

by
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Preface

The unabated devastation of tropical wildlands has become one of the most pressing issues of our times. Not only are the rates of deforestation very high, but also approximately 40% of the existing forest areas have been degraded in recent times. It is estimated that tropical rain forests will largely disappear in about 30 years time, except for those that might be conserved as nature reserves. Obviously there is a need for greater investment in scientific research in ecology, conservation and management of tropical rain forests worldwide.

There are three crucial interrelated issues that a manager of indigenous forests must address: depletion of forest resources, regeneration and restoration of forest ecosystems, and conservation of genetic resources. The challenges generated by the reduction and degradation of forest cover can be adequately met only if serious attempts are made to manage and restore forest ecosystems. Restoration inevitably must involve improved reforestation of degraded lands through plantations of native species, and the extension of forest boundaries by artificial and natural regeneration. Finally, coupled with effective management including restoration, conservation of existing genetic resources is of high priority. The resources to be conserved and the manner in which they ought to be conserved are serious issues requiring strong scientific input.

Most research on the reproductive ecology of tropical forest plants from flowering to regeneration, however, has had strong theoretical underpinnings. The test of predictions emerging from hypotheses relating to coevolution and the structure, organization and dynamics of communities has been a major impetus for much of the work. Nevertheless, many types of basic research in reproductive ecology have strong practical applications in management and conservation of forest resources (Bawa and Krugman, 1990).

In June 1987 a workshop on the reproductive ecology of tropical forest plants was held at Bangi, Malaysia, to review recent research in plant reproductive ecology and to examine the application of such research to the management and conservation of forest resources. Reproductive ecology was defined to include all stages of reproduction from the initiation of flowering to seedling establishment. The workshop was jointly sponsored by the Man and Biosphere...
Program of Unesco and the Decade of the Tropics Program of IUBS, in cooperation with the Malaysian MAB National Committee and the Universiti Kebangsaan Malaysia. It was based on 20 invited papers and some 50 offered contributions, in the form of both oral and poster presentations.

In this report, we provide a brief summary of the invited papers in the context of major issues and points raised by the workshop participants. Sections correspond more or less to the various sessions of the workshop. The full text of the papers is being published as a separate volume in Unesco’s Man and the Biosphere Book Series (Bawa and Hadley, 1990).
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Reproductive cost in relation to stand structure and plantation design

In Asia, the great majority of trees with fleshy fruits are components of the mature phase of the forest in the main canopy (e.g., mangoes, rambutans) and the understory (e.g., mangosteens, also the neotropical Annona fruits). The principal timber trees are emergents, both forest gap and building phase species producing light industrial hardwood often lacking heartwood (e.g., Albizia, Dyera, Alstonia; also Hevea and Ceiba), and quality timber species of the mature phase (Shorea, and the principal leguminous, meliaceous, and lauraceous timbers). However, most of these timber species have dry fruits and seeds, often wind dispersed or gyrating. Dioecy (separate sexes) in tropical trees is associated with fleshy fruits (Bawa, 1980; Givnish, 1980). It is interesting that Ashton (1969) observed an increase in the representation of dioecious individuals from less than 5% in the emergent stratum of Far Eastern Mixed Dipterocarp Forest to more than 30% in the understory, the large representation of emergent juveniles in the latter notwithstanding. Forest fruit and timber trees therefore substantially avoid competition for space.

These facts provide opportunities, long known to subsistence farmers in the tropics but only recently entering into commercial plantation practice, of increasing profitability by more efficient use of space through multiple species, multiple product, plantations. A notable advantage of this approach is that a much earlier return can be made on investment in quality hardwood timber plantation, by interplanting with rattan and fruit trees which can be culled from 6-10 years age onwards. Other advantages are that such plantations are well suited to small-holders and increase labor intensity. They are therefore socio-politically more acceptable than pure timber plantations, and the timber trees included in them are hence more secure.

The genus Parkia is unusual as it includes relatively fast growing trees of the building phase which not only provide light shade favorable to quality hardwood regeneration, but also highly nutritious fruit. Likewise, the durians (Durio section Durio) are mature phase emergents yielding both fruit and qua-
lity timber. There are some 20 species of durian, and up to six species are cultivated in some ancient centers of settled agriculture such as Brunei Darussala. Different species have different soil preferences, several occurring in nature on infertile podsolized soils, thus providing improvement opportunities for agricultural diversification through breeding, and their use for rootstock and for grafting.

In general, though, genetic improvement must be directed to increasing the yield of a single commodity; plants survive by performing at their maximum potentiality for their site and genotype. Increase in yield of fruit by one species can therefore only be achieved at the cost of reduced wood production, and vice versa. Thus, Primack et al. (1989) have found evidence that increment declines drastically in the occasional mast fruiting years during which the meranti and kapurs (Shorea, Dryobalanops, Dipterocarpaceae), prime timber trees, reproduce in western Malesia (Fig. 1). This may be because these trees produce inflorescences instead of a seasonal leaf flush, thus reducing their leaf area by perhaps as much as half. Interestingly, Dayanandan et al. (1990) have found that the exceptionally fast growing tiniya dun (Shorea trapezifolia) of Sri Lanka not only flowers annually, but produces inflorescences and a new leaf flush simultaneously. These properties identify tiniya dun, with its readily available seed (albeit lacking dormancy) and its rapid growth, as a plantation species of unusual promise. The possibility of transferring the gene responsible for its simultaneous reproductive and vegetative growth to other Shorea also arises.

![Fig. 1. Mean growth rates of Engkabang (Shorea splendida) in a plantation and a primary forest given improvement felling in Semengoh Forest, Sarawak, East Malaysia over a 19 year period beginning 1936. The figure shows that growth rates decline dramatically prior to flowering. [From Primack et al. (1989).]](image)
The mangosteen (*Garcinia mangostana*), well known for its slow growth rate, belongs to a genus in which flowers and fruit are presented in the shade of the forest understory. Jamaluddin (1978) and Ashton and Hall (in prep.) have evidence that members of the understory guild, which often start flowering early in life, can manifest exceptionally low maximum girth growth rates. These small trees may include some of the oldest individuals in the forest. Here, it seems, natural selection may have already favored fruit over wood production. This needs to be taken into account in selecting new species for introduction, and in breeding programs.

The mangosteen is dioecious, but the male tree is unknown in cultivation and the tree reproduces apomictically. Bawa (1980) and Givnish (1980) hypothesized that dioecy may be causally associated with seed dispersal by vertebrates, that is with large seeds and fleshy fruits. In this case knowledge of the breeding system is essential to enable increases in fruit production because the number, if any, of male trees to maximize fruit trees in a stand has to be balanced against the loss of space for fruit production which must instead be allocated to males.

There is growing evidence of site-related differences in fecundity among tropical trees. There is evidence of reduction in average fruit size and nutritional value in mixed-species stands with decline in soil fertility (Ashton, unpublished data). Wood (1956) implied that dipterocarps in peat swamps may flower less frequently than in more fertile dry land sites, and this has been confirmed in an unpublished phenological report by the silvicultural staff of the Sarawak Forest Department. Burgess (1972) found that *Shorea leprosula*, a fast growing species of mesic sites, flowers more frequently than others in its section in Peninsular Malaysia. C.V.S. and I.A.U.N. Gunatileke and their students (in prep.) have observed that *S. trapezifolia*, *S. disticha* and *S. worthingtonii*, which respectively occupy the mesic, intermediate and xeric parts of the catena in Sinharaja forest in the wet lowland of southwest Sri Lanka, flower in declining frequency and intensity. These observations imply that poor sites can be expected to yield less timber and also less fruit than favorable sites.
Phenology

Phenology of tropical rain forest plants raises a number of interesting questions. In a seemingly aseasonal climate, what cues do plants use for the initiation of vegetative and reproductive growth? Given the lack of notable variation in climate, why do different species initiate vegetative growth and reproduction at different times? What accounts for tremendous variation in patterns of leaf flushing and flowering among species? Why do some species flower more than once a year, others once a year and still others every two or more years? How is the phenology of plants correlated with the phenology of pollinators and herbivores? How does selection from such diverse forces as herbivores, pollinators, seed dispersal agents and seed predators influence patterns of leafing, flowering and fruiting?

Answers to such questions require characterization of phenological phases with respect to timing, duration and frequency at the level of species. In recent years a number of phenological patterns have been described in tropical forest plants but the possible factors underlying these patterns largely remain obscure. Two out of the three invited papers in this section of the Bangi workshop, one from Malaysia (Yap and Chan, 1990) and the other from Costa Rica (Frankie et al., 1990), summarize data on the phenology of trees, and the third describes the results of an empirical study undertaken in Panama aimed to elucidate factors responsible for the initiation of flowering (Wright and Cornejo, 1990).

General mass flowering at irregular intervals is a notable feature of many aseasonal forests in Southeast Asia. This flowering pattern is characterized by supraannual flowering and may involve one species, a group of related species or a majority of species in the community. Yap and Chan (1990) describe community-wide general flowering in dipterocarp forests. They observed 310 trees belonging to 16 species of Shorea over an 11 year period at four sites. Mass flowering occurred in the years 1976, 1981 and 1983 (Fig. 2). The proportion of species and individuals that participated in mass flowering varied from one episode to another. Moreover, Yap and Chan show considerable site specific variation in phenological response of species. Not only was the intensity of flowering different at the four sites, but also some species flowered at one site but not at the other(s).
Yap and Chan’s study also shows that mass flowering can occur at different times of the year in different episodes. For example mass flowering in Malaysian forests has been generally recorded to occur in the April-May period (Burgess, 1972; Ng, 1977). However, in 1981 mass flowering occurred in September-October. Ng (1981) has shown two leaf flushing peaks in April and October in dipterocarps of Peninsular Malaysia. Generally, the flowering of dipterocarps is associated with the leaf flushing in April, but in 1981 it apparently was also associated with the leaf flushing in October. Dayanandan et al. (1990) also note two periods of flowering for dipterocarps of Sri Lanka, in April-May and November-December.

There is no documentation of the response of pollinator populations to mass flowering. Appanah (1990) remarks that there is general abundance of insect pollinators during periods of mass flowering. In 1976, Ng (unpublished observations) noted a marked increase in the number of pollen collecting bees. One might assume that population densities of pollinators decline during off-years. Yap and Chan have observed that flowering in off-years generally does not result in fruiting. Lack of fruit set could be due to insufficient pollinators or resource depletion from the previous mast fruiting episode.

Janzen (1974) has attributed the evolution of mast fruiting to the pressure from seed predators. According to Janzen, production of large quantities of seeds after intervals of more than one year results in the satiation of seed predators. Satiation allows the escape of many more seeds from the predators than would be the case if trees were to flower every year and produce smaller quantities of fruits. Ashton et al. (1988) have suggested that the cue for floral induction in mast fruiting species is a drop of approximately 2°C or more in minimum night-time temperature for three or more nights.

![Flowering Chart](image)

**Fig.2.** The proportion of 310 individual trees belonging to 16 species of *Shorea* flowering in four study sites in Malaysia during 1973-1983.

[From Yap and Chan (1990).]
Phenology: Key points

What is known

- Each tropical forest community has its own distinctive yearly pattern of flowering and fruiting.
- Flowering and fruiting at the community level are more or less regular in some communities on an annual basis while in other communities flowering and fruiting are highly irregular, abundant in some years and scarce in others.
- Species within a community differ with respect to when they begin flowering, how long they flower and how often they flower.
- For each species, plants in a population may flower at the same time or asynchronously, individuals may flower for a few days or several months, and episodes of flowering may occur several times a year, once a year or once every several years.

What is not known

- The environmental cues that result in the initiation of flowering and subsequent fruiting.
- Why gregarious widespread flowering at several years interval is common in some communities but not in others.
- How different flowering patterns affect the degree of genetic variability in each species.
- How variation in flowering and seed production affects the number of seedlings on the ground and future numbers of adult plants.
- The effect of logging and opening up of the canopy on phenological patterns.

Frankie et al. (1990) summarize the results of their comprehensive studies of phenology and plant-pollinator interactions. In contrast to the Malaysian dipterocarp forests, most tree species in neotropical lowland rain forests in Central America flower annually, though some species do flower biennially (Frankie et al., 1974). In the neotropics, phenology of various species at the population level has also been examined (Bawa, 1983 and references therein). Studies at the population level show considerable year to year quantitative variation in flowering and fruiting.

In order to understand the coevolution between flowers and their pollinators, studies of flowering phenology ought to be coupled with studies of the phenology of the associated pollinators. Frankie et al. (1990) also briefly describe their comprehensive investigations of the biology of bees, including their nesting behavior, feeding and mating ecology and population dynamics. It is apparent that our knowledge of the behavioral ecology and population biology of tropical pollinators is rather limited, yet crucial for the conservation and management of forest resources.

It has often been suggested that water availability is a critical factor in the initiation of flowering in many tropical trees. The suggestion is based on the observation that many species in neotropical forests initiate flowering in the
dry season. Wright and Cornejo (1990) describe the results of an unusual experiment conducted to determine if moisture stress is indeed responsible for the timing of flowering. They continuously irrigated forested areas in Panama during the dry season to maintain water level at a certain threshold. They found that irrigation had no effect on the flowering periodicity. Wright and Cornejo conclude that water availability is not the proximal cue for flowering for many species, but emphasize that long-term observations are required for a firm conclusion.

A vast body of knowledge about leafing, flowering and fruiting periodicity of tropical forest plants, both at the level of communities and of individual species, has been developed during the last two decades. This information has revealed considerable spatial and temporal variation in phenological patterns. Species differ with respect to timing, duration and frequency of flowering and fruiting (Primack, 1985). Moreover, communities differ in terms of overall phenological patterns. For example, the type of mass flowering that has been observed in the Southeast Asian rain forests (Yap and Chan, 1990) has not been noted in the neotropics. Clearly phenological patterns of tropical forest trees are diverse and complex. Equally complex are the factors that regulate these patterns. It is thus not surprising that despite considerable research on phenology in recent years, we are still far from developing any predictive models of flowering or fruiting. Because the patterns of leaf flushing, flowering and fruiting influence populations of herbivores, pollinators and seed dispersal agents respectively, an understanding of phenology — the patterns as well as the underlying factors — is basic to the understanding of a wide variety of species interactions in tropical forests.

The year to year variation in seed and fruit set is also likely to influence population recruitment. Moreover, if the number of mating individuals varies greatly from one flowering episode to another, different cohorts may also differ in the amount of genetic diversity contained within the cohorts. As mentioned earlier, the consequences of temporal variation in seed output on population recruitment and the generation of genetic diversity have not been examined.

The effect of logging on phenological patterns is not known, but is an area that should be of primary concern to the forest manager. Logging may change the environmental regime and the spacing patterns of the conspecific trees. Both changes may influence the amount of flowering and fruit and seed set. Altered spacing and phenological patterns may also change the mating relationships with unknown genetic consequences.

A detailed knowledge of flowering and fruiting patterns is also critical for the successful management of forest genetic resources. Information about seed and fruit set and seedling establishment schedules is required for in situ management of forest stands for conservation as well as production. Characterization of phenological patterns at the level of species-populations is of utmost importance to the tree breeder. In several species, individuals within a population mature seeds asynchronously. Seeds collected at only one point in time in such populations may not adequately represent the genic diversity of the population. Thus adequate sampling for ex situ collections may require gathering of seeds in the years when the maximum number of individuals participate in the reproductive episode.
Plant-pollinator interactions, sexual systems, gene flow and genetic variation

Plant-pollinator interactions, sexual and breeding systems, and levels of gene flow in tropical forest trees are of interest for several reasons. Many species of trees in tropical rain forests have densities of one reproductively mature individual or less per hectare (Hubbell and Foster, 1983). Spatial isolation of conspecifics could result in limited pollen flow and inbreeding unless mating patterns are such that they allow considerable outcrossing. Thus for many years, the extent of inbreeding and outcrossing has been a central issue in the population biology of tropical forest trees (Ashton, 1969; Bawa, 1979). In recent years a great diversity of pollination mechanisms and breeding systems in rain forest trees has been documented (Appanah, 1981; Chan, 1981; Bawa, Perry and Beach, 1985; Bawa et al., 1985; and references therein). The diversity of pollination mechanisms coupled with taxonomic diversity in tropical rain forests has also allowed excellent opportunities to study the degree of coevolution between plants and their pollinators (Feinsinger, 1983). Finally, the study of spatial and temporal distribution of various plant-pollinator interactions at the community level has provided insights into the role of such interactions in community structure (Stiles, 1978; Appanah, 1981; Bawa et al., 1985).

In the lowland wet tropics, pollination mechanisms and sexual and breeding systems have been studied most extensively at two sites: La Selva in Costa Rica and Pasoh forest in Malaysia. Schatz (1990) and Appanah (1990) respectively summarize the results from these two sites. Dayanandan et al. (1990) present results of their comprehensive studies on the pollination ecology of the Dipterocarpaceae in Sinharaja, a premontane wet tropical forest in Sri Lanka. Irvine and Armstrong (1990) examine interactions between plants and beetle pollinators in an Australian rain forest. Young (1990) provides estimates of pollen flow in an aroid herb. Shaanker and Ganeshiah (1990) review the relationship between patterns of pollen deposition and the number of seeds per fruit.
Plant-pollinator interactions

Schatz and Appanah note that at both La Selva and Pasoh, tree species are largely outcrossed via self-incompatibility or by virtue of being dioecious. Apomixis has been reported for some species at Pasoh, but species at La Selva have not been examined from this point of view. Studies of herbaceous species at La Selva reveal a higher incidence of self-incompatibility than encountered in trees (Kress and Beach, 1989).

Pollination mechanisms at both sites are diverse. Bawa et al. (1985, reviewed in Schatz, 1990) have shown that the relative frequencies of various pollination systems are dissimilar in different strata of the forest. Appanah's qualitative observations in Malaysia confirm the quantitative trends noted for the Costa Rican rain forest. Studies at both sites show that the diversity of pollinators is greatest in the understory. Schatz distinguishes between diurnal and nocturnal pollination systems. He points out that the former are driven by visual cues and the latter by odors. The diurnal pollination systems appear to be more common in the canopy and the nocturnal in the understory. Pollination 'guilds' consisting of species sharing the same vectors have been studied extensively in the case of hummingbird pollinated plants (Stiles, 1978) and beetle pollinated plants (Schatz 1990; Irvine and Armstrong, 1990). Irvine and Armstrong note that in Australia, the nocturnal beetle pollination system is encountered in all life forms and at all levels of the forest. They also suggest that beetle pollination may be more common in Australian than in neotropical rain forests.

Dayanandan et al. (1989) report the results of their comprehensive studies of flowering, floral morphology, pollination mechanisms and breeding systems in the Dipterocarpaceae. They show that various species of Shorea differ in their flowering patterns. In Vatteria copallifera, flowering patterns vary among populations. Trees in open, disturbed habitats flower more frequently than trees in closed, undisturbed forests. Dayanandan et al. show that species of Shorea and Vatteria, like other tropical rain forest trees, are mostly outcrossed. The principal pollen vectors are bees. Dipterocarpaceae are a dominant component of the canopy and many species are commercially exploited. The information on reproductive biology provided by Dayanandan et al. should be of considerable importance in the conservation and management of dipterocarps.

Young (1990) describes the reproductive biology with particular reference to the movement of pollen flow in an understory aroid. Estimates of pollen flow and effective population size provide important insights into the dynamics of micro-evolutionary process as well as conservation strategies. There is an urgent need to extend the type of study conducted by Young to other plants.

In many species of plants all ovules do not mature into seeds. Many factors are involved in the abortion of ovules. Shaanker and Ganeshiah (1990) examine the role of pollen deposition patterns in regulating the number of seeds. They note that in many multi-ovulated species a large fraction of ovules develop into seeds. Shaanker and Ganeshiah show that the high level of seed set is due to the deposition of many grains on the stigma. Flowers receiving pollen grains fewer than the number of ovules are aborted. Shaanker and Ganeshiah's research shows the existence of subtle pre-fertilization mechanisms employed by plants to regulate their reproductive output. Elucidation of such
Plant-pollinator interactions, sexual systems, gene flow and genetic variation: Key points

What is known

- A diverse array of animals from insects to mammals pollinate plants in tropical forests.
- The proportion of plant species pollinated by various pollen vectors varies from one stratum to another within the same forest.
- Tropical forest plants also display tremendous variation in sexual systems ranging from apomixis (uniparental reproduction) to obligate cross-pollination.
- In a few canopy species investigated to date, mating systems are such that individuals scattered over a large area appear to interbreed with each other more or less at random. This implies that canopy species have large effective population sizes.
- Tropical species show diverse patterns of genetic variation; some species are apparently genetically uniform, others highly variable.

What is not known

- The extent to which plant-pollinator interactions are specialized.
- The effect of variation in composition of plant species on pollinator populations, and conversely the effect of changes in pollinator fauna on plant populations.
- Variation in the level of inbreeding within species and among species and the effect of plant density on the level of inbreeding.
- The effective population sizes and the levels of gene flow among populations.
- The effect of fragmentation and isolation of habitats on populations of pollinators, and the level of inbreeding in plants.

mechanisms helps us understand the evolution of plant reproductive strategies, as well as the factors limiting seed and fruit set. Such studies also demonstrate the close relationship between pollination and seed and fruit morphology (see also Primack, 1987).

The detailed investigations of specific pollination systems are just beginning and much remains to be learned. Attempts to gather information about pollination of large canopy trees in tropical rain forests are still in a very preliminary stage. For many commercially important species, we have virtually no knowledge about the mode of pollination or the extent to which there is a species specific relationship between the pollen vector and the plant species. Our knowledge about the dynamics of pollinator populations in tropical forests is also poorly developed. As stressed by Schatz, Appanah, Irvine and Armstrong and others, comprehensive data on flowering patterns, floral rewards and sexual systems are required to elucidate the structure and functioning of reproductive systems at the level of species, groups of related species and communities.
Papers in this section of the Bangi workshop revealed the diversity and complexity of reproductive systems of plants in tropical lowland rain forests. At the community level, pollination mechanisms of tropical rain forest trees involve a wide variety of vertebrates and invertebrates as pollen vectors (Table 1). Species specificity in pollination mechanisms is rare, and each species of pollen vector may service many species of plants either at the same or at different times. Thus the maintenance of a particular plant species within an ecosystem may be contingent upon the presence of other plant species which serve as a continuing resource for its pollinators. However, little is known about the extent to which the perturbation of species diversity in an ecosystem might influence specific plant-pollinator interactions.

Community wide studies indicate that the diversity of pollination mechanisms is greatest in the understory and that the maintenance of the understory may be critical to the overall integrity of the interactions in the community. Within the community are the various guilds. Some of these guilds, as for example the hummingbirds and their host plants, are well-studied (Stiles, 1978); others such as the beetles are the targets of intensive studies as pointed out by Schatz and Irvine and Armstrong in their contributions to the Bangi workshop. The number of pollinators as well as plant species involved in these guilds vary among the pollinator guilds as well as geographical regions. The factors that limit the number of species of a guild is an important theoretical issue. The effect of removal of one or more species of plants on other plant species pollinated by the same group of vectors is a significant management issue. At this level the specificity of plant-pollinator interaction is not well understood. Nor is the geographical variation in the interaction well documented. The extent of specificity as well as geographical variation have important theoretical and practical implications.

Table 1. Frequency of pollinator classes among a sample of 143 tree species at La Selva Biological Station, Costa Rica.

<table>
<thead>
<tr>
<th>Pollinator Class</th>
<th>% Tree Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bat</td>
<td>3.0</td>
</tr>
<tr>
<td>Hummingbird</td>
<td>4.3</td>
</tr>
<tr>
<td>Small Bee</td>
<td>14.0</td>
</tr>
<tr>
<td>Medium-sized to Large Bee</td>
<td>27.5</td>
</tr>
<tr>
<td>Beetle</td>
<td>7.3</td>
</tr>
<tr>
<td>Butterfly</td>
<td>4.9</td>
</tr>
<tr>
<td>Moth</td>
<td></td>
</tr>
<tr>
<td>Sphingid</td>
<td>8.0</td>
</tr>
<tr>
<td>Other</td>
<td>7.9</td>
</tr>
<tr>
<td>Wasp</td>
<td>4.3</td>
</tr>
<tr>
<td>Small diverse insect</td>
<td>15.8</td>
</tr>
<tr>
<td>Thrip</td>
<td>0.6</td>
</tr>
<tr>
<td>Wind</td>
<td>2.5</td>
</tr>
</tbody>
</table>

[Source: Bawa et al. (1985).]
Sexual systems

In terms of sexual and breeding systems, there is now overwhelming evidence that a majority of tree species in tropical rain forests are outcrossed. However the presence of apomixis in several species indicates that uniparental reproduction occurs. The challenge is to quantitatively estimate the relative frequency of outcrossing, selfing and apomixis among the progeny of the same individual or population. Genetic markers in the form of allozymes recently utilized to estimate quantitatively the amount of outcrossing in tropical tree species offer the potential to investigate the mating patterns and mating systems in more detail than hitherto possible (O’Malley and Bawa, 1987; O’Malley et al., 1988).

Gene flow and genetic variation

Genetic markers are also expected to be used increasingly to estimate gene flow, effective size of populations and the amount and patterns of genetic variation in populations (Bawa and Krugman, 1990). Despite rapid progress in understanding the reproductive modes of trees, information about their population genetic parameters remains very meager. Yet such information is critical for designing effective strategies to maintain genetic diversity in nature reserves, and ex situ collections.

For example, within a geographical area, even at a local scale, a large continuous population may in fact be a metapopulation, composed of genetically differentiated subpopulations (Lande and Barrowclough, 1987). The extent to which a population may be subdivided depends upon the interaction among genetic drift, inbreeding, selection and migration. Effective population size (Ne) determines the potential for subdivision within a population. Everything else being equal, a large effective population size decreases the potential for subdivision and inbreeding and a small effective population size has the opposite effect. Patterns of pollen and seed movement within a population are the primary determinants of effective population in plant populations.

The boundaries of a nature preserve may not coincide with the boundaries of subpopulations. Moreover, the genetic structure of the metapopulation included in the preserve may differ for various species. While common species may be represented by one or more subpopulations, rare species may have so few individuals that they do not constitute a viable breeding population.

As mentioned earlier, not much is known about the genetic structure of populations in tropical forest trees. Limited evidence indicates that there is little genetic differentiation among forest stands separated by a few to scores of kilometers (Bawa and Krugman, 1990; Hamrick and Loveless, 1989). Thus it seems that at least in some species effective population sizes may be large, requiring extensive area for conservation of tropical forest tree populations.

Although populations show little genetic divergence in the few species investigated so far, genetic diversity within population in terms of polymorphic loci and heterozygosity is high. However, there are also species which show
little genetic variation within populations, but considerable differentiation between populations.

Patterns of genetic variation may also be apparent in patterns of phenotypic variation. Ashton (1969, 1984) has indicated that this might be so among rain forest trees species in Asia. Striking is the general tendency for taxa to manifest extraordinary morphological uniformity throughout their geographical range, which can often be large. Sympatric, closely related, species differ morphologically in small ways which are nevertheless constant throughout their ranges. In Dipterocarpaceae, taxa in which geographical subspecies are recognized, and which have been examined, have been found to be facultatively apomictic, suggesting that facultative apomixis may serve to fix favorable genotypes and thus increase the rate of allopatric differentiation in outbreeders. In the Far Eastern sapindaceous monoecious genera Pometia, Allophyllus and Nephelium, which are known to be highly self-compatible, a complex reticulate pattern of local and regional morphological variation is manifested, often accomplished by ecotypic specialization, which defies narrow species definition (Leenhouts 1968, 1986).

In summary, tropical tree populations are expected to show a wide variety of population genetic structures because of the great diversity of pollination mechanisms, sexual systems and mating patterns. Genetic studies of a representative group of species are urgently needed to characterize major patterns.
Seed dispersal and seeding establishment represent the most critical and sensitive stages in the life history of plants. Since tropical forests are prominently represented among the world's most diverse plant communities, it can be anticipated that the processes of seed dispersal and seedling establishment in them will be accordingly diverse. This is suggested by the presence of many classes of disperser organisms in most tropical forests, and in the varied consequences and levels of pre- and post-dispersal seed predation. However, neither the simple identification of mechanisms, nor even the elucidation of their workings, will necessarily serve to answer more remote and fundamental questions about the density-dependent interactions that control the compositional stability and predictability of particular forest types. Nevertheless, these distant goals are likely to remain elusive until we achieve a detailed understanding of the proximal mechanisms involved.

Howe (1990), Gautier-Hion (1990) and Leighton (1987) — whose research represents, respectively, the neotropical region, equatorial Africa and southeastern Asia (Borneo) — describe plant-animal interactions involved in seed dispersal. Although each offers a different perspective on dispersal processes in their respective forests, the contributions contain sufficient common ground to allow some points of comparison. One is impressed that in certain ways the dispersal biology of these forests is similar, while in others it seems very different. This question of similarities and differences, and their possible underlying causes, is explored below.

Phenological patterns in fruit production

Over the past 20 years, numerous studies of fruiting phenology have been conducted in tropical forests around the world. With unfailing consistency, the results indicate that wherever one takes the trouble to measure it, fruit production fluctuates widely, usually with an unambiguous seasonal rhythm. Strongly sea-
sonal behavior is found in forests growing in a wide range of climates showing markedly different types and degrees of seasonality of rainfall (Terborgh 1986). This finding points to the suggestion that factors other than, or in addition to, climate may be driving these rhythms. Gautier-Hion (1990) suggests three hypotheses.

**Competitive avoidance**

The first of these could be called the 'competition avoidance hypothesis' (Hypothesis #1). Originally proposed by Snow (1966), this view holds that sympatric species of plants that share a common pool of dispersers should stagger their fruiting seasons so as to minimize competition among themselves for dispersers. While this proposal may indeed account for the species of *Miconia* (Melastomataceae) that were the focus of Snow's attention, subsequent evidence has not greatly extended its generality. Moreover, stated in the above form, the hypothesis is nearly impossible to test.

First, it requires that one defines a set of plant species that share a common pool of dispersers. Observers, including the three authors in this section of the Bangi workshop, have maintained vigils at countless tropical fruiting trees and found enormous variation, both within and between tree species, in the number and species composition of potential dispersers. Indeed, one of the points Gautier-Hion makes most strongly about the M'Passa forest in Gabon, is that most species of fruit are taken by many species of consumers, and that a particular fruit can very seldom be associated with a particular disperser or even group of dispersers. Thus, the occurrence of sets of plant species sharing common pools of dispersers is likely to be more the exception than the rule.

Another difficulty intrinsic in this hypothesis is that its prediction of staggered fruiting seasons is sensitive to one's ability to define the sets of plant species that share dispersers, and hence may possibly compete for them. If one fails to include some of the appropriate species, seasonal gaps will be evident in what may truly be a uniform temporal staggering of fruiting periods; conversely, if too many species are included, temporal staggering among some of them can be swamped by the more seasonal behavior of other species extraneous to the interacting set.

Finally, to the extent that competition among plants for dispersers really does lead to staggered fruiting seasons, the trend will result at the community level in a pattern that will most likely be indistinguishable from a random one. This brings us full circle to our opening observation that fruit production in tropical forests is seasonally concentrated, and hence decidedly non-random. We cannot reject the possibility that in many of these forests, certain plant species may mutually avoid each other's fruiting periods, but wherever one looks, the overall statistical pattern is non-uniform.

**Predator satiation**

Complementary to the competition avoidance hypothesis is the 'predator satiation hypothesis' (Hypothesis #2). This states that trees should adjust their fruiting seasons to coincide as a means for overwhelming the appetites of seed pre-
Seed and fruit dispersal:  
Key points

What Is known

- A wide variety of birds, mammals and other vertebrates are important in seed dispersal.
- The seeds of certain tree species can only be dispersed by specialized fruit-eating animals.
- Fruit-eating animals need a constant supply of food in order to survive through the year.
- Seeds which fall under the parent tree are typically heavily attacked by insects and fungi, and have little chance of establishment.

What Is not known

- The impact on seed dispersal if many of the seed dispersers or seed-eating animals are hunted out of an area.
- How selective logging affects the density of animals and seed dispersal.
- If isolated national parks and conservation areas will be able to support viable, self-maintaining populations of vertebrate seed-dispersing animals.
- How changes in top predators influence the populations of seed eaters and consequently the composition of plant species.

dators. The prediction is of a clumped, rather than a temporally uniform distribution, of fruiting periods.

Gautier-Hion offers a test of this hypothesis with data from the M'Passa forest. If the need to sate seed predators were paramount in selecting for fruiting seasons, then one might expect to observe different patterns of seasonality in sets for species that are heavily versus lightly attacked by seed predators. Gautier-Hion identifies two ‘large guilds’ of fruits. One is made up of species that are brightly colored, possessing pulp or arils rich in sugar or lipid, which are dispersed by large birds and monkeys ‘without significant predation’. The other consists of fruits that are ‘dull with a fibrous and nutritionally poor flesh and well-protected seeds’ that suffer from pre-dispersal seed predation by squirrels and ruminants. In Gabon, both types of fruits show marked seasonal fruiting peaks, so the comparison fails to resolve the issue.

In a slightly different approach to the question, Gautier-Hion examined the phenological behavior of zoochorous versus non-zoochorous species (anemochorous plus autochorous species), reasoning that zoochorous species should be under selection to avoid disperser competition (Hypothesis #1, above), while non-zoochorous species should cluster their fruiting seasons to satiate seed predators (Hypothesis #2). Again, both classes of fruits showed strongly aggregated fruiting seasons, so no conclusion could be drawn.
More convincing support for the predator satiation hypothesis is provided by Leighton, who offers the first measurements of seed predation rates in a masting versus non-masting year in a southeast Asian forest. In a non-masting year (1986), the depredations of arboreal seed predators (principally squirrels and primates) at the Gunung Palung site in West Kalimantan (Borneo) were so systematic that very few viable seeds reached the ground (per m² per month). Then, in the early months of 1987 there was a major masting event, the first in several years, and scores of viable seeds per m² rained onto the forest floor, with the subsequent appearance of lawns of seedlings. Leighton’s valuable observations raise some important questions to which we shall later return.

**Optimal time of ripening of fruit crops**

The third suggestion offered by Gautier-Hion may be termed as the ‘optimal time of ripening of fruit crops’. Gautier-Hion presents suggestive evidence in the finding that dehiscent fruits tend to mature in the late dry season when atmospheric conditions may favor dessication of their outer walls, and that fleshy fruits more often mature in the main rainy season, which in Gabon is a time of high insolation that could, in the presence of ample moisture, promote the rapid accumulation of carbohydrates and lipids. In further support of this possibility, she points out that the flowering times of the species belonging to a given morphological type tend to extend over a longer season than the subsequent fruiting periods.

What are we to make of all this? The competition avoidance model clearly does not apply at the community level to any tropical forest yet studied. Information from Panama and Gabon, with strong annual fruiting seasons every year and pronounced masting behavior of forests, along with intense seed predation outside of masting episodes, supports the predator satiation hypothesis.

Aggregated fruit production schedules thus seem to result from different forcing mechanisms in different portions of the tropics, in opposition to whatever tendencies toward uniformity might be furthered by competition among dispersers. One cannot conclude that competition avoidance is negligible or non-existent, but rather that it is a weaker force in selecting for the timing of fruiting than either of the other two.

As a footnote to the above discussion, it is important to stress that neither the predator satiation hypothesis nor the optimal timing hypothesis has yet been subjected to rigorous testing. In fact, since both predict aggregated fruiting peaks, it is not clear how they may be conclusively discriminated. One improvement would be to compare the dispersion of fruiting periods among species known to suffer heavy seed predation with that shown by species that are largely free of seed predation. The comparison of fruits belonging to different morphological categories, as in the Gautier-Hion contribution, is a first step, but the results are evaluated qualitatively without the benefit of statistical criteria. In the end it may prove difficult to distinguish the two hypotheses because the evolution of tightly aggregated fruiting peaks for the avoidance of seed predators is compatible with an evolved timing that takes advantage of the most propitious climatic conditions. Obviously, we are far from having any final answers to these questions.
Fruit morphology in relation to dispersers

Gautier-Hion has reported on the relations between fruit morphology and fruit choice by consumers in the M'Passa forest. It was shown (Fig. 3) that the consumer groups were arranged, first, around the parameter of fruit weight which separated birds from large rodents and ruminants (axis 1); then, around the parameters of fruit color, where monkeys diverged from squirrels (axis 2). Both birds and monkeys were found to be selective feeders. 'Bird fruits' could be defined as small, red or purple, without protection, and more often as dehiscent fruit with arillate seeds. Monkeys mainly took red, orange and yellow fruit either with a succulent pulp or arillate seeds. In contrast, small rodents appeared as opportunistic feeders and squirrels were not very selective. Large rodents preferentially took large-sized indehiscent fruit with fibrous flesh and seeds protected by hard kernels. Ruminants took a large variety of fruits but avoided the smallest. The overlap in fruit choice was not clearly based on taxonomic relatedness but more obviously on foraging levels and energy needs.

A point emphasized by both Howe and Gautier-Hion is that relationships between the taxonomic identity of consumers and fruit morphological traits are loose at best. Both discount the existence of strong coadaptive links in their forests. In Howe's study, oily Virola arils were taken mainly by toucans and other birds, while sugary Tetragastris arils were favored by primates. Nevertheless, primates harvested some Virola fruits, and birds some Tetragastris fruits. A far more extreme example was presented by Gautier-Hion in the case of Trichilia gilgiania (Meliaceae), the fruits of which were taken by ruminants, squirrels, monkeys, porcupines, hornbills and other birds. We may suspect that the frequency with which inappropriate species harvest the fruits of a given tree will vary greatly between species and from one occasion to another, in accordance with the availability of alternative resources. It is often presumed that uncommon visitors are seldom effective as dispersers, but this is generally an unproven contention.

A contrasting picture has been painted by Leighton of the lowland dipterocarp forest he has studied in Borneo. A sizeable fraction of the fruits there is subject to heavy attack by pre-dispersal vertebrate seed predators which consume seeds in the milk just prior to the hardening that accompanies final maturation. A legion of avid seed predators, including numerous squirrels, rats and primates, seem to impose a strong selection on plants to evolve means of protection masting, morphological resistance and chemical defenses. All three types of protection seem to be developed in the Bornean flora to a degree that surpasses what has been reported for African and neotropical sites.

Leighton's presentation to the Bangi workshop included photographs of many Bornean fruits protected by heavy fibrous husks. Such formidable armatures will predictably reduce the number of potential dispersers, increasing the specificity of dispersal in parallel with the increased cost of ancillary structures. One large class of heavily protected dehiscent fruits, comprising some 75 species of predominantly Meliaceous and Burseraceous trees, was exclusively dispersed by hornbills, as only their strong cuneate bills possess the capacity to open the thick husks and extract the large arilate seeds from within. More generally, fruits belonging to the bird and primate morphological syndromes seem to affect greater
Fig. 3. Interrelationships among six groups of consumers and the fruit characters of their food, in the M'Passa forest in Gabon (Gautier-Hion et al. 1985). The consumer community studied included seven large canopy birds, eight species of small rodents, nine squirrels, two large rodents, seven ruminants and six monkey species (a total of 39 species). The fruit morphology of 122 species of plants whose fruits were eaten by at least one consumer group was described in terms of simple characters that accounted for the energy needs of animals as well as their capacities of perception, manipulation and mastication. Such characters included fruit and seed weight, fruit color, the texture of the protective coat preventing access to the flesh and seeds, the type of edible tissue and the number of seeds. The seven categories of parameters defined included 25 variables. The overall relations between these variables and the six consumer groups were tested in a contingency table which was analysed by a multifactorial analysis. The factorial plane 1-2 accounts for 83% of the total inertia. Black circles: active variables for consumers; white circles: active variables for fruit. For further details, see text and Gauthier-Hion et al. (1985).
disperser specificity in the Bornean forest, though this could be a consequence of masting or more potent chemical deterrents. There is much to be learned from pursuing such interregional comparisons, though a lack of standard data gathering protocols so far precludes anything beyond impressionistic speculation.

Another impression gained from Leighton's presentation was that the fruits and seeds of bird dispersed species in families common to Terborgh's study site in Amazonian Peru were consistently larger at the Gunung Palung site. This appeared to be so in families producing dehiscent fruits — Burseraceae, Meliaceae, Myristicaceae, Sapindaceae — as well as in the genus *Ficus*. A striking, albeit anecdotal, corollary of this can be found in comparing dispersers. There are eight species of toucans at the Amazonian site, and eight hornbills filling the equivalent ecological roles in Borneo. Yet the toucans are of modest size, ranging in weight from 200 to 700 gms., while the Bornean hornbills, in contrast, are comparatively gigantic, the smallest of them weighing 1 kg and the largest more than 4 kg. Is this merely a chance outcome of independent throws of the evolutionary dice? Perhaps, but one might think that Borneo's ponderous hornbills were adapted to opening its equally prodigious Burseraceous and Meliaceous fruits, which in turn may have evolved their present remarkable dimensions in response to the unceasing attentions of arboreal seed predators. The Bangi workshop presents us with many more intriguing questions of this type than we can presently answer.

Gautier-Hion stresses that the distinction between seed predators and seed dispersers may often be blurred and cites compelling data to bring the point home. Seeds recovered from stomach contents of *Cercopithecus pogonius* (a guenon) were 50% broken, while those eaten by a close relative, *C. cephus*, were 20% broken, despite close similarities in body size and dentition. Although rodents and ruminants more commonly destroy seeds in the M'Passa forest, rodents frequently serve as critical dispersers through scatter-hoarding (Emmons, 1980), while ruminants (e.g. duikers) have been found to regurgitate seeds during rumination (Dubost, 1984). Scatter-hoarding by seed predators is also an important mechanism of dispersal in the neotropical forest (Smythe, 1970; Kiltie, 1981), but Leighton finds little evidence of it in Borneo. If arboreal, pre-dispersal seed predators are as prevalent in Borneo as Leighton's results indicate, then the abundance of seeds on the ground may not be sufficient to support a scatter-hoarding guild.

Similarly, one can wonder whether the Bornean forest supports a guild of secondary dispersers. In neotropical forests, seeds are often redispersed from feces by mice (Janzen, 1986) or dung beetles (Estrada and Estrada-Coates, 1986), while Africa enjoys a certain renown for the extraordinary diversity and size of its dung beetles. With so much yet to be learned about primary dispersal mechanisms, it is no surprise that secondary mechanisms have been looked at in only a few places.

A message for managers

Seed dispersal biology is highly relevant to the future management of tropical forests. Emerging generalities about seed dispersal mechanisms can potentially
lead to the conscious manipulation of species compositions with the consequent enhancement of economic values. The principal value of primary tropical forests to the logging industry has been in the exploitation of hardwoods, usually only a few species in any given region. Typically, these high value species belong to what are called mature phase species, and very often these are dispersed by large birds and mammals.

Under natural conditions, the balance of pioneer versus mature phase species in any given tract is believed to reflect the size and frequency of disturbance events. Natural disturbances include the mortality of adult trees due to natural causes, as well as induced mortality resulting from windstorms, fires, flooding, landslides, etc. The overwhelming majority of such natural disturbances are small in scale, involving only one to a few individual trees, and the near absence of gap phase pioneer species in many primary forests reflects this. Indeed, the most heavily stocked primary forests are often ones having very low rates of natural disturbance.

Logging of any kind results in disturbance, and the less selective and more extensive the logging operation, the greater the disturbance. Clear cutting is, of course, the extreme case. Inevitably, the regrowth that follows logging is more biased in its composition toward pioneer (gap phase) species than was the original primary stand. Large-scale clear cutting typically leads to the complete dominance of soft-wooded pioneer species (Jordan, 1986). Although these may grow rapidly, the wood they produce is of a lower average value than the wood that was removed from the primary forest. As more and more primary forest is exploited, the availability of prime hardwood species will inevitably decline, inducing a consequent rise in the price per unit volume. At some point the rising value of hardwood should compensate for its slower rate of growth and create incentives for management directed toward increased production. It is expressly this kind of management to which we address the following remarks.

A growing body of research is pointing to the likelihood that the densities of many tree species in natural stands are limited by pre- and post-dispersal seed predation. This is particularly true of the large-seeded species that predominate in the mature phase. In the main, these are dispersed by large birds and mammals, with some assistance from bats. Seeds that are not dispersed — that is, those that fall under or near the parent tree — have a vanishingly small chance of escaping predation, as Howe has so vividly demonstrated. Either they are bored by larvae, eaten by rodents or, upon germination, are damped by fungi. Study after study has now shown that the highest chances for survival are possessed by seeds that have been dispersed many meters away from the parent tree.

To obtain good regeneration of such species, it is thus essential to retain dispersers in the system. Often large birds and/or mammals are the only dispersers of mature phase species, but even in species attracting a wide range of potential dispersers, the larger dispersers are generally found to be more effective because: (1) they tend to be more selective of large seeded mature phase species, (2) they consume more fruits per feeding bout and (3) they tend to carry the seeds farther before regurgitating or defecating. Such observations firmly establish the indispensable role of large vertebrates in the perpetuation of mature phase species in forest stands. Future management plans for tropical forests will therefore have to consist of two components: (1) strategies for main-
taining large vertebrate dispersers in the ecosystem and (2) strategies for increasing the representation of tree species of particular economic importance. Let us consider these two stipulations.

Systematic overhunting frequently extirpates the large vertebrate fauna of tropical forests long before the first advent of loggers. Where some game remains, loggers are likely to eliminate it for their own needs while they remove the trees. Regeneration is thus likely to begin with a deficiency of dispersers, a situation that can only be remedied by controlling hunting. The presence of smaller scatter-hoarders — such as squirrels and other rodents — may, to a degree, be able to mitigate the absence of monkeys or hornbills, but this is as yet an unstudied possibility.

The maintenance of a fauna of large vertebrates will depend not only on controlling hunting but on retaining a high plant species diversity in managed forests. The large vertebrates that play major roles as seed dispersers require a plentiful year round supply of suitable fruits and/or seeds. A forest composed of only a few tree species will create an environment of boom and bust, brief surges of abundance offsetting long periods in which no species is in fruit. Animals cannot survive such conditions. Only through diversity can they obtain the continuous food supply needed to support growth and reproduction.

This conclusion cautions us that management should not be too intensively directed toward one or a few species of special interest. Instead, to maintain adequate plant diversity and the interdependent animal community, management should be based on the exploitation of many species. Heretofore, timbering in the tropics has been largely focused on export markets for cabinet and veneer woods, but taking such a narrow view does disservice to local markets. People in less developed countries use and need wood for many purposes: fuel, thatch, building materials, tool handles, fence posts, etc. In many areas, different species are exploited for each of these purposes. Production that is exclusively export oriented overlooks much of the potential of the forest resource, and consequently leads to waste on a large scale. Residents of the exporting country are deprived of resources that could be theirs.

By including species that have value on local as well as international markets, the evaluation of management options could be radically altered. The perceived worth of a given forest will inevitably be enhanced by the inclusion of additional marketable species. Animals, as well as plants, should enter into the accounting in recognition of their value as game, pollinators and dispersers. Such economic aspects of tropical forest management have been even less explored than some of the arcane biological topics touched upon above.

The point was made above that the disturbances produced by logging in a primary stand will bias the regrowth toward pioneer species of low commercial value. Herein lies the greatest challenge to the manager who wishes to restock the stand with high value hardwoods. In effect, he has to swim against the tide. Is this going to be a practical proposition, even if we grant the presence of large vertebrate dispersers?

The question is an important one to consider seriously, because the success or failure of future management efforts will depend on it. Certainly a haphazard, laissez-faire approach is doomed to failure from the start. Our feeling is that successful management for hardwoods is a serious possibility, though it will require
the application of restraint during extraction procedures and a level of technical expertise that most tropical foresters and tropical forestry departments do not now possess.

In principle, it should be possible to exploit the existing age structure of primary stands to promote the regeneration of mature phase species. Saplings and pole-sized immatures of gap phase species tend to be rare in primary stands. The pole stage individuals that crowd the understory of many primary forests belong mostly to mature phase species. They are following a 'sit-and-wait' strategy of persisting in the shade at negligible growth rates while waiting for openings in the canopy above. Through carelessness and indifference, such pole-size trees are commonly ravaged in logging operations. If judiciously spared, they could provide the key to successful management. Once released from the overtopping shade of a higher canopy, such trees, being half grown already, should quickly reach maturity. The period between successive harvests could be dramatically less than for trees grown from seed. Over the long-run, there might be difficulties in perpetuating a favorable age structure in twice or thrice harvested stands, especially where dispersers were scarce or absent, but from the perspective of today, this long-run is a far distant horizon. By then, there may be few tropical forests, or in a rosier projection, we may have learned enough to manage them effectively.
Seed physiology, seed germination and seedling ecology

Seedling establishment is necessary for tree populations to complete their life cycle. Seedling establishment can be divided into the phase of seed germination and the subsequent growth of the seedling. Three papers in the Bangi workshop focused on this sequence in seedling development. Vázquez-Yañez and Orozco-Segovia (1990) reviewed the literature concerning seed dormancy and the requirements for seed germination. Hladik and Miquel (1990) developed a framework for categorizing seedling types and the processes of establishment in the African rain forest. This framework was then used in comparison with other tropical forests. Augspurger (1990) made an original attempt to consider the role of fungal pathogens in tropical tree populations. All three contributions took a broad view of their subject, and considered a wide range of examples. This survey perspective is appropriate because our general knowledge of seed biology in tropical trees is quite limited. While the contributions treated separate topics in seed and seedling biology, the basic ecological and morphological characters resulted in a certain continuity of ideas that unify the material.

Vázquez-Yañez and Orozco-Segovia (1990) point out that most trees of the mature tropical rainforest produce fruits with large, heavy seeds. These seeds have a high water content, and germinate quickly. Because of the large stored food reserves, the resulting seedlings have an extensive and often deep root development and a comparatively large leaf area. The seedlings are often well-adapted to shady or partially shaded conditions. If these seeds are kept in dry conditions or in some other way prevented from germinating, they will die. Since the seeds of these species lack dormancy, they are not found in the soil seed bank. A second group of trees in the mature-phase forest produce smaller seeds with a lower water content and often a hard seed coat. Certain species are adapted to dispersal by wind while others have fruits that are ingested whole by vertebrate fruit dispersers. These species have a range of germination types but many may remain dormant in the soil if conditions are not suitable for germination. The third group is the pioneer species that invade gaps in the forest canopy and other disturbed areas. These species often produce small seeds of low water content. These seeds are adapted to remain dormant in the soil until
conditions become favorable for germination. Many of these species have a light requirement for seed germination and are sensitive to red/far-red light ratios. These categories of course represent generalizations, and many species do not fit into this simple framework. However, at this stage in our knowledge, such a framework is a starting point in further research.

Research on seed dormancy has considerable relevance to the management of tropical rain forest. Following large scale disturbance of the forest by clear-cut logging, agriculture and forest fire, the primary source of seeds for recolonization of the area will come from dormant seeds in the seed bank. The pioneer species and other species with dormant seeds are pre-adapted to take advantage of such wide-scale disturbance by the high densities of seeds in the soil. When an area is disturbed with the mineral soil exposed and sunlight falling on the ground, these seeds will germinate and quickly form a carpet of seedlings. A knowledge of seed dormancy and the seed bank will allow predictions to be made of the types of species likely to persist following forest disturbance.

A knowledge of seed dormancy is also relevant to forest managers and geneticists interested in storing seeds. Forest managers often wish to store large numbers of seeds for planting one or many years later during a reforestation program. Forest geneticists may wish to store seeds of an economically valuable species from a number of localities in order to preserve the genetic diversity of the species for later use in a genetic improvement program. For many tree species of the moist tropics, such seed storage is presently impossible or very difficult, seriously impeding efforts at reforestation and tree breeding. For example, species of dipterocarps are the most valuable timber trees in Southeast Asia. The seeds are large, have a high water content and lack dormancy. Since the trees only fruit every several years, the seeds of these important timber trees cannot as yet be readily incorporated into the regular forestry planting programs.

One potential reason why so many tree species can coexist in the tropical rain forest is the variety of specializations for establishment niches. Each species may have a particular type of seedling which is best adapted to a particular set of conditions, such as light, moisture, temperature and herbivores. This issue is addressed by the innovative paper of Hladik and Miquel in which seedlings are classified into five morphological types (Fig. 4). These classifications are based on whether the cotyledons are held in the air or at (or under) ground level, whether the cotyledons are thin and leafy or fleshy and whether the cotyledons remain inside the seed coat or come out following germination.

In a comparison of four tropical forests (Fig. 5), the overwhelming majority of seedlings belong to two common types: species that develop into seedlings with upright, leafy cotyledons and species with large seeds in which the cotyledons remain at ground level. The species with leafy cotyledons include most of the small seeded pioneer species and vines and even some of the shade-tolerant tree species. These small seeded species also tend to be dispersed by a wide range of generalized animal dispersers or by wind. In contrast, species with large seeds are mainly trees of the mature forest, and dispersal is more by specialized vertebrates. Seedling surveys in the mature forest also show a surprising abundance of seedlings of species possessing fleshy cotyledons produced
Seed physiology, seed germination and seedling ecology: Key points

What is known

- There is a wide diversity of germination characteristics among tropical trees.
- Many tree species of the mature forest have seeds which must germinate right away and cannot be kept in storage.
- The seeds in the soil generally belong to pioneer and gap-phase species which germinate following disturbance.
- Seeds and seedlings are attacked by fungi, insects and other pests which may cause decreased growth or death.
- The incidence of fungal and insect attack will tend to increase when individuals of a species occur at a high density in natural conditions and in plantations.

What is not known

- How to store the seeds of many important tropical timber species for extended use in planting programs.
- The best mixtures of commercial species and planting densities to minimize fungal and insect damage.
- The adaptive significance of such a wide variety of seed types in the rain forest community.

out of the seed coat above ground in families such as the Leguminoseae, Meliaceae and Burseraceae, and also seedlings of other species with upright, fleshy cotyledons remaining inside the seed coat. Comparatively few species with leafy cotyledons are found within the forest, while such species predominate in disturbed areas.

These results are important in providing an ecological and evolutionary framework in which to classify seedling behavior. By simple observations of seed size and seedling morphology, it is possible to predict its preferred habitat and light requirements. This information can be used by forestry nurseries in developing general methods for propagating different seedling types.

The contribution by Augspurger (1990) considers the importance of fungal pathogens in influencing tropical tree populations. Pathogens appear to be able to attack all phases in the life cycle. The destructive effects of pathogens on tree seedlings is particularly well documented. In the wild and in nurseries, the majority of seedlings can be weakened by fungal growth. The circumstances which favor the growth of fungi are unusually moist conditions, particularly when these follow some disturbance to the environment. Fungal pathogens are often quite specific in their host requirements, and a high density of a particu-
Fig. 4. Five seedling types proposed by Hladik and Miquel (1990): 1-1 = Seedling Type 1 (phanerocotylar, epigeal, foliaceous cotyledons); 1-2 = Seedling Type 2 (phanerocotylar, epigeal, fleshy cotyledons); 1-3 = Seedling Type 3 (phanerocotylar, hypogeal); 1-4 = Seedling Type 4 (cryptocotylar, hypogeal); 1-5 = Seedling Type 5 (cryptocotylar, epigeal). For definitions, see Glossary of Terms.

Fig. 5. Occurrence of the five seedling types (percentages of observed species) is similar in four tropical rain forests (there are no significant differences, p<0.05). Seedling Type 1 is the most common (39%). Seedling Type 5, the "Durian" Type, although rare (5%), is present in all tropical forests. For further discussion, see Hladik and Miquel (1990).
lar plant species facilitates the spread of the pathogen. So in general, fungal pathogens are particularly damaging in forest nurseries where thousands of seedlings are grown together at high density. The poor growth of seedlings, "damping off," is the tangible evidence of fungal growth. The economic and ecological importance of fungal pathogens on tropical woody plants will certainly increase in the future, as the remaining forests are more intensively managed and lands are converted to fast-growing exotic timber species and tropical tree crops.

Fungal pathogens may play a role in restricting the population size of common tree species in the primary forest and holding the density below a certain point. However, once the environment is disturbed by selective logging, with its exposure of the soil, piling up of organic matter and injuring the bark of the remaining trees, the opportunity for an outbreak of fungal pathogens may greatly increase. If one understands that the ecological niche of fungal pathogens in the tropical rain forest involves attacking populations that are at high densities, it make sense that fungi would be particularly destructive in situations where the density of a species has been artificially increased, such as in a forest treated with a management program to encourage certain timber species. Enrichment plantings and plantation forests are particularly susceptible to fungal attack due to the high density of particular species. Many of the extensive plantations of fast-growing exotic timber species in Southeast Asia have had disappointing results due to pathogen attack. Enormous plantations of bananas, cacao, coffee and other tropical crops have been destroyed by fungal pathogens that have been simply performing their ecological role. Understanding the ecology of fungal pathogens in primary forest can give insight into the control of fungal pathogens in environments affected by human activity.

These three contributions thus describe specific aspects of the establishment of new trees in the forest. However, it is interesting to consider the continuity of reproductive characters and to see how dormancy, seedling morphology, habitat requirements and resistance to fungal pathogens are interrelated. At one extreme are tree species which occur in the mature forest and produce large seeds. Only one or a few such seeds are contained in large fruits that are dispersed by specialized vertebrate dispersal agents. These seeds have a high water-content and germinate without any dormancy period. The resulting seedlings will typically have fleshy cotyledons that remain at ground level or above the ground. The mature seedlings will have extensive leaf tissue and a deep radicle that will allow them to persist for a long period even in deep shade and during periods with relatively little rainfall. The seedlings will quickly develop tough lignified tissue in the stem and root which will make them less susceptible to fungal pathogens.

At the other extreme are species of early successional stages, particularly pioneer species with small seeds. The fruits of these species will tend to be small, dry, wind-dispersed fruits or fleshy fruits with small hard seeds that are swallowed whole by generalized fruit-eaters. These seeds, when they land on the ground, can remain dormant for long periods of time until they are exposed to the high-light, moist conditions necessary for germination. Their seedlings are typically small, with leafy cotyledons above ground. The photosynthetic capabilities of these leafy cotyledons are necessary to the rapid growth of the
seedling since it only has a limited energetic reserve. These seedlings must
grow rapidly or die. If they are exposed to shady, moist conditions, which
might occur during a period of rainy weather, or if the canopy closes above
them, then these seedlings may be susceptible to attack by fungal pathogens.

These two common seed and seedling types represent the ends of a range,
with many species possessing intermediate characteristics as well. It is a useful
exercise to consider such interrelationships among seedling characters and to
realize that the plant is an integrated organism equipped to face a succession of
challenges at each phase in its life cycle.
Regeneration

Reproduction in higher plants may be broken down into a series of consecutive phases which affect final reproductive success, such as flowering phenology, pollination and breeding systems, fruits and seed dispersal, seed dormancy and seed germination. The final phase in this process is successful establishment of seedlings and saplings in an environment where they can grow into reproductively mature trees. This successful regeneration allows a species to be maintained over time at a particular forest. Successful regeneration away from the existing population allows each species to extend its range into new habitats. These processes are significant for the understanding of tropical forests and are relevant to the long-term production management of these forests. The contributions to this part of the Bangi workshop examined regeneration in the context of forest structure and forest dynamics (Hubbell and Foster, 1990), small scale disturbance (Clark, 1990), and the growth rates and mortality of trees (Manokaran et al. 1987).

In the last few years, several large, long-term primary forest plots have been set up — at Barro Colorado Island in Panama, La Selva in Costa Rica, Macambú in Brazil, Pasoh Forest in Peninsular Malaysia and Sarawak in Malaysian Borneo — to obtain demographic data from tropical tree populations. Such data include the establishment, growth and survival rates of seedlings, saplings and adults of common timber species. The goals of this research are several-fold. First, information will allow estimates to be made of timber and overall biomass production in these forests. These data will be valuable for comparison with silvicultural plots that have been treated in order to determine how many years are required for a logged forest to return to the characteristic state of the primary forest. Second, these plots are valuable to determine how stable tropical rain forest tree populations are over time. Since a goal of tropical forestry is to manage forests for a high production of particular timber tree species, this may not be possible if populations are unstable at a local scale. And third, such plots are relevant to explaining the great species richness of the rain forests.

Two major hypotheses are currently being debated by ecologists to resolve this question, as described in the paper by Hubbell and Foster. A prediction of
the equilibrium hypothesis is that species may coexist in the rain forest because each species has a specialized niche in which it is competitively superior to all other species. Coexistence of species in an equilibrium can also occur if density- and frequency-dependent mortality caused by predators, herbivores and pathogens limits the population size of individual tree species that begin to become common. This will have the effect of preventing any one species or group of species from dominating a forest. The non-equilibrium hypothesis states that the present species composition and abundance of individual species were determined in part by random factors such as the types of seeds available when canopy gaps were formed. This hypothesis predicts that there will be a species turnover in forests with some species going extinct and other species becoming established.

This academic debate about equilibrium and non-equilibrium models has practical significance to conservation biologists and managers of national parks. If a forest is found to be in a non-equilibrium state, many species will rapidly be eliminated from the forest. In isolated conservation areas with no external sources of seeds, such losses of rare species will be permanent and result in the gradual species impoverishment of the forest. Also, in a non-equilibrium state it may be difficult or even impossible to predict the minimal forest area necessary to preserve particular species.

The largest long-term plot and the one most completely analyzed to date is the 50 ha plot established in 1980 at Barro Colorado Island in Panama by Steve Hubbell, Robin Foster, other collaborators and the Smithsonian Institution. The forest is semi-evergreen and seasonal and is at least 500-600 years old. The plot is relatively flat and at an elevation at 150 m. Within the plot are two specialized habitats: 2 ha of swamp and 1 ha of ravines and creeks. In 1980 all trees and saplings with a diameter at breast height of 1 cm were tagged, measured, identified and mapped. The plot was re-censused in 1985 for tree growth and survival as well as sapling recruitment. In addition the vegetation, canopy gaps and terrain were mapped in great detail.

The overall conclusion of the 1980 census was that the forest was not in a state of equilibrium. While a few species were habitat specialists, many species appeared to have general habitat requirements. Further, the density of virtually all species appears to be far below the levels at which density-dependent factors would begin to influence populations. Consequently, the species richness at Barro Colorado Island could best be explained by a non-equilibrium, island biogeography model in which there is continual species turnover.

The 1985 re-census showed that saplings had higher growth and survival rates when further away from conspecific trees. Such data provide evidence for an equilibrium view of the forest composition controlled by density-dependent effects. However, it is relevant to ask how density-dependent effects can be distinguished from micro-successional effects. If saplings establish in one type of forest and grow up as trees, the forest environment will be altered and may no longer be suitable for the establishment of seedlings and saplings. Such successional effects on a local scale will be indistinguishable from density-dependent effects. Hubbell and Foster's conclusions are that there is a complex mixture of equilibrium and non-equilibrium forces affecting the forest at Barro
Regeneration: Key points

What is known

- Species differ in their requirements for successful seedling establishment and subsequent sapling growth.
- In primary forest, species composition may change over time due to natural processes.
- The growth rates of seedlings and saplings generally increase following both natural disturbance and selective logging.
- The types of tree species and their relative frequencies in the forest often change dramatically following selective logging.

What is not known

- Why the common canopy trees do not continue to increase in abundance and come to dominate the forest, as happens in the temperate zone.
- Why only certain saplings and trees respond to silvicultural treatment, while others show no enhanced growth.
- If certain trees grow rapidly to a large size because they are genetically superior to other trees of the same species.

Colorado Island that defies simple explanations and requires considerable long-term study and analysis.

The paper by Clark (1990) discusses the effects of disturbance on patterns of regeneration in neotropical moist forests. The agents of disturbance and tree fall are varied but include wind, floods, fire, landslides and lightning (Table 2). The tree falls cause changes in the physical environment of the forest floor which affect seedling and sapling regeneration. The primary effects appear to be the quantity and quality of light, temperature, air and soil humidity, and soil nutrients and physical structure. Some trees uproot and fall over, some trees snap off at the trunk, while other trees die standing. Trees that die standing will shed their branches over a period of years, creating many small canopy gaps with little or no exposure of soil. In contrast, trees that fall over and uproot typically cause large canopy gaps and expose a lot of soil. The ecological significance of these modes of tree death remains relatively unexplored but they almost certainly have major consequences on the size and type of canopy gap formed.

Advances in the equipment used to measure light and other physical variables have allowed great progress to take place in understanding the impact of gaps on the physiological ecology of seedlings and saplings. At the center of large gaps, light levels are 10-19% of full sunlight, while light is about 4% at the gap edge and only 1% in the forest understory. Low light levels often appear to limit seedling growth, showing that adult trees preempt a key resource
Table 2. Disturbances in neotropical moist forests.

<table>
<thead>
<tr>
<th>Type of disturbance</th>
<th>Approximate area of effect (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hurricane</td>
<td>$10^3$-$10^5$</td>
</tr>
<tr>
<td>Flood</td>
<td></td>
</tr>
<tr>
<td>Volcanism</td>
<td></td>
</tr>
<tr>
<td>Fire</td>
<td></td>
</tr>
<tr>
<td>Regional wind storm</td>
<td>$10^2$-$10^3$</td>
</tr>
<tr>
<td>Multiple tree fall</td>
<td></td>
</tr>
<tr>
<td>Lightning</td>
<td>$10^3$-$10^4$</td>
</tr>
<tr>
<td>Single tree fall</td>
<td></td>
</tr>
<tr>
<td>Branch fall</td>
<td>$10^2$-$10^4$</td>
</tr>
<tr>
<td>Leaf fall (especially palms)</td>
<td>$10^2$-$10^4$</td>
</tr>
<tr>
<td>Animal effects (nests, rootings, burrows)</td>
<td>$10^2$-$10^4$</td>
</tr>
</tbody>
</table>

[Source: Clark (1990).]

required by seedlings. In an intensive review over twenty years ago, Dawkins has shown that competition models can explain only a small fraction of the variation among adult trees in growth rates. Combining modern competition models with the physiological methods described by Clark could potentially explain a great proportion of this unexplained variation.

Manokaran et al. (1987) discuss some of the characteristic features and problems associated with long-term management of Malaysian dipterocarp forests using selective logging systems. One dominant factor affecting regeneration is the irregular fruiting cycle, with a good fruit crop produced only every three to six years. The net result is that the number of seedlings on the ground fluctuates dramatically over time. Consequently, it is not practical to restrict logging activities only to forests where there is an abundance of seedlings on the ground, since this situation may only occur infrequently. Silvicultural management systems in Malaysia have generally been altered to encourage advanced regeneration in the form of saplings and of small trees since these are more consistently present than seedlings. In the Selective Management System as practiced in Peninsular Malaysia and the Liberation Thinning System as practiced in Sarawak, the assumption is that advanced regeneration (i.e., small trees of desirable timber species) will grow rapidly once the canopy is opened up around them. In fact, many trees of the main timber species fail to respond to silvicultural treatment, with a few trees growing rapidly and most trees growing slowly or not at all. Some of these rapidly growing trees show this enhan-
ced growth for only the first two years following logging, then they also begin to slow down.

A critical need is to determine why only certain trees respond to silvicultural treatment with this enhanced growth. Perhaps modern methods of plant physiological ecology and light detection, as described by David Clark, could identify the critical parameters of light, water and nutrient availability which allow this dramatic growth response. However, the complexity of changes in the physical environment near a particular tree following disturbance, including decreased root and canopy competition with neighbors and physical damage to the roots, trunk and branches by logging, makes this a difficult goal.

A further promising avenue will be investigations to determine if there is a genetic basis to the superior growth rates of certain trees. This problem could potentially be investigated by searching for an isozyme marker associated with fast-growing trees. A more likely method would involve a quantitative genetic comparison of the growth rates of either seedlings or leaf cuttings from fast- and slow-growing trees. The technology of clonal propagation using leaves, described in recent articles in the *Malaysian Forester*, may be the key to conducting such experiments and eventually instituting extensive planting schemes in the absence of seeds and seedlings.

As discussed by Manokaran and his colleagues, work is needed to determine how logging affects the reproductive stock of the forest. During logging, large trees of desirable species and of good form are selectively removed, leaving behind the smaller trees and the poor quality trees. If there is a genetic basis to growth rates and tree form, which seems very probable, then the seeds produced by the remaining trees may be of poor genetic stock. Silvicultural treatments must be undertaken to remove these poor quality trees after selective logging operations.

The species composition of seedlings and adult trees in the forest changes dramatically following logging, and the goal of producing a dense stand of a particular, desirable timber species is often not achieved. In many ways such changes in species composition are not unexpected. The physical and biological environment is so altered by logging that the original common species present on the site may no longer be able to grow there. Also, if the forest is not in an equilibrium state, a timber species might become extinct on the local scale due to random factors, such as weather patterns or the availability of seeds from other species.

In conclusion, these studies have provided a broad review of the factors affecting tree regeneration. The key points are that fruiting is often irregular, resulting in great fluctuations in seedling density on the ground. Further, seedlings and saplings of certain common tree species may be virtually absent in primary forest or after logging, indicating that the species is no longer regenerating on a local scale. Such considerations have implications both to the forester who is interested in encouraging further regeneration of the common, valuable timber species as well as the park manager interested in the preservation of tree species diversity. The forester, in trying to encourage the regeneration of a common tree species through silvicultural treatment, may be bringing the density of the species above a certain critical level, resulting in an explosive growth of destructive pests. Research in measuring light, canopy structure and
the photosynthetic responses of seedlings might serve to identify the best environment for seedling growth. In addition, genetic variation for photosynthetic rates and consequent growth rate also needs to be investigated. The importance of genetic variability in explaining the great phenotypic variation in growth rates is a critical area in which immediate research is required.
Reproductive biology and tree improvement programs

Any discussion of tree improvement must take account of future demand for tree products. This is no easy task, for the working life of a rubber or oil palm tree can extend to thirty years and tree improvement programs such as the celebrated one for rubber can continue to increase tree yield for at least double that time even when conducted, as with *Hevea* rubber trees, on a single provenance. Tree biologists who do turn to resource economists for advice are rarely satisfied. Alan Grainger's (n.d.) predictions of tropical hardwood supply and demand well into the next century provide a rare exception. His predictions are inevitably regarded as controversial.

All the same, World Health Organization predictions of human demographic trends have little margin for error (barring cataclysm). It is therefore certain that, whereas the population of the industrialized, temperate nations may increase by 15% over the next 30 years, those in the nations of the tropics will double. In other words, the relative proportion of the world's population resident in the former will be halved, while that in the latter will double, to well over half the world's population. This fact has profound implications to forestry and for tree improvement.

We must anticipate, if standards of living worldwide are to be maintained let alone improved, that the relative demand for tropical products from the traditional consumers in the currently industrialized nations will steadily decline. This means that, unless there is substantial further industrialization which currently does not seem likely, it is probable that industrial products such as rubber latex will go into overproduction. Others, such as vegetable oil, which are produced by temperate as well as tropical plants, are already beginning to experience overproduction. Yet the need to create new employment in the tropics, and particularly in the rural sector, is obvious and urgent. Already, natural forest in Asia is almost entirely confined to lands unsuited to permanent herbaceous crops. Within thirty years, this will be the case everywhere but for parts of the Amazon valley and, perhaps, Zaire. The *Hevea* rubber tree remains the only plantation species which can be profitably grown on much of that land in the Old World.
The rapid expansion of human populations in the tropics will itself provide major opportunities for market expansion. Consequent lower transportation costs, plus greater familiarity of regional products among local consumers provides opportunities for product diversification, and hence for development of new tree crops for marginal lands. This is doubly fortunate. It not only allows greater opportunities for creating employment through development of a diversified tree-based economy on marginal lands, but it offers much needed opportunities for diversified (hence lower risk), land-use and multiple-species plantations in a climate where pest control in long-lived crops is already expensive and will certainly become more so in the future.

What kind of products will be in demand? Besides industrial products such as rubber latex, it seems likely that the specialized chemical products for which tropical plants are so celebrated, and which are or have been used worldwide as pharmaceuticals, flavorings or cosmetics, are at risk of being replaced by manufactured alternatives. Increasingly, pharmaceuticals are manufactured through culture of microorganisms as well as from fossil fuel byproducts. Vanilla can now be synthesized in tissue culture. On the other hand, the relative price of hardwoods has increased more rapidly than those of any other tropical commodity over the last forty years, and Grainger is probably right in assuming that demand, worldwide, will continue to be high. The spectacular growth of the world trade in rattan in the last decade indicates the promise of forest products which form the basis for craft-based industries whose products are in universal demand. Food crops, notably tropical fruit, are assured of a strong home demand and also, with improved marketing and storage technology, international demand.

In many cases, such as rattan and brazil nuts, most or all harvesting is still conducted in natural forest. Increasingly, culture must be intensified though, as in the case of these two commodities, plantation will only be possible in mixture with other species.

In summary, therefore, we can fairly reasonably predict the kind of forest product on which we should be concentrating research and therefore the species we should select, the attributes which should be enhanced through breeding, and the cultural ground rules which can best ensure high production, low risk and sustainability. Above all, cultivation in the coming decades will increasingly require exploitation of tree diversity in nature.

Several aspects of reproductive biology have implications for success in tree improvement programs and plantation management. Griffin (1990) examines the effects of inbreeding on the growth of trees in plantations. Most forest tree species are highly outbred. Inbreeding can have several deleterious consequences, including reduction in growth. As Griffin argues, seed collected for plantations often have a narrow genetic base. Inbreeding is therefore common in such plantations. Plantations raised from inbred seed may further erode the genetic base of the population and trees in such plantations may continue to show decline in survival and growth rate. Griffin calls for greater care in the selection of seed during domestication of tree crops as part of the process of initial domestication of tree species (Fig. 6).

Brune (1990) also briefly touches upon the consequences of casual collection of seed for plantations. He cites the examples of *Eucalyptus deglupta* in
Reproductive biology and tree improvement programs: Key points

What is known

- Tropical trees possess diverse modes of reproduction with a variety of breeding systems, pollination mechanisms and seed dispersal mechanisms.
- Most trees are outcrossed and inbreeding has a deleterious effect on fitness traits that affect productivity.
- Tropical trees differ in the patterns of genetic variation within and between populations.

What is not known

- Reproductive modes of many commercially important species.
- Patterns of genetic variation in many species of actual and potential importance.
- Effects of inbreeding in plantations with a narrow genetic base.

which case seeds were collected from plants that tended to flower in the first year. Plants grown from these seeds began to flower earlier and showed poor growth because vegetative growth was not vigorous and the trees branched precociously as the primary meristems turned into the reproductive shoots. Brune also discusses other problems in reproduction such as altered flowering seasons and lack of fruit set in the absence of pollinators when plants are introduced into new habitats.

Kageyama (1990) reviews patterns of genetic variation in natural populations of rain forest trees, emphasizing that information about genetic architecture of populations is critical to the success of tree breeding programs. Direct observations of population genetic structure in tropical forest trees are scanty but recent studies by Hamrick and his associates in Panama, Bawa and coworkers in Costa Rica, Ashton and his colleagues in Southeast Asia, and Kageyama in Brazil, have shown that most species contain considerable variation within populations. Less is known about the extent of genetic differentiation between populations; limited data in a few species show little divergence among widely separated populations (Buckley et al., 1988; Bawa and Krugman, 1990). Kageyama emphasizes that patterns of genetic differentiation are likely to be influenced by modes of pollen and seed dispersal as well as successional status of the species, as is the case for other angiosperms (Loveless and Hamrick, 1984). Because the various tropical rain forest tree species differ with respect to their pollen and seed dispersal features as well as their successional status, we might expect a wide variety of population genetic structures to exist.

Longman et al. (1990) describe how flowering can be induced at convenient height in clonal and grafted forest trees. This is an important area of research
because flowers of most canopy species are not easily accessible for controlled breeding work. Methods to induce flowering also need to be developed for those species that flower at very long intervals, such as Shorea and many other dipterocarps in the prehumid regions of the far eastern tropics.

In conclusion, research in many areas of reproductive biology is needed for better management of tree breeding programs and plantations. However, in the context of future likely market needs, almost no appropriate research has been done. We must identify more precisely what kind of tree commodity is likely to be in increasing demand. If trees are to continue to be grown in the tropics for production of goods other than timber, it is certain that new species will be introduced into cultivation and that some of these will merit genetic improvement. Thus interdisciplinary collaboration is crucial between tree biologists including silviculturalists, tree breeders and geneticists, tree nutritionists and pathologists, and economists, market analysts, planners and policy makers. Upon their recommendations, exploration and introduction must be dramatically intensified. Tree improvement must go hand in hand with new approaches in plantation design with the aim of reducing maintenance costs and risk without detriment to production. And both must be advanced hand in hand with better coordinated, and more consistently if not better funded research into the reproductive biology, demography and population genetics of tropical trees growing in nature; and into the structure and predictability of natural mixed species plant communities.

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Fig. 6. Generalized procedure for initial domestication of a fast growing tree species. [From Griffin (1990).]
Conclusions

Clearly many areas of plant reproductive ecology, defined in a broad sense, offer opportunities for the application of basic research to practical problems in forestry management. This viewpoint was echoed in many contributions to the Bangi workshop. However, by no means do we imply that our ability to restore and rehabilitate, and to conserve tropical ecosystems must await more biological information; we already know enough to proceed. Further studies on phenology, pollination and breeding systems, seed biology, regeneration and population genetics, can certainly refine our ability to manage effectively tropical ecosystems for conservation and sustained yield of forest products, though. This is particularly true for species of known commercial value, for many of which we lack information about basic biology. Moreover, at the community level, we are just beginning to unravel interactions that influence the structure and dynamics of forests. Our ability to manage and maintain biodiversity in forests that are increasingly subject to fragmentation and isolation will largely depend upon the basic knowledge of site-specific, key interactions involved in reproduction and regeneration of forest plants.

Another point that needs emphasis is that much of the research in plant reproduction, regeneration and population genetics has been done in isolation of each other. Genetic consequences of various phenological patterns, breeding systems and pollination and seed dispersal mechanisms are virtually unknown in tropical plants. Spatial and temporal variation in reproductive output has generally not been correlated with seedling establishment or the variation in genetic diversity of the resulting seedlings. For example, if recruitment in tropical forest trees is episodic, it might be concomitant with heavy seed production and the release of large amounts of genetic variability. Obviously there is a need to explore correlations among the quantity of seed produced, the amount of recruitment and the level of genetic variation among cohorts produced from different reproductive episodes. Thus not only ought there to be a greater integration of various types of ecological research such as phenology and regeneration but also the ecological studies must be meshed with genetic studies to understand the dynamics of regeneration in tropical rain forests.
The importance of biological information notwithstanding, another major point of consensus among the workshop participants was the need for close interaction between forest biologists and forest managers. Progress in conservation and management of forest resources should be greatly enhanced by closer collaboration than that which exists at present in tropical countries. It is only when priorities for research are jointly determined by the biologists and managers that we are likely to see the resolution of practical problems in the sustained use and conservation of tropical forest resources. For example, ecologists either prefer or are required to work at pristine, isolated field stations where the impact of humans is minimized. Yet the majority of tropical forests have been greatly altered by humans, or soon will be. Forest managers need research results which are relevant to the disturbed forests that they are required to manage.

Instead of speculating as to how human activities such as logging or hunting might affect the reproductive ecology of tropical plants, ecologists need to conduct explicit comparisons of primary forest and disturbed forest. For example, if field studies in a protected forest show that a particular vertebrate is the key fruit disperser of a tree species, what actually happens in nearby unprotected forest when that vertebrate has been hunted out? Does that tree species fail to regenerate? Or does another animal take over the role of principal disperser? As another example, how does the decrease in density of particular timber species following logging affect pollinator flight distances, fruit set and the rate of outcrossing? While forest managers need to learn more about the ecology of the primary forests, ecologists must also be willing to spend their time investigating managed forests that have been affected by human activities.


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Glossary of terms

**Allele.** One of two or more alternative states of a gene.

**Allopatric.** Occurring in different places, geographically separated.

**Allozyme.** An enzyme that is the product of a particular allelic form of a gene.

**Amenochorous.** Pertaining to plants whose seeds are dispersed by wind.

**Apomixis.** Reproduction without sexual union.

**Aril.** The fleshy and often colored outer covering of a seed.

**Autochorous.** Pertaining to plants whose seeds are distributed by their own movements.

**Biomass.** The total quantity of living organisms in a specific volume of soil, air or water.

**Breeding system.** System of mating that determines the prevalence of selfing or outcrossing.

**Canopy.** The covering created by leaves of mature trees in the upper layer of a forest.

**Clonal propagation.** Asexual reproduction or multiplication of plants from a single original individual.

**Coevolution.** The coordinated evolutionary change in two or more species in response to the presence of other species.

**Cohort.** A group of individuals of similar age within a population.

**Cotyledon.** The seed leaf, a leaf-like organ within the seed in which food for the new plant is usually stored.

**Cryptocotylar.** Referring to seedlings with cotyledons hidden in seed coat.

**Dehiscent.** Designating fruit that opens when ripe to release seeds.

**Dioecious.** Having the male and female elements on different individuals.

**Ecosystem.** A major interacting system that involves both organisms and their non-living environment.

**Effective population size.** Number of individuals in an ideal population which has the same level of genetic drift and inbreeding as the population from which it is drawn.

**Epigeal.** Describes seedlings with cotyledons above ground level.

**Ex situ.** Removed from the original location.

**Fecundity.** The rate at which an individual produces offspring.

**Gene fixation.** The condition in which a particular allele becomes the only allele present in a population, due to selection or genetic drift.

**Gene flow.** Exchange of genetic traits between populations by movement of individuals, gametes, or spores.

**Genetic drift.** Random fluctuations in gene frequency due to sampling error.
Genotype. The genetic constitution of an individual, often stated just for one or two genes.

Guild. A group of organisms resembling one another ecologically.

Heterozygosity. The state of having two different alleles at one or more genetic loci.

Hypogeal. Describes seedlings with cotyledons at (or below) ground level.

Inbreeding. The mating of individuals that are closely related genetically.

Inflorescence. An arrangement of flowers on a stem or axis; a cluster of flowers or a single flower.

*In situ.* In the original location or natural setting.

Isozymes. Different molecular forms of the same enzyme.

Leaf flush. A period of renewed growth in a woody plant.

Mast fruiting. A period of massive fruit production.

Mesic. Referring to habitats with plentiful rainfall and well-drained soils.

Microevolution. An evolutionary pattern usually viewed over a short period of time, such as changes in gene frequency within a population over a few generations.

Monoecious. A plant in which the male and female flowers are separate, but borne on the same individual.

Niche. The role played by a particular species in its environment.

Outbreeding. The crossing of genetically unrelated individuals.

Outcrossing. Cross-pollination with other individuals that may or may not be related.

Phanerocotylar. Referring to seedlings with exposed cotyledons.

Phenology. The study of periodical phenomena in plants, e.g. the time of flowering, fruiting and leaf flushing in relation to environmental factors.

Phenotype. The observable characteristics of an organism, often stated in reference to a single trait.

Podsolization. Breakdown and removal of clay particles from the acidic soils of cold, moist regions.

Polymorphic loci. Genes for which there are more than one allele present in a population.

Population. A group of individuals existing together in time and space and capable of interbreeding.

Population dynamics. The study of changes in population densities.

Population genetics. The study of the genetic composition of populations.

Self-compatibility. The ability of a plant to set viable seed from self-pollination.

Self-incompatibility. The inability of a plant to set viable seed from self-pollination.

Selfing. See self-compatibility.

Semi-hypogeal. Describes seedlings with cotyledons exposed at ground level.

Sexual system. Reproductive system characterized by the sexuality of flowers and the gender of individual plants.

Sympatric. Occurring in the same place; having overlapping distributions.

Understory. Those trees of secondary height growing below the upper canopy.

Xeric. Referring to habitats in which plant production is limited by availability of water.

Zoochorous. Pertaining to plants whose seeds are dispersed by animals.
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BULGARIA- Bulgarian Academy of Sciences
CANADA- National Research Council
CHILE- Sociedad de Biología de Chile
CHINA- Association for Science and Technology, Beijing
CHINA- Academia Sinica, Taipei
CUBA- Academia de Ciencias
CZECHOSLOVAKIA- Czechoslovak Academy of Sciences
DENMARK- Det Kongelige Dansk Videnskabernes Selskab
EGYPT- Academy of Scientific Research and Technology
FINLAND- Societas Scientarium Fennica
FRANCE- Académie des Sciences
GERMAN DEMOCRATIC REPUBLIC- Deutsche Akademie der Wissenschaften
GERMANY (FEDERAL REPUBLIC OF)- Deutsche Forschungsgemeinschaft
HUNGARY- Academy of Sciences
INDIA- Indian National Science Academy
IRAQ- Scientific Research Council
IRELAND- Royal Irish Academy
ISRAEL- Academy of Sciences and Humanities
ITALY- Consiglio Nazionale delle Ricerche
JAPAN- Science Council of Japan
JORDAN- Higher Council of Science and Technology
MONACO- Centre Scientifique de Monaco
NETHERLANDS- Koninglijke Nederlandse Academie van Wetenschappen
NEW ZEALAND- The Royal Society of New Zealand
NORWAY- Det Norske Videnskaps Akademie
PHILIPPINES- National Research Council of the Philippines
POLAND- Academy of Sciences
SAUDI ARABIA- King Abdul Aziz City for Science & Technology
SOUTH AFRICA- Council for Scientific & Industrial Research
SPAIN- Consejo Superior de Investigaciones Científicas
SWEDEN- Kungliga Vetenskapsakademien
SWITZERLAND- Swiss Academy of Sciences
UNITED KINGDOM- The Royal Society
U.S.A.- National Academy of Sciences- National Research Council
U.S.S.R.- Academy of Sciences
VENEZUELA- Consejo Nacional de Investigaciones Científicas y Tecnicas
YUGOSLAVIA- Union of Biological Sciences