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The Ecology and Management of Non-Timber Forest Resources

Charles M. Peters

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Charles M. Peters

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Cover: Young boy harvesting rattan cane *(Calamus schistoacanthus)* from the flooded forests of Danau Sentarum, Kapuas Hulu district, West Kalimantan, Indonesia. Cane is used for making fish traps and is also sold in large quantities to timber companies for lashing logs together.

Photo: C. Peters

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Contents

Foreword

Concern about the rapid loss and degradation of tropical moist forest has caused many conservationists and natural resources managers to seek alternatives to exploitative forms of forest utilization such as timber harvesting. The hope is that these alternatives will help to better ensure both the conservation of forests and a sustainable flow of benefits for forest-dependent communities.

Many observers have suggested that Non-Timber Forest Products (NTFPs) are likely to provide such an alternative for sustainable forest conservation and management. However, despite interest in NTFPs there has been little systematic evaluation of the management systems that govern their production. Accordingly, this paper begins by describing the basic ecological characteristics of tropical forests and highlighting those influencing the sustainability of production of NTFPs. It challenges the common assumption that the utilization of NTFPs is automatically ecologically benign and outlines the ecological processes governing the development and function of tropical forests. It suggests that any form of resource utilization will have an ecological impact on the forest, and that the severity of these impacts and the ability of management to mitigate these impacts depend upon the nature and intensity of harvesting and the characteristics of the particular resource being harvested.

The World Bank Environment Department is pleased to publish this important and timely paper and we hope it will prove useful to those involved in management of tropical forests.

Andrew Steer
Director
Environment Department

Abstract

Tropical forests contain an incredible diversity of fruit, nuts, oil seeds, latexes, resins, gums, spices, and medicinal plants of great potential economic value. This report summarizes the current state of knowledge on the ecology of these non-timber resources and outlines a series of management recommendations for their sustainable harvest. The discussion is divided into four chapters.

Chapter I summarizes the basic characteristics of tropical plant populations that limit the nature and intensity of resource exploitation. The major problem areas include the diversity and low-density of tree species, the complexity of flowering and fruiting, the specificity of microsites for successful regeneration and growth, and the labile response of population structure to changes in the level of recruitment.

Chapter II discusses the potential long-term ecological impacts resulting from the selective harvest of different plant tissues such as reproductive propagules (fruits, nuts, and oils seeds), plant exudates (latexes, resins, and gums), and vegetative structures (fibers, medicinals, rattans, and thatch). It is argued that most of the current commercial exploitation of non-timber resources is plagued by destructive harvesting, over-exploitation, and a basic disregard for the functional ecology of tropical plant populations.

Chapter III outlines the basic inventory and yield data needed to develop a program of sustainable resource use. Two different methodologies for defining a sustainable level of harvest are discussed. The first, a conceptually simple, inexpensive, and straightforward process called successive approximation, monitors the population impact of exploitation and sequentially adjusts harvest levels over time to obtain a sustainable yield. The second method uses plant demography, matrix models and computer simulations to estimate the maximum quantity of resources that can be harvested from the forest without damaging the long-term regeneration of the species under exploitation.

Chapter IV provides an overview of conventional and indigenous forms of forest management and proposes a general sequence of silvicultural operations for enhancing the regeneration, growth, and productivity of different non-timber forest resources.

Brief summaries are included at the end of each chapter and boxes are used to present supplementary material and to give examples of certain statistical procedures. A glossary and extensive bibliography are also provided.

Introduction

Non-timber tropical forest products have attracted a lot of attention recently, and innumerable articles, books, seminars, workshops and conferences have focused on the pros and cons of exploiting these plant resources. There is hardly anyone who still refers to them as "minor" forest products, and there is even a cryptic acronym (NTFP) now to describe this eclectic mix of fruits, seeds, resins, fibers and medicinal plants. It is somewhat surprising, therefore, that in spite of all the current analysis, discussion, and debate, several basic questions related to the ecology of non-timber tropical forest products have yet to be addressed.[1] For example, what are the actual ecological impacts of harvesting commercial quantities of non-timber products from a tropical forest? Are some species or resources more resilient to the effects of continual harvesting than others? What can be done to minimize these impacts? What sort of monitoring activities, management practices, and silvicultural techniques can be used to insure that the resources being harvested are not overexploited?

These types of questions define the ecological bottom line of non-timber forest resource exploitation, and it would be unwise to continue ignoring them. The commercial extraction of non-timber resources does have the potential to provide innumerable economic, social and ecological benefits, and it does provide a unique means of integrating the utilization and conservation of tropical forests—but only if the resources are harvested in a sustainable manner. If the supply of forest resources is depleted over time, either through excessive harvesting or the gradual death of adult trees without replacement, no type of new product, marketing scheme, or land tenure will make much difference. As elsewhere, there are no free lunches in a tropical forest.

Given these considerations, the present report summarizes the current state of knowledge on the ecology of non-timber tropical forest products and presents a series of management recommendations for minimizing the ecological impact of harvesting these resources. The procedures described are not a blueprint for eliminating the potential impacts on all components (soils, hydrology, associated plant and animal species) of a tropical forest ecosystem, or for maintaining forests in a pristine condition. The immediate concern is simply that of defining a level of resource harvest that can be sustained over time by the plant populations being exploited. The material is aimed primarily at resource managers, foresters, conservationists, extension agents, researchers, and development workers who are involved in the planning and/or implementation of management strategies for tropical forests. Although a large amount of technical detail is included, policy-makers with a background in biology may also find something of use here.

Method of Presentation

The report is divided into four chapters, each chapter treating a different aspect of the ecology and management of non-timber tropical forest resources. The first two chapters are basic plant ecology; the latter two chapters take a more applied, field perspective.

Chapter I summarizes the potential ecological characteristics of tropical plant populations that limit the nature and intensity of forest exploitation. Chapter II builds on this information by discussing the potential long-term ecological impacts resulting from the selective harvest of different plant tissues such as reproductive propagules (fruits, nuts, oil seeds, and so on), plant exudates (latexes, resins, gums), and vegetative structures (fibers, medicinals, rattans, thatch). Chapter III outlines the basic inventory and yield data needed to develop a program of sustainable resource use, and details specific methodologies designed to collect this type of data. Two different methods for defining a sustainable level of harvest are discussed, and monitoring activities for assessing the response of the plant population to differing harvest intensities are also outlined. Chapter IV provides an overview of conventional and indigenous forms of forest management and proposes a general sequence of silvicultural operations for enhancing the regeneration, growth, and productivity of different non-timber forest resources.

To enhance the reader's comprehension of the material, brief summaries are included at the end of each chapter and an extensive bibliography is provided. A box format is used in several parts of the text to present supplemental material and to give examples of certain statistical procedures. In view of the fact that plant ecology and forest management are both characterized by an overabundance of technical jargon, a glossary is also provided. Finally, an annotated outline summarizing the various ecological, logistic, and operational issues which effect the exploitation and management of non-timber tropical forest resources is included as an Annex to the report. It is hoped that this synthesis will help make the material more accessible to policy makers and government officials who have neither the time, nor the motivation, to wade through the entire text.

Scope

The report is focused exclusively on non-timber plant resources, with particular emphasis on trees. Although the sustainability of harvesting forest fauna is undeniably an issue of great importance, crocodile, butterflies, iguanas, turtles, bird's nests and the many other animal resources and products collected from tropical forests are not discussed here. Whenever possible, specific botanical examples are cited to illustrate key concepts. Reflecting the author's previous field experience, most of these examples[2] have been taken from the tropical moist forests of South America and Southeast Asia. This geographical bias does not imply that there are no interesting or useful plants in the African tropics, that the problems of overexploitation and resource depletion are absent from this region, or that the extensive dry forests found in more seasonal tropical environments are unsuited for sustainable management.

The text is largely concerned with primary forests, either undisturbed or already subjected to some degree of exploitation and the ways in which non-timber resources can be harvested from them with minimal ecological damage. The selective management of pioneer species, tree felling, or the deliberate creation of secondary vegetation within these forest areas, however, fall outside the scope of the present work and are neither advocated nor discussed. The extensive areas of secondary forest that have been created throughout the tropics indeed represent an important source of non-timber products. A discussion of the use and management potential of these habitats, however, falls outside the scope of the present work.

A final caveat. There is no question that economic, social, and political factors play an extremely important role in determining the success or failure of forest exploitation. This report, however, attempts to tell the story strictly from the plant's point of view. The reason *why* too many fruits are removed from the forest is not really the issue here. What we want to know is *what happens* as a result to the plant populations being exploited—and *what can be done about it*. The biological mechanics of overexploitation are the same regardless of whether the fruits are collected by a village cooperative or a multinational corporation, or whether the trees are growing in an extractive reserve, a state forest, or a logging concession.

Notes

1. The basic text of this report was written over an eight-month period from 1991 to 1992 while the author was in residence in West Kalimantan, Indonesia conducting fieldwork. Since this time, several interesting studies focused specifically on the ecological impacts of non-timber forest product exploitation have been published (for example, Nepstad and others 1992; Wong 1992; Cunningham and Mbenkum 1993; Hall and Bawa 1993; Pinard 1993). These studies notwithstanding, the ecological context of non-timber forest product exploitation remains virtually unexplored territory for investigation.

2. The reader is strongly advised to look beyond the examples and to focus on the underlying concepts being illustrated. Tropical moist forests contain different species and exhibit different ecological characteristics than do tropical dry forests, but the basic procedures required to achieve a sustainable harvest are essentially the same in each environment. Similarly, an understanding of population density and yield is as important for managing herbaceous plants, shrubs, and lianas as it is for trees.

I

Introduction to the Ecology of Tropical Forest Resources

> "All planned forestry is applied ecology."
>
> —*Hewetson (1956)*

Plant ecology, in the most general sense, can be defined simply as the interrelationships between a plant and its biotic and abiotic environment. A basic understanding of the nature and extent of these interrelationships is fundamental for developing sustainable systems of forest resource exploitation in both tropical or temperate climates. In both situations, the resource manager inevitably must seek answers to several questions about the ecology, or "life history" of the plant species to be exploited. How abundant is the species in the forest? What pollinates its flowers and disperses its fruits? How successful is the species in regenerating itself and surviving until maturity? And, perhaps most importantly, how much of the desired resource can be extracted from the forest over time without adversely affecting the reproduction, growth, and long-term productivity of the species?

Although the focus of these questions should be similar regardless of the habitat or resource, the ease with which they can be answered differs dramatically in a tropical forest and a temperate forest. Tropical forests are known to be some of the most complex biological systems in the world. They are also some of the least studied and most poorly understood of all terrestrial ecosystems. Faced with such constraints, policymakers and resource managers in the tropics have tended to ignore these ecological questions or have simply assumed that tropical trees behave essentially like temperate trees. Either course of action is ill advised, and the failure of most attempts to manage tropical forests on a sustained-yield basis have repeatedly illustrated this fact. The problem, however, is not so much a lack of understanding about the ecology of tropical forest resources. The real problem is that only rarely has this type of information been applied within a management context, especially one concerned with the exploitation of non-timber tropical forest resources.

The purpose of this first chapter is to briefly summarize the principal ecological characteristics of tropical trees and forests that limit the nature and intensity of resource exploitation. The discussion is by no means exhaustive, and readers desiring a more thorough treatment of tropical forest ecology should consult Richards (1952), Longman and Jenik (1974), UNESCO (1978), Whitmore (1984), or any of the other excellent textbooks available.

It should be noted that the chapter does not discuss nutrient cycling in tropical forests. The reason for this is the observation that the population and community-level impacts of forest tree utilization (for example, gradual elimination of the exploited resource or associated flora and fauna) frequently become apparent long before any ecosystem-level nutrient limitations are manifested. This certainly does not imply, however, that the conservation of existing nutrient capital is an inconsequential or trivial management concern in the tropics. In low-fertility habitats such as the white sand *caatinga* in Brazil (Pires and Prance 1985) or the *kerangas* forests in Borneo (Whitmore 1984), excessive harvesting could easily cause lack of nutrients to become a limiting factor to sustainable use (Jordan 1985; see also chapter 2).

Tree Diversity and Density

One of the most fundamental and well-known characteristics of tropical forests is their great species richness, or their large number of plant species per unit area. To illustrate this point specifically for trees, data collected in floristic inventories of small tracts of tropical forest in Amazonia and Southeast Asia are presented in table 1.1. All data are limited to trees greater than 10 centimeters diameter at breast height (DBH). Although differing sample sizes preclude direct comparisons between the two regions, it is clear that the tropical forests in both Amazonia and Southeast Asia are extremely diverse, and may contain from 100 up to almost 300 different trees species in a single hectare.[1] The strong influence of habitat on the total number of tree species growing within a tropical forest can also be appreciated in this table. The *igapo* (forest seasonally flooded by infertile blackwater) inventoried near Belem, Brazil, for example, contained only sixty tree species per hectare, while the *kerangas* or heath forest growing on poor, sandy podzolic soils near Badas, Brunei was limited to seventy-two tree species per hectare.

An additional feature of tropical forest diversity is its small-scale heterogeneity: adjacent tracts of forests may differ greatly in species composition. The net result of this floristic "patchiness" is that the total number of tree species recorded in a forest inventory is

Table 1.1 Number of Stems and Tree Species in Small Plots of Tropical Forest in Amazonia and Southeast Asia

Site	*Soil/Habitat*	*Sample Area (hectares)*	*Number Trees*	*Number Species*
Amazonia				
Yanamoro, Peru[a]	Alluvial terrace	1.0	580	283
Mishana, Peru[a]	White sand	1.0	842	275
Cocha Cashu, Peru[a]	Alluvial terrace	1.0	650	189
Rio Xingu, Brazil[b]	Terra firme	1.0	567	162
Breves, Brazil[c]	Terra firme	1.0	516	157
Belen, Brazil[d]	Igapo	1.0	564	60
Southeast Asia				
Lalmbir, Sarawak[e]	Yellow sand	1.6	1,025	283
Lempake, East Kalimantan[f]	Red/yellow clay	1.6	712	209
Sungai Menyala, Malaysia[g]	Red/yellow clay	1.6	1,075	197
Kuala Belalong, Brunei[e]	Yellow clay	1.6	712	125
Badas, Brunei[e]	Sandy podzol	0.5	369	72

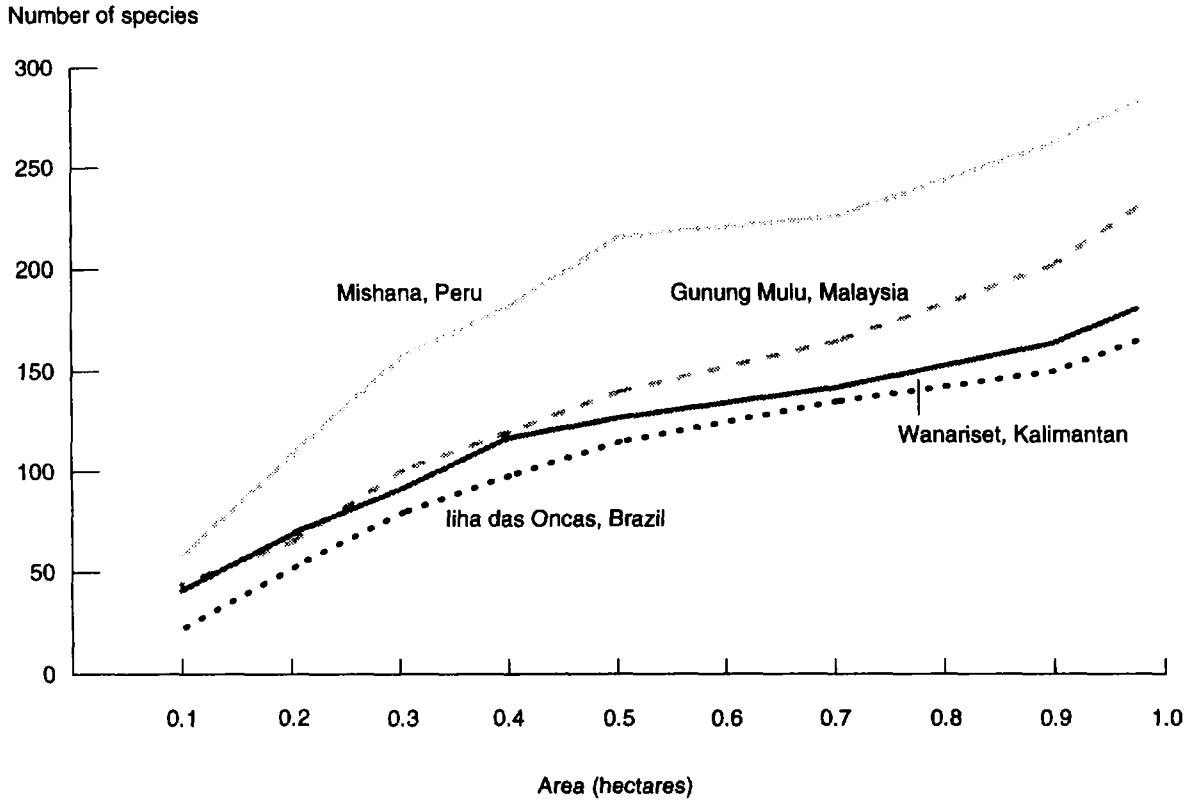
Note: The numbers are for stems and trees equal to or greater than 10 centimeters DBH. Habitat classifications for each site are based on descriptions presented in the source citations.

Source: a. Gentry 1988. b. Campbell and others 1986. c. Pires 1966. d. Black, Dobzhansky, and Pavan 1950. e. Ashton 1984. f. Riswan 1982. g. Wyatt-Smith 1966.

usually directly related to the size of the sample area. The nature of this relationship is traditionally expressed by a species-area curve (McGuiness 1984), which shows the increase in new species encountered on plots of increasing size. Four such curves, constructed from inventory data collected in Brazil, Peru, Kalimantan, and Malaysia, are shown in figure 1.1. There is a steady increase in the number of tree species recorded within each forest up to plot sizes of 1.0 hectare. The curves for Mishana and Gunung Mulu exhibit the steepest slopes, these two forests apparently possessing the highest degree of small-scale heterogeneity. The fact that none of the curves have started to flatten out at the 1.0 hectare mark suggests that this plot size may be too small to accurately describe the diversity of tree species growing in some tropical forests (Heinsdijk and de Bastos 1965; Ashton 1984; Campbell 1989). The implications of this for developing effective inventory procedures will be discussed in detail in chapter 3.

Given the large number of tree species per unit area, it is not surprising that most tropical forests contain an astounding variety of economic resources—edible fruits, nuts, oilseeds, medicines, building materials, latexes, gums, resins, and so on. A few examples should suffice to illustrate the renowned resource richness of these plant communities.[2] The forests of Southeast Asia have been estimated to contain from 200 to 300 species of native fruits alone (Jacobs 1974; Williams, Lamoureaux, and Wulijarnri-Soetjipto 1975;

Figure 1.1 Species-Area Curves for Trees ≥ 10.0 cm DBH from Two Amazonian and Two Southeast Asian Forests



Source: Data taken from Ilha das Onças, Brazil (Anderson and Jardim, 1989); Mishana, Peru (Gentry, 1988); Wanariset, Kalimantan (Kartawinata and others, 1981) and Gunung Nulu, Malaysia (Procter and others, 1983).

Soepadmo 1979), including nine species of durian (*Durio* spp.), thirty species of mangosteen (*Garcinia* spp.), at least ten species of mango (*Mangifera* spp.), and thirty-five species of wild rambutan (*Nephelium* spp.). Similarly, studies conducted near Iquitos, Peru along the Upper Amazon have shown that 139 different species of native fruits are consumed in this region, 120 of these species being harvested exclusively from local forests (Vasquez and Gentry 1989). An additional finding of interest from the Peru study is that 48 percent (fifty-seven species) of these wild-harvested fruits are actually sold in the Iquitos market.

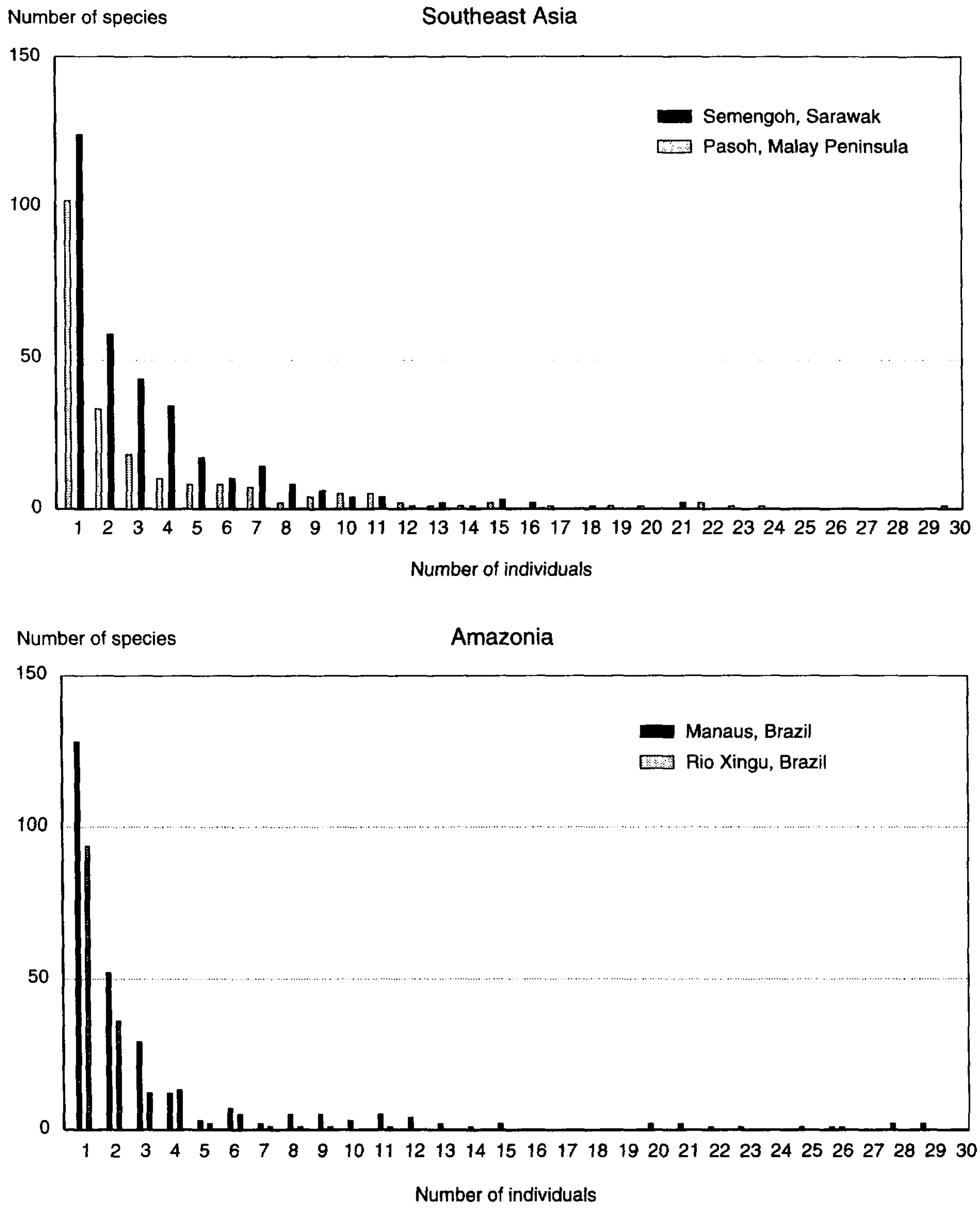
In spite of the obvious economic potential of these native fruit resources, an inevitable correlate to high species or resource diversity is that most conspecific individuals (trees of the same species) occur at extremely low densities within the forest. Whitmore (1971), for example, reports that in a sample of 676 hectares at Ulu Kelantan, Malaysia the density of most wild fruit species was only one adult tree (defined as larger than 40 centimeters DBH) every 4–7 hectares. Similar results were obtained from a recent 50 hectare sample of primary forest in the Pasoh Forest Reserve, Peninsular Malaysia in which the average density of adult fruit trees was found to be 0.2 trees per hectare (Saw and others 1991). This general trend of high species diversity coupled with low species density within tropical forests is illustrated graphically in figure 1.2. The data used for this figure were collected from plots of 4 hectares (Sarawak and the Malay Peninsula), 3 hectares (Rio Xingu, Brazil), or 1 hectare (Manaus, Brazil). As the histograms clearly document, the great majority of tree species recorded in both the Southeast Asian and Amazonian sites are represented by only one or two individuals. Less than 10 percent of the species recorded contained more than four trees per hectare.

The low density of conspecific adult trees and high diversity characteristic of many tropical forests is a major constraint to sustainable resource exploitation and a chronic management problem. Economic species that occur at densities as low as only one adult tree every 3–4 hectares are difficult for collectors to locate, and the travel time and the overall distance or circuit required to carry the product back to the point of origin can be very long. Furthermore, yields per unit area are also likely to be quite low. One of the basic tenets of optimal foraging theory (Charnov 1976) states that as search, travel and carrying times increase, the overall return from a resource, as well as the specific preference for that resource, will correspondingly decrease. The "boom and bust" history of forest product extraction in the tropics seems to have repeatedly proven this theory. Without question, one of the first objectives of any management plan for exploiting species-rich tropical forests sustainably must be to increase the density of selected forest resources.

Fortunately for management, there are exceptions to the rule of high species diversity in tropical forests. Although the fact is seldom mentioned in much of the literature on forest extraction, dense aggregations of a single tree species are known to occur in habitats where severe flooding, shallow soils, or frequent disturbance preclude the formation of species-rich forest (Janzen 1974a; Connell and Lowman 1989). These oligarchic forests (in which a few species dominate) have been reported for almost every region of the wet tropics; notable examples include the *Shorea albida* forests of Sarawak (Anderson 1964; Brunig 1964), the *Gilbertiodendron dewevrei* forests of Central Africa (Gerard 1960; Letouzey 1970; Hart, Hart, and Murphy 1989), the *Mora excelsa* forests of Guiana and Trinidad (Davis and Richards 1933; Beard 1946), and mangrove (*Avicennia, Rhizophora*) forests throughout the world. Forests containing only a few palm species are especially common in tropical freshwater swamps (Moore 1973; Ruddle and others 1978).

Oligarchic forests are also known to occur in Amazonia (Ducke and Black 1953; Pires 1973; Pires and Prance 1985). The salient feature of the low-diversity aggregations found in this region, however, is that in many cases

Figure 1.2 Population Densities of Four Tree Species in Small Tracts of Amazonian and Southeast Asian Forest



Note and Source: Inventory data collected from 4.0 ka sample plots in Semengoh, Sarawak and Pasoh, Malay Peninsula (Ashton, 1984); 3.0 ka sample plots were used at Rio Xingu, Brazil (Campbell and others, 1986), and 1.0 ha sample plots in Manaus, Brazil (Prance and others, 1976).

the dominant species produce fruits, nuts, or oilseeds of economic importance (Peters and others 1989). As is shown in table 1.2, oligarchic Amazonian forests may contain from 100 to 1,200 conspecific adult trees per hectare and annually produce up to 11 metric tons of fruit per hectare. In yield, these forests rival many of the commercial fruit plantations in the tropics (Purseglove 1975; Williams 1975). Not surprisingly, the rural inhabitants of Amazonia are well aware of these benefits, and the oligarchic forests of the region are actively harvested and even occasionally managed (see Anderson and others 1985; Anderson 1988). Given the impressive productivity and relative ease of managing these plant communities, it is unclear why all of the recent extractive reserves in Brazil have been established only in species-rich forests.

Flowering, Fruiting and Reproductive Dynamics

Temperate trees, as a general rule, occur in high-density populations, flower and fruit in response to well-defined environmental cues, are monoecious (bisexual individuals with both male and female flowers), and have their flowers pollinated and their fruit dispersed by an abiotic vector such as wind or gravity (Whitehead 1969). Successful fruit set by these trees is therefore an almost predictable phenomena that is frequently taken for granted by resource managers. Tropical trees, on the other hand, reproduce in a more aseasonal environment, and there is tremendous variability in the flowering and fruiting phenologies, the pollination and seed dispersal syndromes, and the sexual systems exhibited by these forest species. The reproductive biology of tropical trees is complex and, to date, poorly understood. It is, however, a subject of great importance to any resource manager working in the tropics, regardless of the species or product being exploited. Maximizing the production of fruits, nuts, or oil seeds may not be the goal of every forest management system, but insuring the continual regeneration of the species under exploitation will always be a key component of sustainable forest use (Bawa, Ashton, and Nor 1990).

Phenology of Flowering and Fruiting

Studies in Malaysia (McClure 1966; Medway 1972; Ng 1977; Yap 1982; Appanah 1985), Costa Rica (Frankie, Baker, and Opler 1974), Panama (Smythe 1970; Croat 1978), subtropical Brazil (Jackson 1978), and Amazonian Peru (Terborgh,1983) have shown that tropi-

Table 1.2 Density and Yield for Selected Forest Species in Amazonia

Dominant Species	*Primary Uses*	*Habitat*	*Adult Density (trees/ha)*	*Fruit Yield (tons/ha/yr)*
Euterpe oleracea	Edible fruits Palm hearts	Seasonally flooded forest	267	1.2 ± 0.7
Grias peruviana	Edible fruits	Seasonally flooded forest	192	2.3
Jessenia bataua	Edible fruits Oil	Seasonal swamp forest	104	3.5
Mauritia flexuosa	Edible fruits Oil	Permanent swamp forest	138	6.1
Myrciaria dubia	Edible fruits	Seasonally flooded riparian	1,224	11.1 ± 1.6
Orbygnia phalerata	Oil Animal feed	Disturbed upland forest	223	1.5 ± 0.1

Note: Yield data are expressed on a fresh weight basis; mean production and standard error shown when fruiting measured for more than one year or when replicate sample plots were used (see source for study sites and sampling methodologies).

Source: Peters and others 1989.

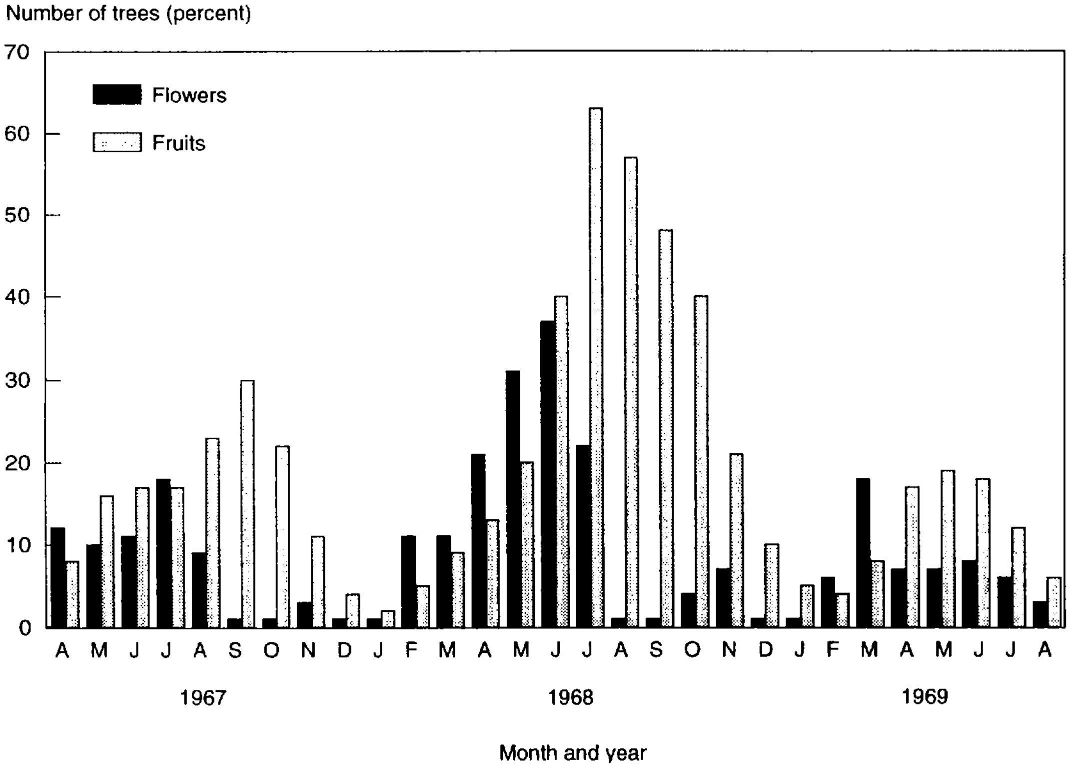
cal trees vary greatly in the timing, duration, and intensity of their flowering and fruiting. Different species may produce flowers supra-annually (only once every couple years), annually, or even several times a year (Bawa 1983). Similarly complex patterns occur in the periodicity of fruit production (Janzen 1978).

In spite of the diversity of different phenologies exhibited by individual tree species, community-wide flowering and fruiting patterns have been found to be remarkably seasonal in many tropical forests. In both Panama (Croat 1978) and Peru (Terborgh 1983), distinct peaks in fruit production have been noted at the start (November-December) and toward the end (February) of the rainy season. In Costa Rica, a single fruiting peak was observed from August to October during the second dry season (Frankie, Baker, and Opler 1974), while in Malaysia, the highest percentage of trees produced flowers between March and July during the early dry season and fruited from July to October (McClure 1966; Medway 1972). The occurrence of these seasonal peaks, however, should not obscure the fact that a significant number of tree species were also producing flowers and fruits during other months of the year. The Costa Rica study, for example, found that at least 37 of the 187 tree species surveyed had flowers or fruits during any month of the year (Frankie, Baker, and Opler 1974).

One of the most interesting and notable examples of synchronous or "gregarious" flowering and fruiting is exhibited by the Dipterocarpaceae, a family of dominant canopy trees in Southeast Asia.[3] At irregular intervals of from two to ten years, numerous dipterocarp species will more or less simultaneously start to flower within the forest (Wood 1956; Cockburn 1975; Appanah 1985; Ashton, Givnich, and Appanah 1988; Ashton 1989; see also the Malaysian phenology studies cited above). This supra-annual, mass flowering phenomena is usually followed by an extremely abundant level of fruit production known as "mast" fruiting. Mast fruiting may occur in a region as small as a single river valley, or in some years may extend over an area as large as all of northeastern Borneo (Ashton, Givnish, and Appanah 1988). In an especially intense mast year, almost every dipterocarp and up to 88 percent of all canopy trees may burst into flower (Medway 1972). A graphic depiction of this phenomena is presented in figure 1.3, which shows the phenological behavior of forty-five large-canopy species before, during, and after a mast year at the Ulu Gomback Forest Reserve in Peninsula Malaysia. Although gregarious flowering and fruiting is also known to occur in neotropical forests, it is usually limited to individuals of the same species and rarely occurs with the synchronicity, or intensity, of that exhibited by the canopy trees of Southeast Asia.

The environmental cues responsible for stimulating flower and fruit production by tropical trees are, as yet, poorly understood. Seasonal water deficits during the dry season have been shown to trigger the opening of flower buds (anthesis) in many Central American trees (Janzen 1967; Daubenmire 1972; Borchert 1983), and several canopy species in the seasonally flooded forests of Amazonia appear to flower at the onset of flooding (Peters and Hammond 1990). A variety of explanations have been offered to explain the gregarious flowering of dipterocarps, including brief dry periods (Foxworthy 1932; Boswell 1940; Baillie 1972), an increase in daily irradiation (Wycherley 1973; Ng 1977), or a slight drop in minimum night temperatures (Ashton, Givnish, and Appahah 1988). Whatever the proximal cue may be, Janzen (1974b) has argued that the mass flowering and subsequent mast fruiting of many tree genera in Southeast Asia are ultimately driven by the need to satiate seed predators. According to this theory, mast fruiting limits the abundance of frugivores and seed predators in the forest by concentrating their food supply into one brief period every few years when they are swamped by more food than they can possibly eat. The theory seems to be supported by

Figure 1.3 Flowering and Fruiting Phezology of 45 Canopy Tree Species Growing at the Ulu Gombak Forest Reserve in Malaysia



Note: Over 85% of the tree species were reproductively active during the last-fruiting event shown in 1968; 40–50% of the species produced flowers or fruits during 1967 and 1969.

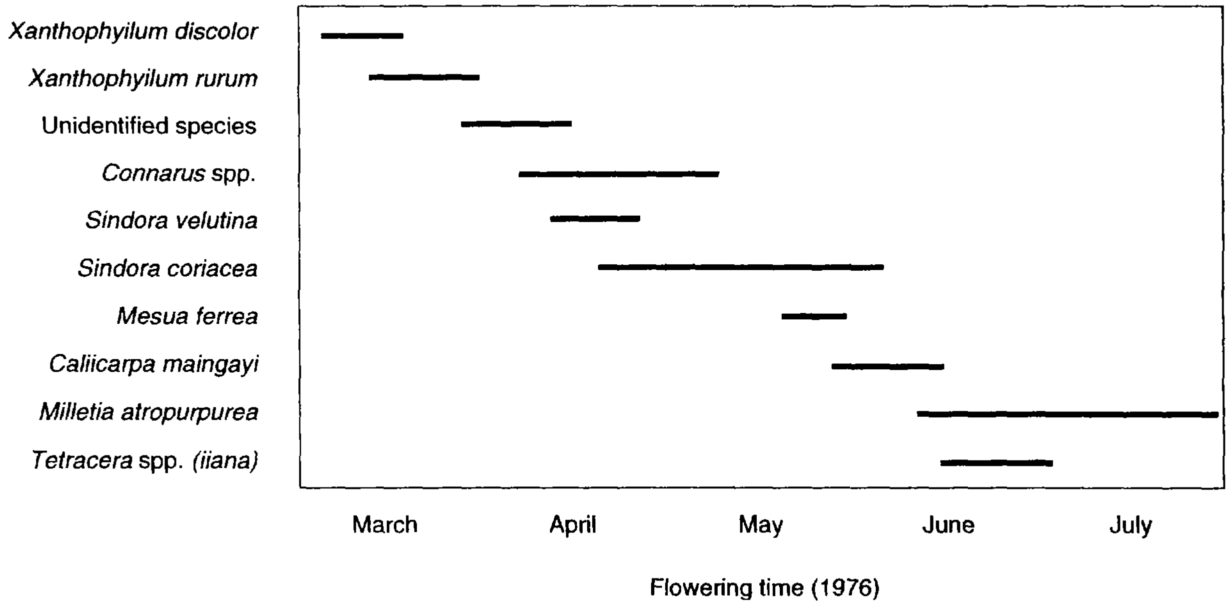
Source: Medway, 1972.

the observation that trees that occasionally fruit out of synchrony with the rest of the population experience high levels of predation (Burgess 1975).

A final aspect of the phenology of tropical trees—that also reflects the important influence of forest animals—is the sequential flowering of congeners or related taxa sharing the same pollinators. Staggered flowering times of various tree species has been observed in both Central America (Stiles 1978) and Southeast Asia (Wood 1956; Appanah 1985; LaFrankie and Chan 1991) and may be a common strategy to avoid competition for limited pollinators. This phenomena is illustrated in figure 1.4, which presents the timing and duration of flower production by nine tree species and one liana growing in the Pasoh Forest Reserve, Malaysia. All of the species produce large, conspicuous flowers that are pollinated by carpenter bees (*Xylocopa* spp.). As can be seen in this figure, the flowering sequences of the ten species are arranged in such a manner that the bees can easily switch from one species to another. When the floral resources of one species are finally exhausted, those provided by the next species increase. Each of the plant species is able to maximize pollination efficiency, and the pollinators are provided with a reliable food source for a longer period of time.

Clearly, the use and management of tropical forests would be considerably easier if flowers and fruits appeared more regularly and predictably. In fact, an ideal economic tree species would produce abundant fruit crops at well-defined intervals throughout the year. Unfortunately, few forest trees

Figure 1.4 Timing and Duration of Flower Production of Nine Tree Species and One Liana (Pasoh Forest Reserve, Malaysia)



Note: All ten species are pollinated by carpenter bees (*Xylocopa*).
Source: Adapted from Appanah 1979.

would be able to maintain this level of production, and even if they did, the fruit crops would probably be devastated by the frugivore and seed predator populations that had expanded on such a reliable food source.

The intricate phenological patterns of tropical trees have evolved to facilitate pollination, seed dispersal, and the growth and survivorship of seedlings. Although these ecological necessities are also important to the resource manager trying to develop a sustainable program of forest use, such basic economic considerations as yield per unit area, ease of harvesting, and resource availability in response to market demand may ultimately determine the success or failure of the business. For example, it is hard to imagine a more difficult situation to manage than one in which the key species produce fruit for only a few months at unpredictable intervals of from two to ten years—but this is exactly the challenge of the illipe nut (*Shorea* spp.) trade in northwestern Borneo.[4] Phenological patterns can frequently be an ecological bottleneck to commercial resource extraction, and resource managers would be well advised to learn as much as they can about the temporal dynamics and causality of the flowering and fruiting behavior of the species under their control.

Pollination

The low density and scattered distribution of individuals within many tropical tree populations presents a dilemma for pollination. Outcrossing, or the exchange of genetic material between conspecifics, is the desired objective, but how can pollen be transferred from one tree to another when they may be more than 100 meters apart? Table 1.3, which lists the principal pollinators of twelve commercially important tropical plant resources, provides a partial answer. Tropical trees have apparently solved the problem of long-distance pollen transfer by coevolving relationships with a variety of animals, ranging from tiny thrips and midges to bees and large bats, to shuttle pollen between conspecific individuals. These relationships can be quite specific, with one type of insect being solely responsible for pollinating the flowers of a particular species, or even genus, of forest trees (Wiebes 1979). Numerous studies (for example, Baker 1973; Heithaus 1974; Toledo 1977; Appanah 1981) have documented the diversity—and ingenuity—of these pollination systems. Interestingly, flowers of similar morphology, color, fragrance, or presentation are frequently used by different tree species to attract the same type of pollinator, such that a number of general pollination syndromes can be recognized. Several of the more important pollination syndromes exhibited by tropical trees are discussed briefly below, and a general listing of the main characteristics of each floral type is presented in box 1.1.[5]

Ecologists have long puzzled over which animal vector is responsible for pollinating the gregarious, supra-annual flowering Dipterocarpaceae of Southeast Asia. What animal could possibly respond to such a massive increase in floral resources and still survive the long periods between mass flowering events? Several studies (Appanah 1979, 1985; Chan 1977; Appanah and Chan 1981) have shown that thrips (*Thysanoptera*)—small, seemingly insignificant, insects—perform this vital service. A useful characteristic of these insects is their capacity to rapidly increase in numbers on an unpredictable food source. They have an eight-day life cycle and a single female can produce up to twenty-eight eggs (Appanah and Chan 1981). The millions of floral buds produced by several dipterocarp species (*Shorea* section *Mutica* and *Hopea*) become the breeding grounds for these tiny insects. Adult thrips quickly emerge after oviposition and begin to feed on, and become covered with, the petals and sticky pollen of the newly opened flowers. In the morning, the thrips, together with the shed corollas, fall to the ground. New flowers begin to open in the evening and as the penetratingly sweet floral odor lures the thrip pollinators back up into the crown, hundreds of their pollen-ladened bodies slowly

Table 1.3 Pollinating Agents of Selected Commercially Important Tropical Plant Resources

Species	*Common Name*	*Use*	*Pollinator*
Shorea spp.[a]	Illipe nut	Oil seed	Thrips
Hevea brasiliensis[b]	Rubber	Latex	Thrips/midges
Theobroma cacao[b]	Chocolate	Oil seed Edible fruit	Midges
Mangifera indica[b]	Mango	Edible fruit	Flied
Artocarpus heterophyllus[b]	Jackfruit	Edible fruit	Flies/beetles
Orbiguya martiana[b]	Babassu	Oil seed	Beetles
Bactris gasipaes[c]	Pihuayo	Edible fruit Palm heart	Beetles
Bertholettia excelsa[d]	Brazil nut	Edible seed	Bees
Euterpe oleracea[c]	Acai	Edible fruit Palm heart	Bees
Ceiba pentandra[e]	Kapok	Fiber	Bats
Durio zibethinus[f]	Durian	Edible fruit	Bats
Parkia speciosa[g]	Petai	Edible fruit	Bats

Note: The animals listed represent the principal pollinators; the flowers of each species may also be visited by other pollinators.

Source: a. Appanah and Chan 1981. b. Purseglove 1975. c. Anderson 1983. d. Henderson 1986. e. Mori and Prance 1987. e. Baker 1973. f. Soepadmo and Eow 1977. g. Baker and Harris 1957.

Box 1.1 Basic Characteristics of Various Pollination Syndromes

Pollinator	Anthesis	Floral Characteristics			
		Color	*Odor*	*Shape*	*Nectar*
Insect Pollinators					
Beetles	Day and night	Usually dull	Fruity or aminoid	Flat or bowl shaped; radial symmetry	Undistinguishable, if present
Carrion and dung flies	Day and night	Purple, brown or greenish	Decaying protein	Flat or deep; radial symmetry; often traps	Rich in amino acids, if present
Syrphid and bee flies	Day and night	Variable	Variable	Deep; usually radial symmetry	Hexose-rich
Bees	Day and night or diurnal	Variable but not red	Usually sweet	Flat to broad tube; bilateral or radial symmetry	Sucrose-rich or hexose-rich
Hawkmoths	Nocturnal	White, pale or green	Sweet	Deep, often with spur; radial symmetry	Ample and sucrose-rich
Settling moths	Day and night or diurnal	Variable but not red	Sweet	Flat or moderately deep; bilateral or radial symmetry	Sucrose-rich
Butterflies	Day and night or diurnal	Variable; pink very common	Sweet	Upright; radial symmetry; deep or with spur	Variable; often sucrose-rich
Vertebrate Pollinators					
Bats	Nocturnal	Drab, pale, often green	Musty	Flat "shaving brush" deep tube; radial symmetry; much pollen; often upright, hanging outside of foliage, or displayed directly on branch or trunk	Ample and hexose-rich
Birds	Day	Vivid, often red	None	Tubular, sometimes curved; radial or bilateral symmetry; robust corolla	Ample and sucrose-rice
Abiotic Pollinators					
Wind	Day or night	Drab, green	None	Small, sepals and petals absent or much reduced; large stigmata; much pollen	None or vestigial
Water	Variable	Variable	None	Minute; sepals and petals absent or much reduced	None

Source: Adapted from Howe and Westley 1986; with data from Faegri and van der Pijl 1971; Procter and Yeo 1972; and Baker and Baker 1983.

spiral upward in the weak air currents of the forest interior.

Bees undoubtedly rank as some of the most important and ubiquitous pollinating agents in tropical forests, especially among trees of the upper canopy (Appanah 1990; Baker and others 1983). Large, solitary bee species such as *Euglossa* and *Xylocopa*, for example, have been found to move systematically from the crown of one conspecific individual to another during a flowering event, often covering a distance of up to 23 kilometers in a single day. This interesting behavior, which Janzen (1971a) has termed "trap-lining," is obviously of great benefit in facilitating the cross-fertilization of tall, widely spaced individuals. Other bee species (for example, *Trigona*) are specialists at foraging within the low visibility of the forest understory. According to Faegri and van der Pijl (1971), bee flowers are usually zygomorphic (bilateral symmetry), of bright colors such as yellow, blue or bluish-green, and produce copious amounts of sucrose- or hexose-rich nectar (see box 1.1). Many of these flowers even contain a strategically located "landing platform" for the pollinator where it can rest and drink nectar while inadvertently covering its body with pollen.

Pollination by vertebrates is also well represented in tropical forests, and bats perhaps provide the best example of these syndromes. Floral visitation by bats in the Asian tropics is limited to members of the suborder Megachiroptera (for example, *Eonycteris*), while the Microchiroptera (*Artibeus* or *Glossophaga*), which are insectivorous in Southeast Asia, are the predominate bat pollinators in the neotropics (Baker 1973). Depending on the species of bat and the quantity of available nectar or pollen rewards, these animals may forage either singly or in groups. Several studies from both Central America (Heithaus, Fleming, and Opler 1975) and Southeast Asia (Gould 1978) suggest that bats may also "trap-line" between scattered conspecific trees. Start (1974) reported that the nectarivorous Malaysian bat *Eonycteris spelaea* may fly up to 50 kilometers from its roost in a single night and visit the flowers of several different tree species along the way.

Bat-pollinated flowers are known to occur in two distinctively different forms: either large, sturdy single flowers or "bottle brush" inflorescences (Faegri and van der Pijl 1971). Both floral forms open at night; have a drab or whitish color; exude a strong, musty odor; and produce large quantities of pollen and nectar. There are also marked differences in the location or presentation of bat flowers. The flowers either hang from a long, stout pedicel (as in *Parkia* spp.) so that the bat can fly freely clear of limbs and foliage, or they are clustered near the tips of large branches (*Ceiba pentandra*) so that the bat can easily land to eat pollen or drink nectar (Start and Marshall 1976).

Although necessarily brief, these few examples are sufficient to illustrate the diversity and complexity of the interactions between tropical forest trees and their animal pollinators. A reasonable question that has not been addressed up to this point, however, concerns the frequency of occurrence or relative importance of these coevolved relationships. Are these plant-animal interactions of any real concern to tropical resource managers? What percentage of the trees growing in tropical forests actually rely on a specific animal vector to carry pollen?

Fortunately, the answer to these questions has already been provided, at least for one specific area in the neotropics, by a landmark study that catalogued the pollination syndromes of all tree species found within a small tract of lowland forest in Costa Rica (Bawa and others 1985b). The results from this study are presented in table 1.4, and several points of interest should be noted. First, 139 (96.4 percent) of the 143 tree species surveyed were pollinated exclusively by animals; only 4 (3.6 percent) subcanopy species were pollinated by abiotic means. Second, medium to large-size bees were by far the most common pollinators, followed by moths, small diverse insects (an artificial category containing small beetles, flies, wasps, and butterflies), and small bees. Finally, notable differences in pollination syndromes were detected between canopy and subcanopy trees, with subcanopy species exhibiting the greatest diversity of syndromes. Hummingbirds, beetles, and sphingid moths were particularly important as pollinators in the lower canopy; bees were clearly the principal vector of pollen movement in the overstory.

Based on these findings, it is obvious that the conservation and management of tropical trees must include measures to ensure adequate levels of pollination. Appanah (1990), in fact, has argued that pollinator availability is what ultimately determines the upper limit on the number of species, or the number of individuals of the same species, that can occur together within a tropical forest. This would seem to be especially true for those forest species that have a high degree of specialization with their pollinator. In these cases, as Bawa and Krugman (1991) succinctly point out, "the management of the pollinator population becomes as important as the management of the tree population serviced by these pollinators."

There is an urgent need to learn more about the life histories and population dynamics of important pollinator groups and to document their response to changes in forest composition and structure. Furthermore, there needs to be a greater appreciation of the fact that land-use patterns far away from the immediate management area can be extremely disruptive to populations of wide-ranging animals such as bats or even bees. The current situation of the nectarivorous bat, *Eonycteris spelaea*, is a dramatic and unfortunate example of this.

In Peninsula Malaysia, *Eonycteris* bats are apparently the exclusive pollinator of four species of Parkia trees and eleven species of *Durio* trees (Appanah 1990). Both of these tree genera produce edible fruits of commercial importance (see table 1.3). The bats, however, feed preferentially on the flowers of *Sonneratia alba*, a coastal mangrove that occurs in dense natural populations and produces a few large flowers almost continually throughout the year (Start and Marshall 1976). In order to forage on this reliable food source, *Eonycteris* bats must fly 20–40 kilometers from their roost every night. During this

Table 1.4 Frequency of Different Pollination Syndromes

Pollinator Type	*Percentage of Canopy Species*	*Percentage of Subcanopy Species*
Bat	3.8	2.7
Hummingbird	1.9	5.4
Small bee	7.7	17.0
Medium to large bee	44.2	19.6
Beetle		10.7
Butterfly	1.9	6.2
Moth	1.9	10.7
Sphingid	1.9	10.7
Other	11.5	6.2
Wasp	3.8	4.5
Small diverse insect	23.1	12.5
Thrip		0.9
Wind		3.6

Note: These data were taken from a survey of 143 canopy and subcanopy species in a lowland tropical forest of Costa Rica. The small bee category contains mostly Halictidae, Megachilidae, and Heliponinimi; the medium to large bee category contains Anthophoridae; the small diverse insect category includes such small insects as bees, beetles, flies, wasps, and butterflies.

Source: Adapted from Bawa and others 1985b.

journey, *Parkia* and *Durio* trees that they may encounter in flower are pollinated almost as a dietary afterthought. Any management plan aimed at maintaining a viable population of pollinators for the *Parkia* and *Durio* trees in Malaysia must inevitably address the fact that the principal food source of *Eonycteris spelaea* is being currently decimated by coastal development.

Breeding Systems

The synchronized flowering and well-developed pollination mechanisms exhibited by tropical trees greatly facilitate the transfer of pollen from one flower to another. From an evolutionary perspective, however, the essence of plant reproduction goes beyond the simple transfer of pollen. The really important issue here is the nature and origin of the actual flower to which the pollen is transferred. During a single synchronized flowering event, thousands of conspecific blossoms will open and await visitation by potential pollinators. Clearly, most pollinators will forage on several different flowers within a single tree crown before moving on to another tree. There is therefore a large probability that at least some of these flowers will be pollinated, in one of two ways. Geitonogamy, or the transfer of pollen from the anther of one flower to the stigma of another flower on the same tree is the most likely result of the pollinator's foraging. Autogamy, or the transfer of pollen from the anther of one flower to the stigma of the same flower, may occur with or without pollinator assistance. It should be noted that the genetic effect of both types of pollination are essentially the same—self-fertilization and inbreeding.

To reap the benefits of cross-fertilization (Ghiselin 1974; Lloyd 1980), autogamy and geitonogamy must somehow be avoided so that the flowers on one tree remain receptive to the pollen produced by other trees. Not surprisingly, tropical tree species have evolved a wide variety of different floral strategies and breeding systems to achieve this objective. The exact nature and relative efficiency of the mechanisms used by tropical trees to avoid self-pollination have long been of interest to ecologists and biologists concerned with gene flow, speciation, and the evolution of diversity in tropical forests. These mechanisms should also be of interest to forest managers, especially those concerned with maximizing the quality and quantity of the seeds and seedlings produced by tropical trees.

Avoiding self-pollination would seem to be especially problematic given that the great majority of tropical trees produce hermaphroditic or perfect flowers.[6] Many of these species, however, have evolved flowers that display a distinct physical or temporal separation of the anthers and stigma. The bat-pollinated flowers of *Ceiba acuminata* (Bombacaceae), for example, possess a long stigma that is exserted so far away from the anthers that only through the action of the appropriate animal can pollination be achieved (Baker and others 1983). The small, globose flowers of *Brosimum alicastrum* (Moraceae), on the other hand, display a different strategy: the anthers dehisce (split) and release pollen at a time when the stigma is not receptive (Peters 1989). Staggering the timing of pollen release and stigma receptivity (dichogamy) is an extremely common floral characteristic which can be expressed as either protandry (anthers develop prior to stigma) or protogyny (stigma develops prior to anthers. Protandry seems to be the most frequently encountered form of dichogamy among hermaphroditic tropical trees. Although both physical and temporal mechanisms greatly reduce the possibility of autogamic self-pollination, a significant level of geitonogamy may still occur.[7]

Genetic incompatibility systems are the most subtle and effective barrier to self-pollination (De Nettancourt 1977; Lewis 1979). These ingenious biochemical adaptations enable the stigma, style, or ovary to differentiate between self and outcrossed pollen and to selectively inhibit the germination or growth of all pollen grains except those produced by different conspecific genotypes. Unfortunately, the difficulties of performing controlled pollinations on the flowers of large tropical trees have severely limited the amount of research conducted on this important topic. The few studies that are available, however, suggest that self-incompatibility mechanisms may be a common feature of the breeding systems of tropical trees.

Based on research conducted in a tropical lowland forest of Costa Rica, Bawa, Perry, and Beach (1985a) report that twenty-three (82 percent) of the twenty-eight hermaphroditic tree species subjected to controlled pollinations were found to be self-incompatible. An earlier study of semi-deciduous forest in Costa Rica found that twenty-seven (79 percent) out of thirty-four hermaphroditic trees were self-incompatible (Bawa 1974). A high incidence of self-incompatibility among hermaphroditic trees has also been noted in the montane forests of Venezuela (Sobrevila and Arroyo 1982) and in the mixed dipterocarp forests of Malaysia (Kaur and others 1978; Chan 1981). Contrary to expectations, it would appear that a large percentage of the tropical trees producing bisexual flowers are obligate outcrossers.

A second breeding system used by tropical trees to promote outcrossing is monoecy, or the production of unisexual male and female flowers on the same tree. By separating the male and female flower functions within a tree, the possibility of autogamy is eliminated. Bawa, Ashton, and Nor (1985a) report that 9.5 percent of the canopy trees and 12.2 percent of the subcanopy trees on their Costa Rican study site were monoecious. Croat's (1978) survey of the flora of Barro Colorado Island in Panama found that 15 percent of the medium to large trees and 12 percent of the small trees and shrubs were monoecious. It should be noted that the unisexual flowers of many monoecious taxa contain fully formed, yet nonfunctional, organs of the opposite sex. This characteristic makes it extremely difficult to assess the sexuality of a flower solely from its morphology, and, not surprisingly, many tropical tree species originally described as hermaphroditic have been found to produce flowers that are functionally unisexual as recorded by Styles (1972) for the Meliaceae.

Some tropical tree species have taken the spatial separation of staminate and pistillate floral functions to its ultimate extreme by evolving separate male and female trees. This breeding system, known as dioecy, clearly eliminates any possibility of self-pollination by either autogamy or geitonogamy. Dioecious tree species have been found to be very common among tropical taxa, representing a surprisingly constant 20 percent of the tree species surveyed in Central America (Bawa and Opler 1975; Croat 1979; Bawa, Ashton, and Nor 1985a), South America (Zapata and Arroyo 1978) and Southeast Asia (Ashton 1969). Among this group are many important fruit trees such as nutmeg (*Myristica fragrans*), mangosteen (*Garcinia mangostana*), wild rambutan (*Xerospermum* spp.), and several species of *Baccaurea* (Purseglove 1975; Whitmore 1973; Yap 1982). Interestingly, most of the dioecious tropical trees populations that have been studied exhibit a sex-ratio skewed in favor of male trees (Opler and Bawa 1978; Yap and Razali,1980). Apparently, a preponderance of male trees is essential for maximizing pollen transfer and fruit set in these species.

In contrast to the large number of species that are obligate outcrossers, a final group of tropical trees have recently been discovered to reproduce by apomixis, or asexual embryogenesis. This curious breeding system is an extreme form of self-fertilization and effectively eliminates all gene flow between conspecific individuals. Apomixis has been verified in two dipterocarp tree species from Southeast Asia (Ashton 1977; Kaur and others 1978), and inferred for a wide variety of other taxa, including several genera of cultivated fruit trees (for example, *Citrus*, *Eugenia*, *Garcinia*, *Lansium*, and *Mangifera*). Apomictic species are frequently characterized by the production of multiple seedlings from a single seed, a high degree of self-compatibility, low pollen germination, irregular meiosis, and polyploidy. Although the occurrence of potentially high levels of apomixis in tropical forest trees goes against all theoretical predictions, Appanah (1985) has argued that the evolution of this breeding system is a logical response to the intense competition for pollinators experienced during many mass flowering events.

The particular breeding system used by a forest tree population can either complicate or greatly simplify management activities. In hermaphroditic tree populations, for example, the fact that every individual can potentially set fruit, even autogamic or geitonomic, self-fertilized fruit, is a major asset.[8] Hermaphroditic species with well-developed incompatibility mechanisms, however, may exhibit significantly lower rates of total fruit production than populations of more "promiscuous" individuals. The difference in reproductive output between facultative and obligate outcrossers could become even more pronounced in the event of a shortage, or complete displacement, of available pollinators. Dioecious tree species present a special management problem. Less than half of the individuals in these populations will produce fruit and maintaining an optimal number and distribution of staminate trees could be exceedingly difficult (Ng 1983; Bawa and Krugman 1991). A tropical forest dominated by strictly apomictic populations of useful tree species would undoubtedly be the best-case management scenario. Unfortunately, given the paucity of information on this topic and the difficulty of actually proving asexual embryogenesis in large canopy trees, it is highly improbable that this situation would be recognized even in the unlikely event such a forest should occur.

Irrespective of the species, habitat, or type of forest resource to be managed, a basic understanding of tree breeding systems is of considerable practical importance. The main concepts of plant pollination and breeding systems are illustrated in figure 1.5.

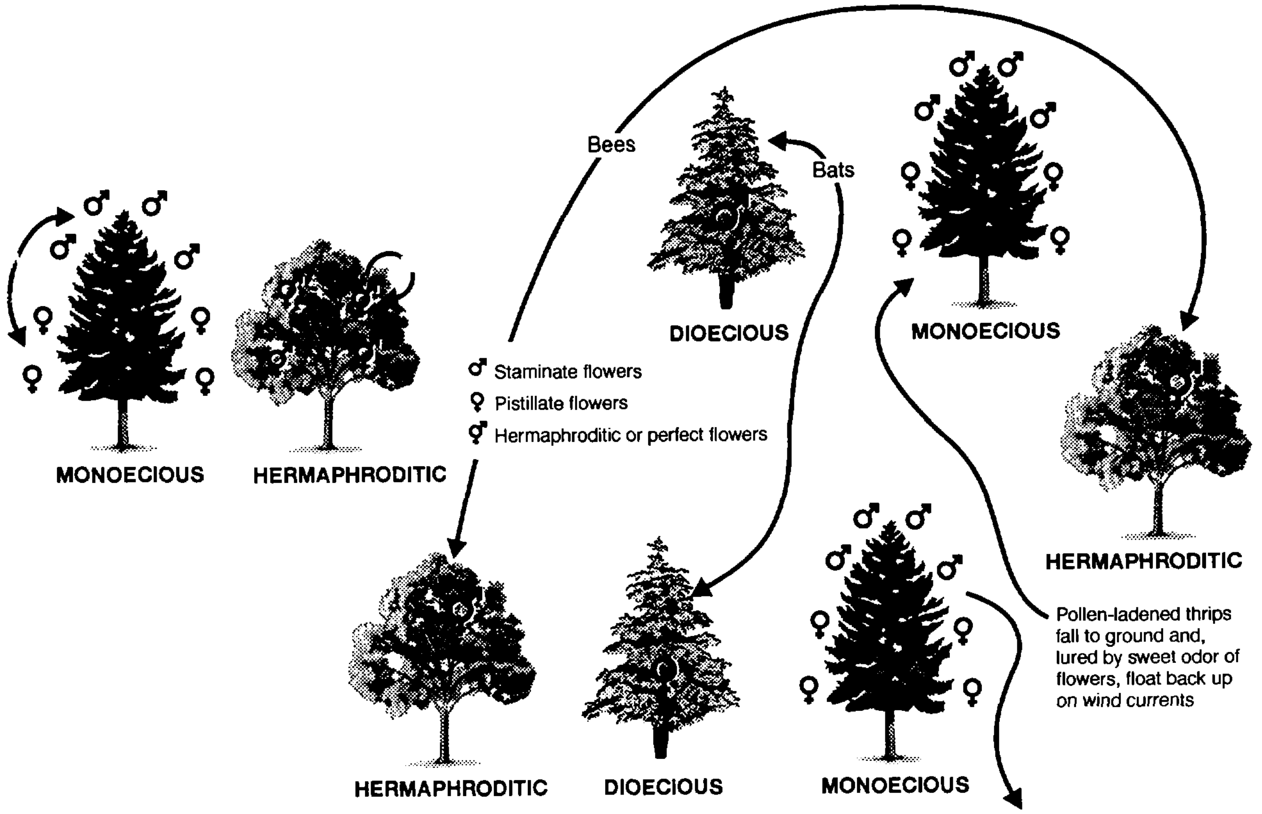
Seed Dispersal

The importance of animals in the reproductive biology of tropical trees does not end after pollination. Once fruits and seeds have been successfully nurtured to maturity, the next problem faced by flowering plants is what to do with these progeny. Given the incredible diversity of tree fruits, many of which are extremely rich in protein, starch, or sugar and are quite costly in terms of resources to produce, it is obvious that they have not been evolved to simply drop to the ground beneath the parent tree. Rather, it seems more likely that these fruits have been specifically designed to be eaten—and the intact seeds within the fruit effectively dispersed to a new location.

Seed dispersal offers at least three ecological benefits to the fruiting individual (Howe and Smallwood 1982). The first of these is that a dispersed seed has a greater probability of escaping the excessive competition and mortality that occurs among conspecific seedlings under parent trees. Dispersal may also allow a seed to colonize new habitats or to spread its parent's genotype into different breeding populations. Finally, some types of dispersal may even position a seed in the precise microsite necessary for its successful germination and growth within the forest. As can be appreciated, these benefits are not mutually exclusive and all three may occur depending on the tree species, the dispersal agent, and the immediate environment. There is, however, an ecological cost associated with seed dispersal, especially when animals are involved. During the process of handling, transporting, or feeding on fruits, frugivores may destroy a large proportion of the seeds inside.

The prevalence of tropical trees with animal-dispersed fruits suggests that the actual costs of biotic dispersal are greatly outweighed by the potential benefits. Studies conducted in Rio Palenque, Ecuador, for example, have shown that 93 percent of the canopy trees and 91 percent of the subcanopy trees produce fruit adapted for consumption

Figure 1.5 Plant Pollination and Breeding Systems



GEITONOGAMY
Self-fertilization and inbreeding reduces gene flow and potential for genetic recombination

Methods of avoiding self-pollination:
- separation of anthers and stigma physically or temporally (protandry or protogyny) in hermaphroditic flowers
- genetic incompatibility in hermaphroditic flowers
- unisex flowers in monoecious species (geitonogamy still possible)
- unisex trees (dioecious species)

OUTCROSSING OR CROSS-FERTILIZATION
is biologically preferable. Pollen transfer between trees is facilitated by birds, bees, bats, and insects such as thrips

by birds or mammals (Gentry 1982). Similarly, Croat (1978) estimates that 78 percent of the canopy trees and 87 percent of the subcanopy trees at Barro Colorado Island in Panama have animal-dispersed fruit, while Hartshorn (1978) reports a figure of 91 percent for the tree species at the La Selva research station in Costa Rica. Although no detailed surveys of this type have yet been conducted in Southeast Asia, related research indicates that animals are also important dispersal agents there (Wilson and Johns 1982; Leighton and Leighton 1983; Johns 1988). Clearly, bats, birds, primates, peccaries, and a wide assortment of other vertebrates are responsible for moving an enormous quantity of seeds around in a tropical forest. These animals may either remove fruits or seeds directly from the tree (primary dispersers), or they may forage on fruits that have already fallen to the ground and split open (secondary dispersers).

Tropical trees attract potential dispersal agents by the color, odor, presentation, or composition of their fruits. Just as human consumers in the fruit section of their local supermarket exhibit specific preferences, different animals have also been found to be attracted to certain types of fruits. The characteristics of a fruit that attract a particular animal vector or predispose it to an abiotic means of dispersal are known collectively as dispersal syndromes. A concise listing of these syndromes is shown in box 1.2, together with descriptive information about the color, odor, form and reward exhibited by each fruit type.[9]

Birds, bats, and arboreal frugivores (primates and procyonids) are probably the most common animal dispersers used by tropical trees (Howe 1986). This pattern has recently been quantified at Cocha Cashu in Peruvian Amazonia where 172 (66 percent) of the 258 different tree fruits sampled displayed the morphological characteristics of bird or mammal dispersal (Jansen 1983). A further finding of interest from this research is that birds and monkeys select and preferentially feed on distinct fruit types and do not forage solely in response to relative fruit abundance. Numerous previous studies (Howe 1977; Howe 1980; Howe and Vande Kerckhove 1981; Wheelwright and Orians 1982), in contrast, have contended that tropical fruits dispersed by only one or a few animals are very rare.

The interactions between birds and forests fruits have been surprisingly well researched, and at least two good surveys of the food plants of different frugivorous birds are available (Snow 1981; Wheelwright and others 1984). Based on these surveys, avian dispersers can be divided into two main groups—obligate or "specialist" frugivores and opportunist or "non-specialist" frugivores (McKey 1975). Obligate frugivores such as toucans and cotingas in the neotropics or hornbills in Southeast Asia are almost completely dependent on a diet of fruit. Fruits adapted for dispersal by these large forest birds are usually either large, lipid or protein-rich drupes of a green or purple color, or bright, contrastingly colored capsules or follicles of red and black that dehisce to expose large arillate seeds (see box 1.2). Fruits adapted for dispersal by opportunist frugivores, on the other hand, are smaller (5–10 millimeters), rich in lipids, proteins, sugars, or starch, and of a black, blue, red, or orange color. It is interesting to note that Snow's (1981) survey lists a total of 61 avian frugivores feeding on 171 plant genera from neotropical forests, compared with only 32 frugivores and 90 plant genera from Southeast Asia.

Bats also play an important role in transporting the seeds of many tropical trees (Fleming and Heithaus 1981; Bonnaccorso, Glanz, and Sanford 1980), and the unique feeding behavior of these animals make them particularly well suited for long distance dispersal. Neotropical microchiropteran bats such as *Artibeus* spp., for example, will remove mature fruits from a tree, fly back to their roost (which may be several kilometers away), and then carefully feed on the pericarp or fruit pulp. The intact seed is later dropped to the ground (Peters 1983). A similar behavior is exhibited by the flying foxes (*Pteropus* spp.) of Southeast Asia, the only difference being that these huge bats have wingspans of up to 1.5 meters and can carry fruits weighing as much as 200 grams (Medway 1969). Bat fruits compensate for their basically dull coloration (green, whitish, or pale yellow) by a strong, often musty, aroma and a dangling or pendant presentation. The fruit pulp is frequently rich in starch or lipids. A wide variety of commercially important fruit genera (*Achras, Annona, Bacccaurea, Lansium, Mammea, Mangifera, Manilkara, Persea, Psidium,* and *Spondias*) represent the bat dispersal syndrome (van der Pijl 1972).

Fruits adapted for dispersal by arboreal frugivores (such as monkeys) are a large and varied group. Research at Cocha Cashu, Peru has shown that five species of monkeys feed on the fruits of over 170 plant species from 55 different families (Terborgh 1983). Large (greater than 14 millimeters), often highly protected, fruits of a brown, green, orange or yellow color were found to be the preferred foods of these Amazonian primates (Jansen 1983), and a similar syndrome of fruit characteristics has been reported from Bornean forests (Leighton and Leighton 1983). Monkey fruits are often aromatic and frequently possess a fruit pulp that is rich in protein, sugar

Box 1.2 Basic Characteristics of Dispersal Syndromes

Dispersal Agent	*Color*	*Odor*	*Form*	*Reward*
Self-dispersal				
Gravity	Various	None	Undistinguished	None
Explosive Dehiscence	Various	None	Explosive capsules or pods	None
Abiotic Dispersal				
Water	Various, usually green or brown	None	Hair, slime, small size, or corky tissue that floats	None
Wind	Various, usually green or brown	None	Minute size, wings, plumes or balloon-like structures	None
Vertebrate Dispersal				
Hoarding mammals	Brown	Weak or aromatic	Tough, thick-walled nuts; indehiscent	Seed
Hoarding Birds	Green or brown	None	Rounded wingless seeds or nuts	Seed
Arboreal frugivorous mammals	Brown, green white, orange, or yellow	Aromatic	Often arillate seed or drupes; often compound	Aril or pulp
Bats	Green, white, or pale yellow	Aromatic or musty	Various; often pendant	Pulp
Terrestrial, frugivorous mammals	Green or brown	None	Tough, indehiscent; often greater than 50 millimeters long	Pulp
Highly frugivorous birds	Black, blue, red, green, or purple	None	Large arillate seeds or drupes; often dehiscent; seeds greater than 10 millimeters long	Pulp
Any frugivorous birds	Black, blue, red, orange, or white	None	Small to medium-size arillate seeds, berries, or drupes; seeds greater than 10 millimeters long	Various
Insect Dispersal				
Ants	Undistinguished	None	Elaiosome attached to seed coat	Oil

Source: Adapted from Howe and Westley 1986, with data from van der Pijl 1972, Wheelwright and others 1984, and Howe 1986.

or starch (see box 1.2). Seed dispersal is achieved by either gnawing on and dropping the fruit or by ingesting the fruit and later defecating the seeds.

A somewhat curious example of seed dispersal by animals has been observed in tropical riverine forests. As documented by Gottsberger (1978) and Goulding (1980) in

Amazonia, a large proportion of the tree species in seasonally flooded habitats drop their fruits into the water. These fruits are subsequently eaten by fish that defecate out the seeds, usually after swimming a considerable distance. The seeds either sink to the bottom to await the end of the flood cycle, or float to the nearest bank. Not surprisingly, the seeds that sink have evolved well-developed dormancy mechanisms to avoid germinating under water (Peters, unpublished data). The fruits of the riparian shrub *Myrciaria dubia* are actually used as bait by many Amazonian fishermen. Anecdotal evidence of fish dispersal has also been reported from the peat swamp forests of Southeast Asia (Anderson 1961; Whitmore 1984).

In spite of the prevalence of animal dispersal in tropical forests, several important tree taxa produce fruits that are adapted for wind dispersal. The Dipterocarpaceae of Southeast Asia are probably the best example of this. Most dipterocarp fruits have from two to five long wings (Ashton 1984) that enable them to slowly spiral down from the upper canopy. Given the lack of wind in the interior of most tropical forests, however, this mode of dispersal does not appear to be very efficient. Burgess (1975), for example, estimates that approximately 83 percent of the fruit crop produced by *Shorea curtisii* falls within 20 meters of the parent tree. The fruits of *Shorea macrophylla*, which can weigh up to 20 or 30 grams (Anderson 1975), undoubtedly display an even more limited pattern of dispersal.

A final aspect of seed dispersal that merits discussion concerns the inherently stochastic and opportunistic nature of this reproductive process. Although dispersal syndromes provide a useful ecological taxonomy, many tropical trees may, in fact, use a number of different vectors to transport their fruit. The fruits of *Spondias mombin*, a widely distributed canopy tree in the neotropics, are picked from the crown by monkeys (*Cebus, Alouatta, Ateles*), procyonids (*Nasua, Potos*), frugivorous bats (*Artibeus*), variegated squirrels (*Sciurus*), and various marsupials (Janzen 1985). All of these animals carry the fruits as far as 100 meters away from the tree, chew off the pulp, and drop the seed. Fruits that fall unaided to the ground are later foraged on by collared peccaries (*Tayassu*), white-tail deer (*Odocoileus*) agoutis (*Dasyprocta*), pacas (*Agouti*), and tapirs (*Tapirus*) that either defecate, regurgitate, or simply drop the seeds after eating the pulp. *Spondias* fruits are also known to float and may be effectively dispersed by water in riverine habitats such as lowland Amazonia (Peters and Hammond 1990). Clearly, it would be extremely difficult to determine which of these dispersal vectors is the most important during a given fruiting season or even to distinguish between the animals that disperse seeds and those that simply destroy them.

The presence of frugivorous animals in a tropical forest presents a dilemma for resource managers. On the negative side, these animals damage or consume large quantities of fruit, and their activities quickly become a nuisance when the species being eaten is a commercially important one. Herds of wild pigs (*Sus barbatus*) can ravage the crop of illipe nuts (*Shorea* spp.) produced during a mast year, drastically reducing the total available yield from the forest (Medway 1969). Frugivorous bats and parrots are notorious for the damage they cause on potential market fruits such as *Baccaurea, Brosimum, Durio, Manilkara, Mammea,* and *Spondias*. It is not surprising that a common solution to this problem has been simply to eliminate the animals from the forest.

On the positive side, however, forest frugivores play an extremely important role in dispersing the seeds of many commercial tree species. Some seeds, in fact, will not even germinate without first being cleaned by animals. Ng (1983) reports that the seeds of *Canarium, Xanthophyllum* and *Calophyllum* must have the pericarp removed before germination can occur, while *Sloanea* requires that the aril be cleaned away. The intact pericarps of the fruits of *Calamus*, the most important genus of rattan, and *Xerospermum*, a wild rambutan, have also been shown to inhibit germination (Yap 1976; Manokaran 1978). The distribution and abundance of the regeneration of a forest tree population is frequently controlled by the action of dispersal agents, and the great majority of these dispersers are animals. To fail to conserve a viable breeding population of these animals would be a serious, and perhaps irreparable, management error.

Regeneration and Growth

Safe arrival from the parent tree to the forest floor does not, by any means, guarantee that a seed will germinate and successfully become established within the forest. The seed must avoid being eaten, it must have the appropriate light, soil moisture, and nutrient conditions for germination, and it must be able to germinate and grow faster than all of the other competing seeds that are trying to establish themselves on that microsite. Moreover, all of these ecological barriers or "filters" must be overcome before the young seedling has a fully functional photosynthetic system. After the seedling becomes independent from its seed reserves, a whole array of new barriers are presented. The seedling must be able to photosynthesize and grow in the environment within which it finds itself, or at least be able to survive until these conditions change. It must be able to recuperate from the damage caused by herbivores, or be able to chemically defend itself against them. It must avoid falling branches, stay free of pathogens, continually produce new leaves and meristematic tissues, and push its way up into the forest canopy.

Tropical trees have evolved a variety of different life history strategies[10] to facilitate the critical transition from seed to established seedling. None of these strategies, however, are equally successful in all habitats. Under some conditions a species may exhibit an abundance of seedlings, saplings, and poles, while in other environments its regeneration may barely compensate for the mortality of adult trees. The scattered distribution and low density of many tree species indicate that the latter scenario occurs with great frequency in tropical forests. Maintaining a continual supply of newly established seedlings is basic to the survival of a forest tree population. It is also the essence of sustainable forest use. Stated simply, management activities which ignore the regeneration and growth requirements of the species under exploitation have little chance of long-term success.

Germination and Early Survival

There is a high probability that a seed will come in contact with an animal during the lapse between dispersal and germination. In most cases, this contact proves fatal for the seed. In terms of total numbers, seed predation is unquestionably one of the most severe sources of mortality during the life cycle of a plant (Harper 1969, 1977). A few examples should suffice to illustrate the importance and complexity of the plant-animal interactions that occur at the level of the seed. More than 98 percent of the seeds of *Virola surinamensis*, a large canopy tree native to the neotropics, are destroyed by rodents (*Agouti, Dasyprocta*) and weevils (*Conotrachelus* spp.) during the first twelve weeks following dispersal (Howe, Schupp, and Westley 1985). *Spondias mombin* loses more than 95 percent of its seeds to bruchid beetle (*Amblycerus*) seed predators (Janzen 1985), and the seeds of the small understory palm, *Astrocaryum mexicanum*, have less than a 0.05 percent chance to survive until germination (Sarukhan 1978). Seed predation is also a fact of life in Southeast Asian forests, and mortality rates of 40–98 percent have been reported for various dipterocarp species (Daljeet-Singh 1974; Burgess 1975; Turner 1990). Rodents, ants and weevils are the most frequently cited seed destroyers in these forests.

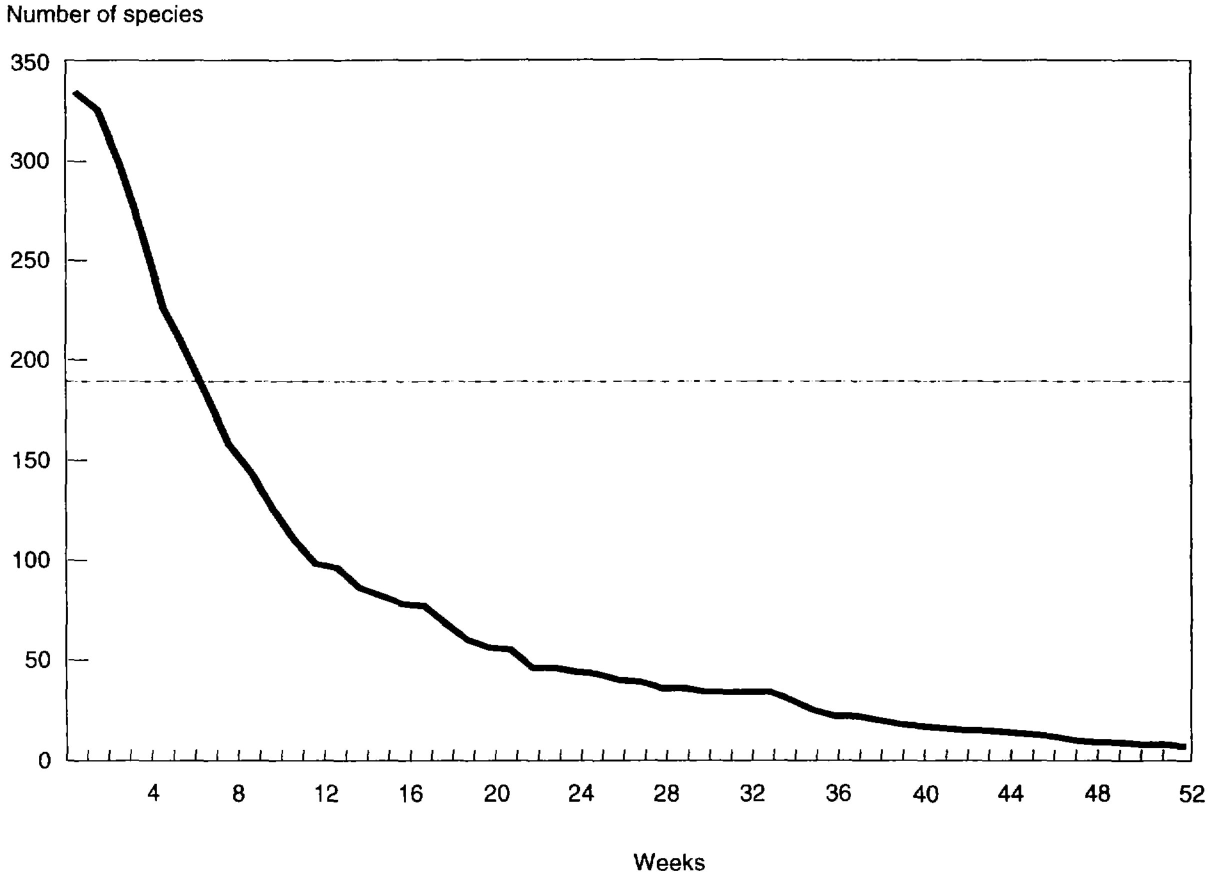
Janzen (1969, 1970, 1971b) has provided an excellent theoretical framework for assessing the evolutionary dynamics of seed predation. According to these theories, two classes of seed predators can be recognized based on their foraging behavior. Predators may be either "density responsive," with the intensity of predation increasing directly with the density of seeds, or they may "distance responsive," with distance to the fruiting individual being the key factor controlling the intensity of predation. In trees without well-developed dispersal mechanisms, a large percentage of the fruits will fall directly under the crown. This situation attracts both density and distance responsive predators and usually leads to an excessively high level of seed destruction (Clark and Clark 1984; Becker and Wong 1985; Howe, Schupp, and Westley 1985). Janzen (1970), in fact, has argued that the scattered occurrence of many tropical tree species is attributable to the effects of this type of seed predation.

One strategy that many tropical trees use to reduce the intensity of predation is to chemically protect their seeds. Chemical defenses seem to be especially common among species with large seeds. In addition to gums, latexes, and resins that may make a seed unpalatable to a seed-eating animal, numerous taxa have evolved seeds that contain alkaloids, phenolics, tannins or other toxic or repellent compounds. The family Leguminosae, for example, is notorious for producing chemically defended seeds. Although a detailed discussion of the chemical ecology of tropical seeds and seed predators is beyond the scope of this chapter, excellent reviews of this subject can be found in Feeny (1975), Levin (1976), and Rosenthal and Janzen (1979). An additional method of escaping predation is simply to germinate as rapidly as possible, and a large percentage of tropical forest trees have been found to exhibit this behavior. In one of the most extensive surveys of tropical seed germination to date, Ng (1980) conducted controlled nursery experiments on 335 different Malaysian tree species, approximately 10 percent of the local tree flora. The results from these experiments are presented as a frequency histogram in figure 1.6, which shows the number of species plotted against the time required to complete germination. Over half of the species (dotted horizontal line in figure 1.6) had finished germinating in only six weeks and two-thirds of them within twelve weeks. Most of the species with rapid germination were large-seeded, upper canopy trees.

A frequent correlate with rapid germination is an equally rapid loss of viability. Based on their storage physiology, seeds can be classified as either "orthodox" or "recalcitrant." The longevity of most seeds is increased in a predictable manner by decreases in temperature and moisture content, and seeds with these characteristics are said to have orthodox viability. Recalcitrant seeds, on the other hand, are killed if their moisture content or temperature is reduced below a critical level. Many tropical forest trees, including several important commercial species such as *Durio* and *Nephelium*) and all of the dipterocarps that have been studied, have recalcitrant seeds (Tang 1971; Tamari 1976; Sasaki 1980). These species usually germinate in the forest within a few days following seedfall and rarely can survive even minimal levels of desiccation (Cockburn and Wong 1969; Burgess 1975).

A second group of species, shown on the right side of figure 1.6 and representing about 7 percent of Ng's (1980) sample, exhibited some type of dormancy and required at least 12 weeks before they started to germinate. Dormancy in seeds has been extensively studied (Harper 1959, 1977; Taylorson and Hendricks 1977; Angevine and Chabot 1979; Cook 1980), and three basic types are usually recognized: *innate*, which prevents the seed from germinating while still attached to the parent tree; *induced*, which is caused by some stimulus that the seed experiences after ripening; and *enforced*, in which germination will not take place until some environmental constraint or limitation is removed. Enforced dormancy is probably the most frequently encountered type among the innumerable viable seeds that accumulate in the soil of a tropical forest. Recent research in the neotropics has shown that the environmental stimulus necessary to trigger the germination of many dormant seeds is either a change in the intensity or quality (for example, increased red wavelengths) of sunlight

Figure 1.6 Germination Times of the Seeds of 355 Malaysian Tree Species



Note: All seeds were sown under light shade in a nursery. Dotted horizontal line shows that 50% of the species exhibit complete germination within six weeks.
Source: Ng, 1980.

or a marked increase in temperature at the soil surface (Vazquez-Yanes and Orozco-Segovia 1984).

The ecological consequences of rapid germination versus dormancy are drastically different. Rapid germination forces the new seedling to photosynthesize, to grow, and to adapt to its environment as best it can. Characteristically, this is an extremely low-light, high-competition microsite within the forest understory. The fact that many seeds with rapid germination are also quite large and contain substantial seed reserves undoubtedly helps the young seedling to survive in such an adverse environment. Seeds with well-developed dormancy mechanisms, on the other hand, manifest a more opportunistic strategy. Their germination is keyed into a specific set of environmental conditions and they remain dormant—and susceptible to predation—until these prerequisites are met. Seeds with rapid germination struggle to survive in a highly competitive, resource limited environment. Dormant seeds sit and wait for things to get better.

Even assuming that a seed has successfully germinated, a new seedling's root system is firmly implanted in the soil, and the first leaves have expanded and started to photosynthesize, there is still a very small probability that the seedling will become established on that site. The first year of life for a seedling is plagued with difficulties. To begin with, the light levels in the understory of a tropical forest are usually so low (1–2 percent of full sun; Chazden and Fetcher 1984a) that it is very difficult for the new seedling to maintain a positive carbon balance.[11] Added to this is a high probability that it will be either browsed on by a herbivore, outcompeted by its neighbors, smashed by a falling tree, or completely desiccated by wildly fluctuating soil moisture levels. The few studies that have actually monitored the survival of new seedlings indicate that over 50 percent of a cohort dies within four to seven months after germination (Fournier and Salas 1967; Hartshorn 1972; Liew and Wong 1973; Sarukhan 1981; Peters 1990). Total survivorship at the end of one year may be as low as 3–4 percent.

A useful method for analyzing survivorship patterns of tropical seedlings is to plot the number or proportion of seedlings surviving against a time axis. Survivorship curves constructed in this manner for *Brosimum alicastrum* (Peters 1989) and three species of *Shorea* (Turner 1990) are shown in figure 1.7. *Brosimum alicastrum* is a widely distributed, upper-canopy tree from the neotropics; all three *Shorea* species are native to Malaysia. Seedling survivorship in these four species ranges from a high of 28 percent for *S. curtisii* to a low of only 3 percent for *B. alicastrum*. "Half-lives," or the time required to kill off 50 percent of the initial cohort, vary from two to five months. Turner (1990) reports that drought and excessive soil temperatures were the major sources of mortality for the three *Shorea* species, although damage by small rodents was also a significant factor. None of the seedlings had produced more than three leaves by the end of one year. Taking into account seed predation, germination, and early seedling survival, Turner (1990) estimates that only 1 percent of the dispersed seeds of *S. curtisii* were still present as seedlings in the forest understory after one year.

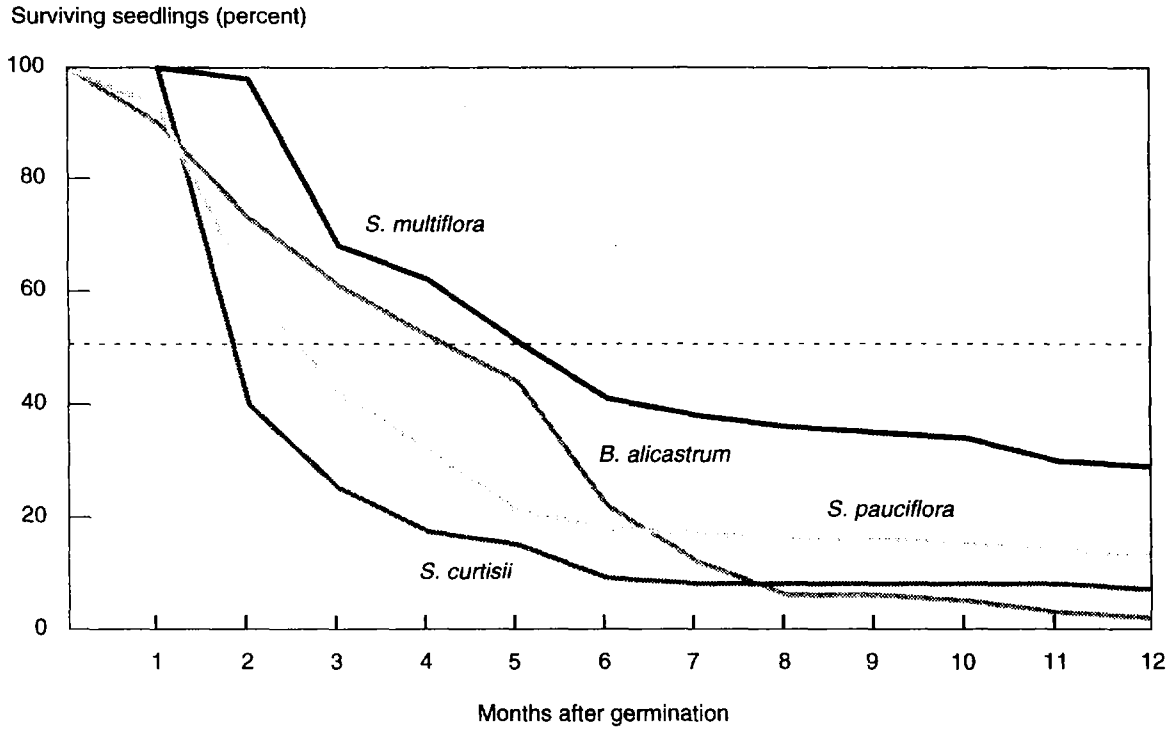
Seedling survivorship by *B. alicastrum* was particularly low, with most of the mortality in this species attributable to desiccation or damage by falling debris (Peters 1989). The sharp increase in mortality shown in figure 1.7 at five to seven months after germination reflects the severity of the dry season in Veracruz, Mexico where the study was conducted. Although the overall shape of the survivorship curves for *S. curtisii* and *B. alicastrum* are quite different, the net demographic effect is surprisingly similar. Of the over 247,000 seeds per hectare produced by *B. alicastrum*, only 3,500 seedlings (about 1 percent) remained alive at the end of one year.

The excessive mortality in the early stages of a tree's life cycle raises a critical management question. Where are the few surviving seedlings located? What type of microsite provides the necessary conditions for germination and, at the same time, allows a new seedling to express an optimal level of photosynthesis and growth relative to its competitors? The specific combination of environmental conditions that describe such a site may be thought of as the "regeneration niche" (Grubb 1977) of a species, and, to a large extent, the area and distribution of suitable niches are what ultimately regulate the number of seedlings that will be established in a tropical forest. Documenting the regeneration niche of a species is one of the most important prerequisites to successful forest management. Fortunately, ecologists and foresters have greatly simplified this task by discovering that the establishment microsites of a large percentage of tropical trees have one feature in common—they are all in some way linked to the sporadic occurrence of tree falls.

The Importance of Canopy Gaps

Tropical trees may blow down, get struck by lightening, topple in landslides, or simply die and slowly fall down. Each of these events produces an opening or gap in the forest canopy that allows direct sunlight to

Figure 1.7 Seedling Survivorship Curves for Three Species of *Shorea* Growing at the Pantai Acch Forest Reserve in Peninsula Malaysia and for *Brosisum alicastram* in Central Veracruz, Mexico



Note: Dotted horizontal line represents the "half-life" of each seedling cohort, i.e. the time interval within which 50% of the seedlings die.

Source: Turner 1990; Peters 1989.

enter the understory. The actual increase in irradiance levels on the forest floor depends on the size, shape, and orientation of the gap, but increases up to 10 percent full sun in a gap of 200 square meters and up to 20–35 percent full sun in a 400 square meter gap are probably good averages (Whitmore and Wong 1959; Schulz 1960; Chazdon and Fetcher 1984b). In addition to an increase in available sunlight, tree fall gaps usually exhibit lower humidity, higher temperatures, and higher soil moisture levels than those found under a closed canopy (Fetcher, Oberbauer, and Strain 1985; Vitousek and Denslow 1986; Uhl and others 1988).

These abrupt changes in the micrometeorological conditions of the forest understory have a notable effect on most of the seedlings in the vicinity, as well as on the seeds lying dormant in the soil (Richards and Williamson 1975; Brokaw 1985, 1987). In smaller gaps, many of the more tolerant seedlings that have managed to survive in the dense shade will display a significant increase in photosynthesis or growth in response to the higher light levels (Schulz 1960; Nicholson 1960; Sasaki and Mori 1981; Langenheim and other 1984; Chazdon 1986; Peters 1989). Numerous dipterocarp species and a wide variety of upper-canopy trees in Amazonia have been found to exhibit this behavior (Richards 1952; Rollet 1969; UNESCO 1978; Whitmore 1984). The seeds germinate in the shade and the young seedlings grow until they have produced about two or three leaves. The seedlings then appear to enter a state of suppression in which they exhibit little or no height growth. There are only two possible outcomes to this physiological condition. The seedlings slowly die over time, or they are "released" by the canopy opening up overhead.

In larger gaps, on the other hand, the drastic change in the quantity and quality of light and the rapid increase in soil temperature may trigger the germination of species with dormant seeds (Bazzaz 1979; Whitmore 1983; Young, Ewel, and Brown 1987; Fetcher and others 1987). The seedlings produced by these seeds characteristically exhibit rapid growth (Coombe 1960; Coombe and Hadfield 1962) and possess a photosynthetic system that is specifically adapted for higher light levels (with high compensation point and maximum photosynthetic rate). Large gap sites are quickly swamped with these aggressive species, and the slower-growing, more shade tolerant seedlings are soon outcompeted. Classic examples of such "light-demanding" species include *Cecropia*, *Trema*, and *Ochroma* (balsa wood) in the neotropics and any of the 280 species of *Macaranga* in Southeast Asia.

Canopy gaps clearly play a major role in the establishment and growth of tropical trees. Hartshorn (1978), in fact, has estimated that 75 percent of the 320 tree species at the La Selva Research Station in Costa Rica require the occurrence of a tree fall to regenerate. The problem, however, from a management perspective is that there is absolutely no way to predict exactly when and where a canopy gap will be created. Gap size is also a key variable in this respect. Different species are thought to use gaps of different sizes and configurations or even to selectively partition the different microsites within a single gap (Denslow 1980). Even if a predictable, periodic series of canopy gaps were created within a forest, given the competitive interactions between trees there is very little guarantee that the desired species will colonize them. This ecological caveat has made sustained-yield forestry in the tropics an extremely frustrating endeavor.

Regeneration Guilds

The preceding discussions in this chapter have illustrated the great diversity of different strategies used by tropical trees to pollinate their flowers, disperse their seeds, and to establish recruits of new individuals into their populations. It has long been noted, however, that tropical tree species can be grouped into distinct ecological categories based on similarities in the regeneration and growth strategies they employ. Light tolerance (shade-tolerant or light-demanding), for example, is one of the most frequent ecological characteristics used to group species. The reason for grouping species is not to obscure the variety of life histories found in a tropical forest, but to provide a tool that resource managers can use to understand more rapidly the ecological requirements and responses of the forest species under their control.

Although several different classification schemes have been proposed for tropical trees (Richards 1952; Budowski 1965; Whitmore 1984), for the purpose of this analysis it is useful to define three guilds of canopy species based on their regeneration requirements and overall life-history patterns: primary, "climax," or mature forest species; early pioneer or "secondary" species; and late secondary species (Hubbell and Foster 1986). Despite the names applied to these different groups, all three types of species can occur in mature tropical forest. A schematic listing of the basic ecological characteristics of each guild is presented in box 1.3.

Primary tree species germinate in the shade and can survive in the understory for a considerable time until a canopy gap opens overhead. Their seeds are usually large and few, with abundant seed reserves and little or no dormancy. As a group, these species are highly shade-tolerant and have a photosynthetic system adapted for growth in low light levels. Growth is relatively slow and wood density, as a result, can be extremely high. Primary trees may live for several hundred years and attain heights of over 60 meters. Many commercial species of tropical timber fall into this guild, together with most of the Dipterocarpaceae and several important fruit or oil-seed trees (*Bertholletia*, *Brosimum*, *Caryocar*, and *Manilkara*, for example).

Early pioneers frequently persist for long periods as dormant seeds in the soil. Their seeds, which are small and produced in abundance, require the stimulus (increased soil temperature or light intensity) of a large gap opening to germinate. After germination, these species exhibit high maximum rates of photosynthesis and growth, and their growth response to increased light levels is considerably more pronounced than that displayed by primary species. Given their rapid growth rates, wood density is light. Early pioneer species mature rapidly and reproduce early, often flowering at a height of only 4–8 meters; their life spans are correspondingly short (about 10–25 years). Common examples of this group belong to the Moraceae, Tiliaceae, Ulmaceae, and Urticaceae families.

Late secondary species are an intermediate guild between primary and early pioneer trees. These species are typically light-demanding, but their seeds neither exhibit the stringent dormancy of early pioneers nor require smaller gap sizes are required for germination. Seed dispersal into gaps is facilitated by wind, birds, bats, or ground mammals. Late secondary species exhibit the fast growth and maximal photosynthesis of many pioneer trees, but they grow to a much larger size and persist for longer periods of

Box 1.3 Basic Ecological Characteristics of Tropical Tree Species in Early Pioneer, Late Secondary, and Primary Forests

Characteristic	*Early Pioneer*	*Late Secondary*	*Primary*
Geographic distribution	Very wide	Very wide	Usually restricted; many endemics
Seed dormancy	Well developed	Slight to moderate	None
Seed viability	Orthodox	Orthodox	Recalcitrant
Seed or fruit size	Small	Small to intermediate	Large
Seed dispersal	Birds, bats, wind	Mainly wind, but also mammals	Mammals, birds
Shade tolerance	Very intolerant	Intolerant	Seedlings very tolerant, late intolerant
Gap size requirement	Large	Intermediate	Small
Seedling abundance	Very scarce	Usually scarce	Abundant
Growth rate	Very fast	Fast	Slow to very slow
Wood density	Light	Light to medium	Very hard
Life span	10–25 years	40–100 years, sometime more	100+ years

Source: Nomenclature for the different regeneration guilds from Hubbell and Foster 1986; categories and descriptions adapted from Budowski 1965; Hallé, Oldeman, and Tomlinson 1978; and Swaine and Whitmore 1988.

time in the canopy. Most of the "emergent" trees (species that grow taller than the general canopy) so characteristic of tropical forests are members of this guild. Wood density is variable, but usually lower than that of primary species. Many valuable timber species such as mahogany (*Swietenia*) and tropical cedar (*Cedrela*) are late secondary species.

It should be noted that not all tree species fall neatly into one of these groups. There are varying degrees of shade tolerance and a complete spectrum of responses to varying degrees of light, soil moisture, and competition from other tree species. Even within a single species, the genetic uniqueness of different individuals causes great variability in growth rate, wood density, fruit production, seed germination, and seedling establishment. To truly understand the specific ecological behavior of forest trees, resource managers are forced to rely on careful observation and detailed study. The more detailed the understanding of the component species, the higher the probability of attaining a truly sustainable form of forest resource extraction.

Population Structure

The ultimate criteria by which the regeneration and growth strategies of tropical trees must be measured is, of course, their effectiveness in recruiting new individuals into the population. One method of measuring this success is simply to monitor the frequency and abundance of seedling establishment over a period of several decades and to record the resultant increase, or decrease, in population size over time. This laborious and time-consuming procedure has been employed in several regions to study the long-term dynamics of tropical forests (see review in Swaine, Lieberman, and Putz 1987). Fortunately, however, the recruitment history of a particular tree species is frequently reflected by the size or age distribution of the individuals within its population. In many cases, a rapid appraisal of population structure alone can provide detailed information about the ecological behavior of a species. It can show, for example, whether a species is regenerating or not, and whether recruitment occurs continuously or periodically. It can also demonstrate the degree to which a tree species is dependent on canopy gaps for regeneration. As will be discussed in detail in chapter 3, the analysis of population structure is an extremely useful tool for orienting management activities and, perhaps most importantly, for assessing the impact of resource extraction.

Population structure data have long been used by foresters and ecologists to investigate the regeneration characteristics of tropical trees (Aubreville 1938; Barnard 1956; Fox 1967; Knight 1975; DeCarvalho 1981). Given the lack of well-defined growth rings and the difficulty of accurately determining tree age in the tropics (Bormann and Berlyn 1981), almost all of these studies have defined population structure in terms of the size-class or diameter distribution of individuals. The basic procedure is quite simple. After conducting a forest inventory, frequency histograms showing the number or percentage of individuals in different size classes are constructed for each species. The overall shape or slope of these frequency histograms are then compared visually; some studies have used statistical techniques to derive a descriptive equation for each distribution (UNESCO 1978). Interestingly, most analyses of this type have found that tropical tree populations are characterized by a limited number of different size-class distributions. Knight (1975), for example, reported that the diameter distributions of over 150 tree species at Barro Colorado Island, Panama could be described by only five basic models. Bongers and others (1988) identified three distinct types of population structure in a lowland tropical forest in Mexico, and Rollet's (1978) study in Venezuela lists seven basic types. Differences in the size-class intervals, sample sizes, and minimum diameter limits used in these studies are at least partially responsible for the varying results.

Three of the most common size-class distributions exhibited by tropical tree populations are shown in figure 1.8 together with a representative example of each type. The type I size-class distribution, illustrated by *Shorea atrinervosa*, displays a greater number of small trees than large trees, and an almost constant reduction in numbers from one size class to the next. This type of population structure is characteristic of shade-tolerant canopy trees that maintain a more or less constant rate of recruitment. There is a large probability that the death of an adult tree will be replaced by the growth of individuals from the smaller size classes. A type I structure is considered by many authors the ideal of a stable, self-maintaining plant population (Meyer 1952; Leak 1965).

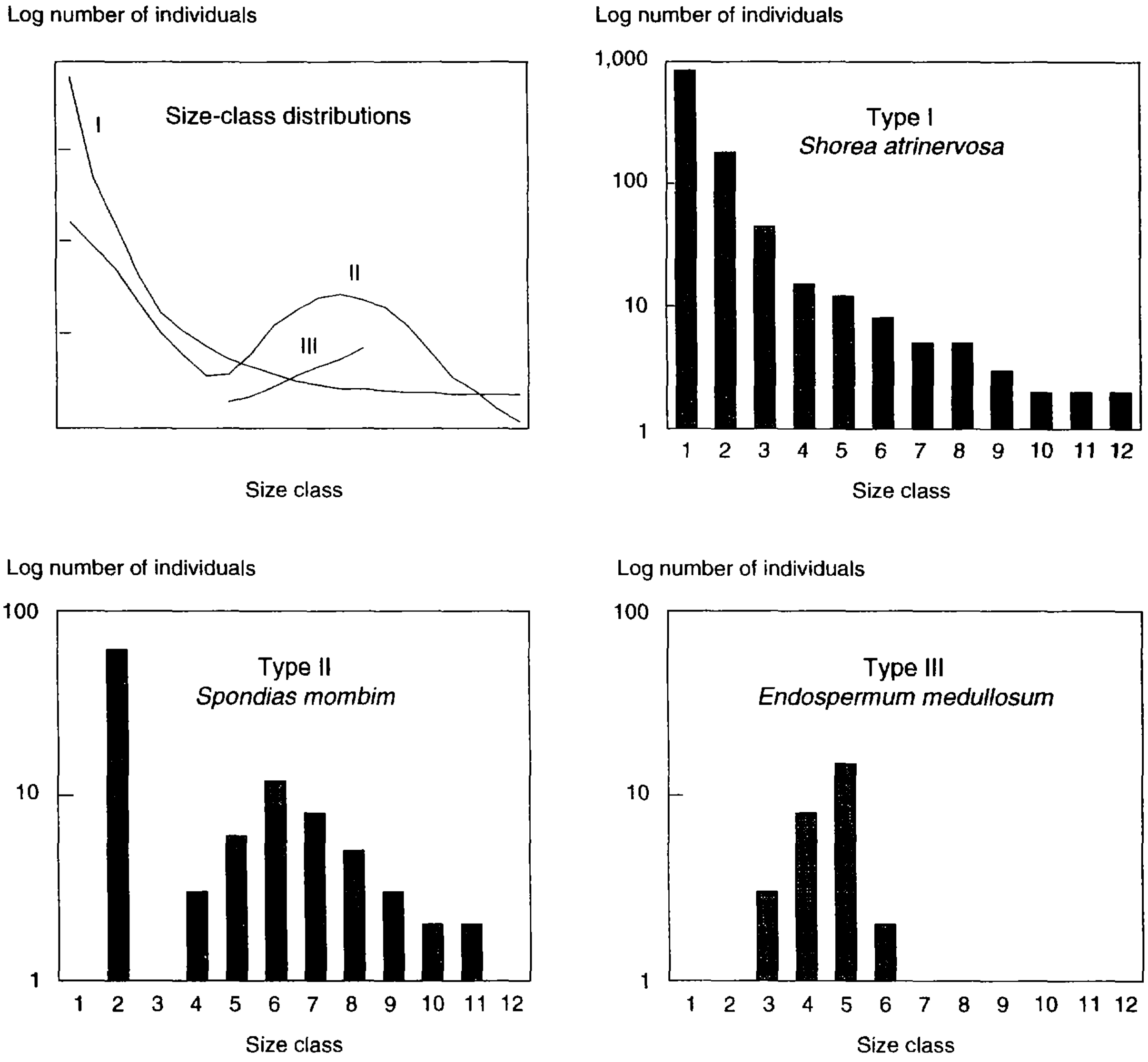
The "inverse J" shape of a type I diameter distribution can be described mathematically using either a negative exponential or a power function model (Mueller-Dombois and Ellenberg 1974). The negative exponential model is preferred when the decrease in numbers from one size-class to the next is uniform, implying that the risk of mortality[12] is constant among all adult trees in the population. Graphing the number of individuals per size-class on a $\log_{10}$ scale should yield a straight line if the diameter distribution conforms to a negative exponential. The $\log_{10}$ population data shown in figure 1.8 for *S. atrinervosa*, however, is far from linear. This population would be better described using a power function model as there is some evidence that the risk of mortality decreases proportionally with increasing diameter. It should be noted that although *S. atrinervosa* is a type of illipe nut tree from the family Dipterocarpaceae, the species appears to bear fruit every year in West Kalimantan where the population shown in figure 1.8 was studied. Annual fruit production undoubtedly helps to enhance recruitment in a primarily mast-fruiting forest.

A type II size-class distribution, as illustrated by *Spondias mombin*, is characteristic of species that show discontinuous or periodic recruitment. The actual level of seedling establishment may be sufficient to maintain the population, but its infrequency causes notable discontinuities in the structure of the population as the newly established seedlings and saplings grow into the larger size classes. This type of diameter distribution is quite common among late secondary species that depend on canopy gaps for regeneration. The large number of individuals recorded in the second size class of the *S. mombin* histogram suggests that gap colonization by this species was particularly successful approximately 15–20 years ago.

The final size class-distribution, type III, reflects a species whose regeneration is severely limited for some reason. Most of the individuals in the population are more or less the same size or age, and although many of them may be reproductively active, no seedlings have been successfully recruited. Type III distributions are frequently encountered among light-demanding, early pioneer species that require large canopy gaps for regeneration. In the absence of such a disturbance, these species may temporarily disappear from the forest, the former population represented only by the seeds lying dormant in the soil. A type III size-class distribution, however, is not restricted to early pioneers. *Endospermum medullosum*, for example, is a late secondary tree dependent on moderate to large size canopy gaps. The lack of regeneration exhibited by this species may have resulted from limited dispersal into gaps, a temporary reduction in the occurrence of appropriately sized gaps, excessive competition for these niches, or a host of other factors. Whatever the reason, the *E. medullosum* population depicted in figure 1.8 is in a very precarious ecological situation.

In general, the three types of size-class distributions exhibited by tropical trees correlate well with the different regeneration guilds discussed in the preceding section. This correlation, however, should not detract from the fact that the population structure of a particular tree species is extremely dynamic and extremely sensitive to environmental conditions. A type I size-class distribution can easily change into a type II if existing recruitment levels are diminished or

Figure 1.8 Three Idealized Size-Class Distributions Exhibited by Tropical Tree Populations and a Specific Example of Each Type



Note: Note log-scale on y-axis; minimum diameter limits and size-class intervals are 10 ca DBH in all histograms.
Source: Population data for *S. atrinervosa* (Peters 1991), *S. mombim* (Knight 1975), and *E. medullosum* (Whitmore 1984).

interrupted. Further constraints on regeneration may drive the population to a type III distribution. It is, perhaps, most useful to view these three structural types as a single sequence through which a population passes on its way to extinction. The occurrence of a type III size-class distribution in a population of shade-tolerant canopy trees is an obvious signal that something is wrong. The analysis of size-class distributions is a simple, yet reliable, method to monitor the health or vigor of a forest tree population. As will be demonstrated in chapter 3, periodic monitoring of this important parameter can be used to guarantee the long-term sustainability of non-timber forest product extraction.

Chapter Summary

1. Policymakers and resource managers in the tropics have tended to ignore the ecological necessities of the species under their control or have simply assumed that tropical trees behave essentially like temperate trees. Either course of action is ill advised, and the failure of most attempts to manage tropical forests have repeatedly illustrated this fact.

2. Tropical trees display a variety of ecological characteristics that can limit the nature and intensity of resource extraction. The major problem areas are: the diversity and density of tree species, the complexity of flowering and fruiting, the specificity of microsites for successful regeneration and growth, and the labile response of population structure to the level of recruitment.

3. Tropical forests are characterized by large numbers of tree species per unit area. As a result of this extreme species-richness, tropical forests contain a large number of non-timber resources such as edible fruits, nuts, oilseeds, medicines, thatch, latexes, gums and resins. Most of these economic species, however, occur at densities of only one or trees per hectare.

4. Although tropical trees vary greatly in terms of the timing duration and intensity of flowering and fruiting, the phenologies of most species exhibit a marked seasonality. Gregarious, supra-annual flowering and fruiting is exhibited by the dipterocarps of Southeast Asia at irregular intervals of from two to ten years. Species sharing the same pollinator frequently stagger their flowering times.

5. The great majority of tropical trees rely on animals (insects, birds, bats, and so on) to pollinate their flowers. In spite of the large distance between conspecific trees, most species are obligate outcrossers. Temporal or spatial separation of staminate and pistillate flowers within a tree, dioecy, or genetic incompatibility mechanisms are the main strategies employed to avoid self-pollination. Seed dispersal is primarily by biotic vectors (birds, bats, primates and rodents) and there is much wastage.

6. A large proportion of seeds die before germination due to predation. Many tree species have evolved chemical defenses or rapid germination to escape excessive seed predation. A lesser number of species produce seeds with well-developed dormancy. Mortality is still extremely high following germination, and over 90 percent of the new seedlings may die before becoming established. Each tree species possesses a specific regeneration niche within which seedling establishment and growth is enhanced.

7. The regeneration niches of many species are linked to the occurrence of tree fall gaps. Based on the gap requirement and shade tolerance of different species, three regeneration guilds can be recognized: early pioneer species, late secondary species, and primary species. The establishment, growth, reproduction, longevity, and management potential of the species within these guilds are markedly different.

8. The population structure or size-class distribution of tropical trees can be described by three basic types. These types correlate well with the regeneration guild of a species, although a single species may exhibit any of these types depending on the environment and level of recruitment. Periodic monitoring of size-class distributions is an easy, yet reliable, method to assess the ecological health of a tree population.

9. The sustainability of tropical forest management can be disrupted by ecological processes occurring at any of the life cycle stages of a tree species. The greater the understanding of the ecology of the species being managed, the greater the potential for achieving a truly sustainable system of non-timber forest resource extraction.

Notes

1. It has long been contended within the scientific (see, for example, Ashton 1977; Whitmore 1984) and popular (Caufield 1985) literature that the low-

land forests of Southeast Asia are richer in tree species than those of Amazonia. The recent data reported by Gentry (1982) from the fertile forests of Upper Amazonia, however, seem to have resolved this debate.

2. A more complete discussion of the innumerable plant resources found within tropical forests can be found in Mors and Rizzini, (1966), Cavalcante (1972 1974 and 1979), Balick (1985) and Prance (1989) for the Amazonian region, or Burkhill (1935), Meijer (1957), Lemmens and others (1989) and de Beer and McDermott (1989) for Southeast Asia.

3. In Southeast Asia, supra-annual, gregarious flower and fruit production is also exhibited by numerous other canopy trees from such families as the Burseraceae, Fabaceae, Myristicaceae, and Sapotaceae (Appanah 1985).

4. Illipe nut is the commercial name for the winged seeds produced by about twenty species of *Shorea* (Dipterocarpaceae) trees (Anderson 1975). The seeds contain an oil that is remarkably similar in chemical and physical properties to cocoa butter oil. The oil content of the seeds may be as high as 50 percent. Large quantities of illipe nuts are collected and sold internationally to be used in the manufacture of chocolate, soap, candles and cosmetics. In 1987, a recent mast year, over 13,000 tons of illipe nuts valued at almost US$5 million were exported from West Kalimantan, Indonesia alone (Biro Pusat Statistik Indonesia 1988).

5. See Procter and Yeo (1972) and Faegri and van der Pijl (1971) for a complete review of pollination biology in both temperate and tropical plants.

6. In a recent study from Costa Rica (Bawa, Perry, and Beach 1985a), 65.5 percent of the 333 tree species examined were hermaphroditic. Similar results have been reported from Malaysia (Ashton 1969), Venezuela (Zapata and Arroyo 1978), and Panama (Croat 1979).

7. A useful summary of the floral strategies used by plants to avoid inbreeding is provided in Briggs and Walters (1976).

8. It is assumed for the purpose of this discussion that the short-term objectives of the resource manager—producing the maximum quantity of edible fruits, nuts, and oil seeds, or procuring sufficient regeneration of a useful species—may, in some cases, be at odds with certain evolutionary imperatives. Initially, the resource manager may be more concerned with fruit quantity than with gene flow, outcrossing rates, or the genetic quality of these fruits. These issues, however, will take on a greater importance as managers ultimately strive to increase the frequency of certain valuable genotypes within the forest.

9. A more extensive treatment of dispersal syndromes with numerous examples from both the neotropics and Southeast Asia can be found in the texts of Ridley (1930) and van der Pijl (1972).

10. Life history strategies are physiological, morphological, or behavioral adaptations that have been evolved to increase survival and reproductive fitness during any of the various stages of a tree's life history. A theoretical review of this important concept is provided by Stearns (1976 1977).

11. The seedling fixes carbon dioxide through photosynthesis, and it loses carbon dioxide through respiration. Over time, the net flux of carbon must be positive for the seedling to produce new tissues and grow. Studies of gas exchange have demonstrated that the seedlings of many tropical species have low respiration rates, low compensation points (the light level at which photosynthesis equals respiration), and a high photosynthetic response to slight increases in irradiance (Bjorkman and Holmgren 1963; Koyama 1978; Langenheim and others 1984; Chazdon and Pearcy 1986). All species, however, require a minimum amount of light to photosynthesize. At extremely low irradiance levels, photosynthesis may decrease to the point where it is equal to or only slighter greater than respiration. This is a life-threatening situation for a seedling. For a more comprehensive review of the ecophysiology of tropical plants, see Bazzaz and Pickett (1980) and Medina, Mooney, and Vazquez-Yanes (1984).

12. The assumption that the decrease in numbers from one size-class to the next in a type I diameter distribution represents mortality is not necessarily true. A rapidly growing population experiencing little mortality between progressively larger size-classes could still exhibit a type I distribution. Diameter distributions encode the structure of a population at only one moment of time. Without actual long-term measurements of size-specific mortality or a documented relationship between age and tree size, it can be very misleading to infer mortality rates from a static description of population structure (Peters 1989; see also chapter 3).

II
Ecological Impacts of Forest Resource Extraction

"It's not just a question of some fruit that you take from the forest. The fruit has a history. The people eat it, the animals and birds eat it. You need a respect for the fruit..."

—Paolo Cipasse
Xavante Indian leader
Mato Grosso, Brazil

As the complex interrelationships and ecological processes discussed in chapter 1 indicate, almost any type of resource extraction from tropical forests will have an ecological impact. Unfortunately, the exact nature of this impact can be extremely difficult to predict. The delicate ecological balance maintained in a tropical forest is easily disrupted by human intervention, and land use practices that at first glance seem very benign can later have a severe impact on the structure and dynamics of forest tree populations. In general, the ecological impact of forest utilization depends on the florisitic composition of the forest, the nature and intensity of harvesting, and the particular species or type of resource under exploitation. Sporadic collection of a few forest fruits, for example, may have little impact on the long-term stability of the tree populations being exploited. Intensive, annual harvesting of a valuable market fruit or oilseed, however, can gradually eliminate the species from the forest. The felling of large adult trees can produce a similar ecological result in a much shorter time period.

The purpose of this chapter is to summarize what is currently known about the ecological impacts of non-timber resource extraction, assess the potential impacts of existing patterns of resource use, and, whenever appropriate, point out ways in which the ecological impacts might be reduced through management activities. Given that the initial impact of resource extraction is largely determined by the specific type of plant tissue harvested, the following analysis employs an ecological, rather than a commodity, approach. From a market or use perspective, fruits, nuts, arils and oilseeds are completely different products. The act of harvesting these products, however, produces a similar ecological effect: extraction removes plant embryos from the site, and hence reduces the total number of seedlings that potentially can be recruited into the tree population under exploitation.

The chapter opens with a brief discussion of the ecological impacts of logging for several reasons, the most important being that the ecological impacts of timber extraction have been relatively well documented in both Amazonia and Southeast Asia. The immediate effects of tree felling are also relatively easy to observe, and they provide a useful illustration of how a single human intervention can precipitate a series of ecological changes within a tropical forest (Terborgh 1988). Finally, the collection of non-timber forest products in many tropical regions unfortunately involves destructive harvesting (the trees are cut to collect the fruit, latex, or other useful product), and in these situations, the ecological impacts of non-timber forest product extraction are no different from those produced by commercial logging.

Timber Extraction

Selective logging is usually regarded as the most common form of forest exploitation in the humid tropics (UNESCO 1978).[1] It is certainly the most damaging way to exploit a tropical forest, and numerous studies conducted in Papua New Guinea (Enright 1978), Indonesia (Tinal and Palenewen 1978; Hamzah 1978; Abdulhadi, Kartawinata, and Sukardjo 1981), Malaysia (Burgess 1971, 1973; Liew and Wong 1973; Johns 1988), Surinam (Jonkers 1987), and Brazilian Amazonia (Uhl and Guimaraea Vieira 1989) amply document the nature and extent of this damage. Most of these studies have shown that the ecological impacts of timber extraction are quite extensive, with forest structure, floristic composition, soil properties, site fertility, water relations, and wildlife all being adversely effected.

Impact on Vegetation

In species-rich tropical forests, only a small proportion of the total number of trees produce high-quality, merchantable timber. Rankin (1985), for example, reports that as few as six tree species (for example, *Ocotea*, *Cedrela*, *Hura*, *Calophyllum*, *Swietenia*, and *Carapa*) account for over 80 percent of all the sawlogs harvested in Brazilian Amazonia. Most of these timber species occur at relatively low densities in the forest, and harvest rates of only 5–15 trees per hectare are very common. Given the small volumes of timber extracted, it is easy to assume that selective logging has a negligible impact on forest structure. The problem, however, is that commercial timber trees are normally large canopy individuals that have crowns of 15–20 square meters. The crowns of at least some of these individuals are invariably lashed to neighboring canopy trees by a profusion of lianas, vines or climbers (Putz 1985). When the timber trees are felled, they pull down other canopy trees with them, crash through the lower canopy snapping tree boles and breaking branches, and flatten a considerable proportion of the forest understory.

As is shown in table 2.1, the ecological impacts of selective logging are far from selective. Harvesting a small number of timber trees can destroy up to 55 percent of the residual stand, and seriously damage an additional 3.0–6.0 percent of the standing trees. The level of damage appears to decrease at lower harvest intensities, but even felling as few as four timber trees per hectare can still kill about 25 percent of the trees in the immediate vicinity. In addition to the damage caused by falling trees, the bulldozers and skidders used in mechanized logging can uproot or topple trees during the construction of roads and log-loading areas and severely scar the trunks of standing trees as the logs are dragged out of the forest. Johns (1988) estimates that approximately 15 percent of the trees inventoried within a logging concession at Pahang, West Malaysia were destroyed by heavy machinery.

Eliminating up to 50 percent of the trees in a stand has an immediate effect on forest structure and the micrometeorological conditions within the forest understory. By reducing the total percentage of canopy cover by as much as a half (Uhl and Guimaraes Vieira 1989), logging causes a drastic increase in

Table 2.1 Summary of Selected Studies on Logging Damage to Forests

Logging Activity	*Gunung Tebu, Malaysia*	*Pahang, West Malaysia*	*Paragominas, Brazil*
Logging Density			
Basal area logged (m^2/ha)	—	24	3–5
Trees/ha logged	—	18	4–8
Percentage total stems logged	10.0	3.3	1.7
Logging Damage during Harvest			
Killed (%)	55.0	47.6	23.0
Damaged (%)	—	6.0	3.0
Undamaged Residuals (%)	35.0	43.1	74.0

— Data not available.

Note: These studies were conducted in Southeast Asia and Amazonia on trees 10 centimeters DBH. Sources of tree mortality included uprooting during road-building activities, crown damage by falling trees, and bark damage from skidding and hauling.

Source: Data for Gunung Tebu, from Burgess 1971; for Pahang, from Johns 1988; and for Paragominas, from Uhl and Guimaraes-Vieira 1989.

light levels and soil temperatures and a reduction in relative humidity. These conditions favor the germination of the dormant seeds of early pioneer trees and lianas, and many of the suppressed seedlings and saplings of late secondary species that have escaped damage may also respond to the improved light environment (Uhl 1982; Saulei 1984; Raich 1987; Uhl and others 1988a). The established seedlings of residual primary forest species are rapidly outcompeted in the race to revegetate the site. In many respects, this process mimics the successional development that occurs in a large tree fall gap. The importance difference, however, is the relative scale of the disturbance. Natural tree fall gaps normally occupy about 5–15 percent of the area within primary forest (Poore 1968; Hartshorn 1980; Sanford, Braker, and Hartshorn 1986), not the 50 percent or more characteristic of selectively logged forests. If the logged area is quite extensive and large volumes are removed, it is highly probable that the successional development of the site will be permanently deflected. In place of the tall, multi-storied forest that was originally logged, a low, impenetrable tangle of vines and scrub will develop (Uhl and Guimaraes Vieira 1989).

Logged-over forests remain highly susceptible to disturbance even after all tree felling has ceased. Because of the patchy, fragmented condition of the forest, the crowns of residual trees are completely exposed and vulnerable to being toppled over by gusts of wind. There is also a large amount of slash (broken branches, boles, and other woody debris) left in the forest after logging. The high temperatures and low humidity in the understory allow the slash to rapidly dry out and become a fire hazard. Uhl and Buschbacher (1985) estimate that a period of only five or six rainless days is sufficient to dry this material below a threshold of combustion. Any ignition source from adjacent areas (such as burning for agriculture or ranching) can cause a fire in selectively logged forests. Several recent reports indicate that these types of forest fires are becoming increasingly common in regions subjected to periodic logging (Malingreau, Stephens, and Fellows 1985; Adriawan and Montiaga 1986; Uhl and others 1988b; Uhl and Kauffman 1990). In Brazilian Amazonia alone, as many as 8 million hectares of forest burned in 1987 (Booth 1989). Of even greater extent, in 1982 tens of thousands of square kilometers of selectively logged forest caught fire in East Kalimantan, Indonesia (Leighton and Wirawan 1986). Recurrent disturbances such as windfalls and fires severely inhibit the normal successional process of forest recovery following logging and, in some cases, can lead to irreversible site degradation.

Finally, uncontrolled selective logging can also reduce the local abundance of certain valuable timber species. Given the small number of commercial timber species and the low population density at which they normally occur (see chapter 1), rates of extraction that seem very low can eliminate many, if not all, of the reproductive adults of a particular species. There is a very small probability that these adult trees will be replaced by individuals of the same species. For example, if only 5–10 percent of the tree species within a forest are logged (table 2.1), the probability that these same species will be able to replace themselves in the forest should, on average, also be about 5–10 percent. Without some effort to ensure the natural regeneration of these species, continued extraction will cause them to become extremely rare in the forest. Unfortunately, a common response to this situation is simply to intensify the search for the last remaining merchantable trees. Gentry and Vasquez (1988) attribute the disappearance of *Ceiba* trees from the forests around Iquitos, Peru to a similar process of overexploitation.

Impact on Soils and Site Fertility

The building of roads and skid trails for extracting timber causes soil compaction, decreases water infiltration capacity, and increases the rate of soil loss due to erosion. Depending on the intensity of logging, the extent of this soil damage can be quite extreme. Nicholson (1979) reports that 15–50 percent of the soil surface within a tropical forest may be damaged by mechanized logging. At Gunung Tebu in Peninsula Malaysia, Burgess (1973) found that up to 27 kilometers of logging roads were constructed for every 100 hectares of dipterocarp forest that were logged. Slightly lower results were obtained in Paragominas, Brazil where 9 kilometers of roads and skid trails, about 8.0 percent of the total area, were built to service a 52 hectare tract of upland forest (Uhl and Guimaraes Vierira 1989).

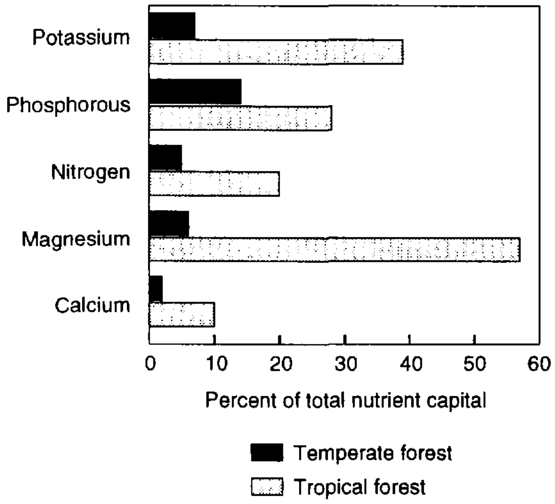
Much of the bare soil within logging areas has been seriously compacted by the heavy, repeated traffic of bulldozers, skidders, and sawlogs. In addition to providing a difficult substrate for seedling establishment, compacted soils can reduce the normal rate of water infiltration by as much as 80–90 percent (Abdulhadi, Kartawinata, and Sukardjo 1981; Hamzah 1978). Water that cannot be absorbed into the soil must move overland, and often the result is erosion. Almost every study of erosion in relation to timber extraction has found that soil loss increases dramatically both during and after logging (see review in Ewel and Conde 1976; Marn and Jonkers 1981). Liew (1974) found that selective logging along a 350 meter slope in Sabah resulted in a loss of 450–500 cubic meters of soil per hectare. Hamzah (1978) reports that there was thirty-three times more silt load in local streams as a result of commercial logging operations in East Kalimantan. These high initial rates of soil loss, however, usually decline somewhat as the denuded soil within the logging area starts to revegetate.

Erosion represents an irreplaceable loss of nutrient capital from a forest ecosystem. It should be noted, however, that a significant quantity of nutrients is also removed in the sawlogs that are hauled out of the site. This nutrient loss is considerably greater in a tropical forest than in a temperate forest.[2] To illustrate, the percentage of total nitrogen, potassium, phosphorous, magnesium and calcium removed by intensive timber harvesting is shown in figure 2.1 for both a temperate and a tropical forest ecosystem. The results for potassium, phosphorous and magnesium are the most notable. Logging a tropical forest can remove up to 28 percent of the potassium, 39 percent of the phosphorous, and 57 percent of the magnesium from the site. A harvest of similar intensity conducted in a temperate forest would result in net losses of only 14 percent, 7 percent and 6 percent for these same respective elements. Based on these findings, nutrient considerations alone would seem to argue quite strongly against the long-term sustainability of timber extraction in tropical forests.

Impact on Animal Populations

Most of the discussion in chapter 1 about forest animals was focused on the various ecological services (pollination and dispersal) they provide for tropical trees. The relationship, however, is obviously reciprocal: tropical trees provide forest animals with shelter, a variety of climbing, perching and roosting sites, and, most importantly, a continual source of food. Selective logging seriously limits the capacity of the forest to fulfill these basic needs for resident animal populations.

Figure 2.1 Percentage of Total Ecosystem Nitrogen, Potassium, Phosphorous, Magnesium, and Calcium Removed by Intensive Logging of a Temperate and Tropical Forest



Source: Histograms constructed from data presented in Buel and Conde 1976.

The impact of logging on animal populations is not so much that a few fruit trees are extracted for timber. The real problem is a bit more complex. Fruit production in a tropical forest is markedly seasonal (see discussion in chapter 1), and periods of high fruit abundance are generally separated by long intervals of relative scarcity. What do frugivorous animals eat during these intervals? Recent studies conducted in Amazonia (Terborgh 1983) and Southeast Asia (Leighton and Leighton 1983) have shown that a very small number of "keystone" plant species provide the food resources necessary to sustain different animal populations during periods of fruit scarcity. At Cocha Cashu in Peru, for example, a mere 12 species (the total estimated flora is in excess of 2,000 species) sustain the entire frugivore community for almost three months each year (Terborgh 1986). Figs (*Ficus* spp.), Annonaceaous climbers, and several species of Myristicaceae and Meliaceae have been found to play a similar role in the dipterocarp forests of Southeast Asia. These keystone plant species are what ultimately determine the carrying capacity of a tropical forest environment for animals. If a sufficient quantity of such fruit resources are destroyed or damaged through tree felling, obligate frugivores have no choice but to migrate to more productive habitats, or starve.

Several studies have examined the effect of logging on animal populations, especially in Southeast Asia: for example, Wilson and Wilson (1975) and Wilson and Johns (1982) in East Kalimantan; Rijksen (1978) and Aveling and Aveling (1979) in north Sumatra; and Yong (1978) and Johns (1986) in Malaysia. The results from these studies have shown that some animal populations are extremely susceptible to logging disturbance, others appear to be more resistant. Large mammals such as orangutans (*Pongo pygmaeus*), sun bears (*Helarctos malayanus*), gibbons (*Hylobates* spp.) and proboscis monkeys (*Nasalis larvatus*) are conspicuously absent in logged-over forest, and all of these species have become severely endangered as a result of habitat destruction. Smaller langurs or leaf monkeys (*Presbytis* spp.) apparently migrate off-site during logging, but return shortly thereafter if the intensity of the timber extraction is not too severe. Large avian frugivores such as hornbills, trogons, and toucans are particularly sensitive to the effects of logging (Leighton and Leighton 1983; Wheelwright 1983), while smaller, "generalist" frugivores (for example, bats and many species of birds) appear to be able to adapt their foraging patterns. The long-tailed macaque (*Macaca fascicularis*), an omnivorous and highly adaptable primate, seems to thrive in disturbed habitats.

As long as there are sufficient islands of primary forest within which animals can take refuge and forage, many of the species that survive the critical period immediately following timber extraction will probably be able to persist in logged-over forests (Johns 1985). The rapid expansion of the timber industry in the tropics, however, has caused a drastic reduction in the areal extent and distribution of intact forest. This fact is particularly worrisome since tropical frugivores are especially prone to extinction when confined to small, isolated tracts (Terborgh and Winter 1980). If continued at its current intensity, there is no question that the commercial exploitation of tropical timber will push many forest animals to the edge of extinction. The total impact of these extinctions on the distribution, abundance, and productivity of the plant resources found within the remaining areas of intact forest will probably never be fully understood or appreciated.

The ecological impacts of logging extend to almost every component of a tropical forest ecosystem, and these impacts can precipitate a series of irreversible changes in the structure and function of the ecosystem. There are, however, ways to minimize the damage caused by logging. By mapping logging sites prior to extraction so that the terrain characteristics and location of merchantable trees are known, roads and skid trails can be positioned to minimize erosion and directional felling can be employed to reduce damage to the residual stand (Jonkers and Schmidt 1984; Jonkers 1987; Schmidt 1987). Cutting woody vines prior to logging can also help to reduce the damage caused by falling trees (Fox 1968). Experimental work in Sarawak has shown that preharvest planning, careful positioning of skid trails, and directional felling can reduce logging damage to about half of that found in adjacent areas logged by conventional methods (Marn and Jonkers 1981).

The problem of keystone wildlife species can also be ameliorated through conscientious management. Once these species have been identified for a particular habitat, they can be flagged and special care taken to avoid damaging them during harvesting operations. It might also be possible to actually enhance the wildlife carrying capacity of the forest by selectively favoring the regeneration and growth of particularly important food plants. Because keystone species, by definition, are only a small percentage of the total species diversity of the forest, retaining or favoring them through management should have little effect on timber yields. There is clearly no lack of technological solutions to reducing the impact of logging in tropical forests. There is, however, a lack of interest in or motivation for applying these solutions. As was pointed out for the neotropics, "for every hectare of forest in tropical America under intensive management, there are 35,000 hectares not so managed" (Wadsworth 1987). The current situation in Southeast Asia is not much different.

Non-timber Forest Product Extraction

One of the most basic and rarely questioned assumptions underlying much of the current interest in non-timber forest products is that the commercial extraction of non-timber forest products has little or no ecological impact on a tropical forest.[3] This assumption, which is both incorrect and potentially harmful to the forests, seems to have originated from two simple observations: local people have been harvesting fruits, nuts and latex from tropical forests for thousands of years; and a tropical forest exploited for non-timber products, unlike a logged-over forest, maintains the appearance of being undisturbed. Two qualifiers, however, should be annexed to these observations. In the first place, the intensity of subsistence harvesting as traditionally practiced by forest peoples is usually quite a bit lower than that of commercial extraction. Second, the gradual extinction of a plant species over time is rarely a visible phenomenon. Collecting fruit and tapping latex are clearly less damaging than felling trees or building roads, but this certainly does not imply that the former activities are entirely benign ecologically. Every non-timber forest resource has a site-specific, maximum sustainable level of harvest. If this harvest level is exceeded, the plant populations being exploited, as well as the community of animals that depend on them, will all be adversely effected.

In this analysis, the enormous variety of non-timber resources produced by tropical forests have been grouped into three categories based on the type of plant tissue or compound exploited: reproductive propagules, plant exudates, and vegetative structures. This classification scheme is illustrated in box 2.1, which presents specific examples for each resource group and type of plant product from both Amazonia and Southeast Asia. All taxa listed are primarily forest species, but in some regions certain plants may also be cultivated. Although all three categories contain several well-known commodities of value, reproductive propagules appear to be an especially prevalent and important group of forest products. It should be noted that the listing in box 2.1 is far from exhaustive. For the Southeast Asia region alone, Burkhill (1935) lists over 2,400 species of native plant resources grouped into 102 use categories. About half of these plants (approximately 1,283 species), or one-sixth of the total estimated flora of over 8,000 species, are non-timber resources found only in lowland primary forest (Jacobs 1982).

Reproductive Propagules

To determine the ecological consequences of collecting fruits, nuts and oilseeds from a tropical forest, it is important to first identify the negative effects of destructive harvesting. As noted earlier, an increasingly common practice in many tropical regions is to simply cut down a forest tree to harvest its fruit. This damaging, short-sighted and wasteful practice is under no circumstances sustainable, and it can have a drastic impact on the distribution and abundance of fruit resources within a forest.

In Peruvian Amazonia, for example, female trees of the dioecious aquaje palm (*Mauritia flexuosa*) are frequently felled by commercial fruit collectors. After very few of these harvest cuts, the forest is left with a preponderance of barren male trees, and eventually, the species disappears completely from the forest (Kahn 1988; Vazquez and Gentry 1989). Uncontrolled felling has virtually eliminated the aquaje palm from the forests surrounding Iquitos, Peru, and local collectors are now forced to travel up to three days to find unharvested palm stands (Padoch 1988). Destructive harvesting has also seriously reduced the abundance of the ungurahui palm (*Jessenia bataua*), the babassu palm (*Orbygnia phalerata*), and a wide variety of other important Amazonian fruit trees such as *Parahancornia peruviana*, *Couma macrocarpa*, and *Genipa americana* (Peters and others 1989). Clearly, no program of commercial fruit extraction will ever be sustainable so long as harvesting involves an axe.

Even in the absence of destructive harvesting, the collection of commercial quantities of fruits and seeds can still have a significant ecological impact. The many difficulties experienced by tropical trees to germinate and establish seedlings were described in detail in chapter 1. Periodic fruit harvests can make the process of seedling recruitment even more problematic. In terms of simple demographics, if a tree population produces 1,000 seeds and 95 percent of the new seedlings

Box 2.1 Selected Examples of Tropical Non-Timber Forest Products, by Plant Part and Resource Category

Resource Category	*Plant Part*	*South America*	*Southeast Asia*
Reproductive Propagules	Fruit	Aguaje (*Mauritia flexuosa*) Camito (*Pouteria* spp.) Camu-camu (*Myrciaria dubia*) Charichuelo (*Rheedia* spp.) Huasam (*Euterpe precatoria*) Shimbillo (*Inga* spp.) Uvos (*Spondias mombin*) Zapote (*Quararibea* spp.)	Asam (*Garcinia, Mangifera*) Bangkong (*Artocarpus* spp.) Durian (*Durio* spp.) Jambu (*Eugenia, Syzygium*) Kedongdong (*Spondias* spp.) Keranji (*Dialium* spp.) Rambutan (*Nephelium* spp.) Tampui (*Baccaurea* spp.)
	Nut/Seed	Almendro (*Caryocar* spp.) Castaqa (*Bertholletia excelsa*) Tagua (*Phytelephas macrocarpa*)	Petai (*Parkia speciosa*) Melinjau (*Gnetum gnemom*)
	Oilseed	Ungurahui (*Jessenia bataua*) Babassu (*Orbignya phalerata*)	Tengkawang (*Shorea* spp.) Kemiri (*Aleurites* spp.)
Plant Exudates	Latex	Shiringa (*Hevea* spp.) Balata (*Manilkara bidentata*) Leche caspi (*Couma macrocarpa*)	Gutta percha (*Palaquium*) Jelutong (*Dyera costulata*)
	Resin[a]	Copal (*Protium, Dacryodes*)	Damar (*Dipterocarpus*) Gum damar (*Shorea*) Gharu (*Aquilaria* spp.)
	Floral nectar		Aren (*Arenga pinnata*) Nipa (*Nypa fruticans*)
Vegetative Structures	Stem fiber	Pona (*Socratea, Iriartea*)	Rattan (*Calamus*) Bambu (*Bambusa*)
	Leaf fiber	Chambira (*Astrocaryum* spp.) Various *Palmae*	Pandan (*Pandanus* spp.) Various *Palmae*
	Root	Barbasco (*Lonchocarpus* sp.)	Tuba (*Derris* spp.)
	Bark	Chuchuhuasa (*Maytenus* sp.)	Medang (*Litsea* spp.)
	Apical bud	Huasal (*Euterpe precatoria*)	Aren (*Arenga pinnata*)

a. Resins are a complex mixture of terpenes and terpenoid compounds that may be solid or semi-liquid. They are always water insoluble.

Note: The listing is far from exhaustive.

Source: Scientific nomenclature follows Burkhill 1935; Whitmore 1980; Cavalcante 1972, 1974, and 1979); and Dunn 1975. Local names from personal observation.

produced from these seeds die during the first year, the population has still recruited fifty new progeny. If, on the other hand, intensive fruit harvesting removes all but one hundred of these seeds from the site prior to germination, the maximum number of seedlings that can be recruited into the population is reduced to only five. A seedling mortality rate of 60 percent during the second year would reduce the actual size of these two cohorts to twenty and two individuals, respectively.[4] This tenfold shortfall in recruitment rate can radically change the structure and dynamics of the tree population being exploited.

Although the preceding example illustrates an important demographic concept, the assumption that mortality rates remain constant regardless of the number or density of seeds in the forest is overly simplistic. Seed predation, herbivory and intraspecific competition are all density-dependent phenomena (Janzen 1970, 1971). A more realistic scenario would have mortality rates changing in response to seed and seedling densities. Unfortunately, density-dependent seedling mortality has never been studied in tropical forests under exploitation, and therefore the direction and magnitude of the shifts in mortality that will occur as a result of fruit collection are difficult to estimate. In spite of this, several probable outcomes can be offered as speculation.

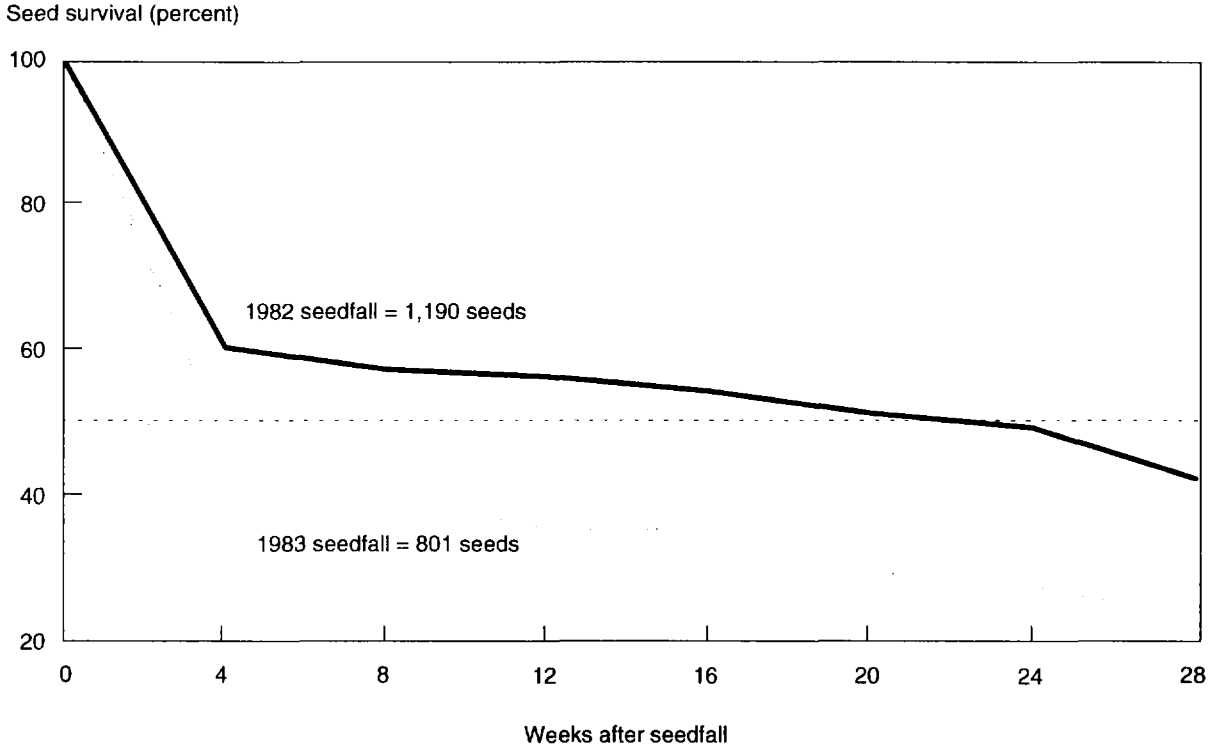
The fruits and seeds left in the forest after harvesting will almost certainly be subject to an unusually high level of consumption by animals. Commercial collectors are, in effect, competitors with forest frugivores, and their activities reduce the total supply of food resources available to ground-foraging animals.[5] Decreased fruit densities could mean increased foraging and a corresponding increase in the overall percentage of fruits and seeds destroyed. An example of this is found in *Faramea occidentalis*, an abundant forest tree on Barro Colorado Island in Panama (Schupp 1990). The seeds of *Faramea occidentalis* are subject to post-dispersal predation by a variety of mammals such as spiny rats (*Proechimys centralis*), agoutis (*Dasyprocta punctata*) and pacas (*Agouti paca*). As shown in figure 2.2, a decrease of only 30 percent in the number of seeds found on the forest floor resulted in a significant increase in rates of seed predation. Although the effect of fruit collection was not specifically addressed in this study, the observed result can be usefully applied within a management context (Schupp 1990). As larger quantities of fruit are extracted from a tropical forest, the survivorship of the remaining seeds will probably decrease. This is an important concern because fewer surviving seeds invariably lead to fewer established seedlings.

Rather than increasing their search for a constantly diminishing food source, it is very possible that less-adaptive frugivores will simply migrate to more isolated tracts of forest in response to commercial fruit collection (Leighton and Leighton 1983). This response could have a serious impact on seedling establishment for those species whose seeds require scarification by animals to germinate (Ng 1983; Pannell 1989). Additionally, some of the frugivores that migrate off-site may have played an important role in dispersing the seeds of certain tree species. Without a dispersal agent, a relatively higher proportion of the fruits and seeds produced by these species will fall directly under the crown of the parent tree where they are more easily harvested by collectors, more easily encountered by potential seed predators, and more susceptible to the effects of intraspecific competition (Augspurger 1983; Clark and Clark 1984; Howe, Schupp, and Westley 1985; Schupp 1988).

All of these sources of mortality interact synergistically to inhibit the recruitment of new individuals into a tree population. Over time, this lack of recruitment will drastically alter the size-class distribution of the population being harvested. If commercial fruit collection continues uncontrolled, the target species can be completely eliminated from the forest. This process of gradual population disintegration is illustrated in figure 2.3 by comparing the size-class distributions of an exploited tree population at various times. Following general convention, the number of individuals per size-class in each histogram are plotted on a logarithmic scale. The size-class intervals depicted are equivalent to 10.0 centimeters DBH; each time period is approximately thirty years.

As is shown at Time 0 in figure 2.3, the hypothetical population initially displays the "inverse J" shaped distribution of a shade-tolerant canopy tree with adequate recruitment (the type I size-class distribution as dis-

Figure 2.2 Seed Survival Rates for *Faramea occidentalis* (Rubiaceae) over a Seven Month Period during Two Years of Differing Seedfall

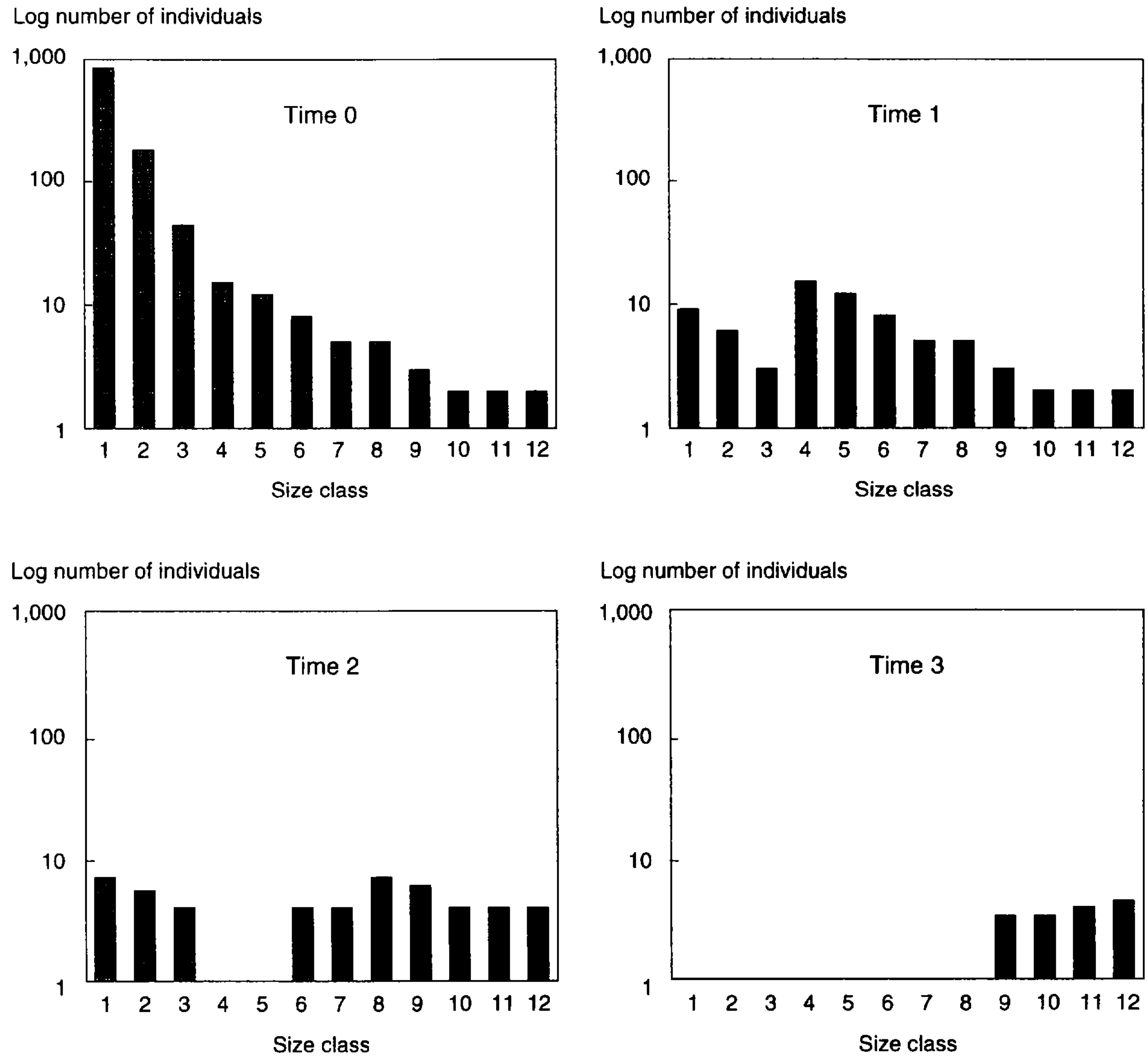


Note: Dotted horizontal line at 50% survival represents the "half-life" of each seedling cohort. Data collected on Barro Colorado Island in Panama.
Source: Schupp 1990.

cussed in chapter 1). After several decades of fruit collection, however, the structure of the population has been notably modified (Time 1). The infrequency of seedling establishment has caused a reduction in the number of individuals in the smaller size-classes; the relatively large number of stems in the intermediate size-classes reflects the growth of saplings that were established prior to exploitation. This type of discontinuous, uneven population structure represents a type II size-class distribution. By Time 2, the structure of the population has been degraded even further. There are complete gaps in the intermediate size-classes, and the existing level of saplings and poles appears to be insufficient to restock these classes. Finally, the histogram shown for Time 3 represents the culmination of a long process of overexploitation. The population consists only of large, old adult trees, none of which are regenerating (type III size-class distribution). In the absence of remedial action, it is only a matter of time before this tree species becomes locally extinct.

The example depicted in figure 2.3 represents an extreme case of uncontrolled overexploitation and does not necessarily imply that every level of harvesting involving reproductive propagules leads directly to species extinction. Some species and populations will obviously be more susceptible to overexploitation than others. The key ecological parameters to consider here are

Figure 2.3 Schematic Representation of Gradual Change in Size-Class Distribution Experienced by a Forest Tree Population Subjected to Intense Collection of Fruits, Nuts, or Oilseeds



Note: Note logarithmic scale on y-axis; size-class intervals are equivalent to 10.0 cm DBH. Each time period is approximately 30 years.

the initial density of the tree population, the intensity of fruit or seed collections, the obligate nature of the plant-animal interactions that occur on the site, and perhaps most importantly, the specific regeneration and growth requirements of the species being exploited. The major challenge for resource managers is simply to ensure that the level of fruit extraction does not adversely effect the long-term regeneration of the species in question—that it is sustainable. This harvest level will probably be greater for high-density species that exhibit abundant regeneration, are not subjected to extreme post-dispersal seed predation, and are pollinated and dispersed by either generalist animals or abiotic vectors. Conversely, low-density populations with type II or type III size-class distributions that display an obligate relationship with a specific pollinator or seed disperser will have a much lower sustainable yield of fruit and will be much more prone to overexploitation. Most of the forest populations of Brazil nut (*Bertholletia excelsa*) currently being intensively exploited in Amazonia exhibit all of these latter characteristics (Mori and Prance 1990). Not surprisingly, there is some evidence that these populations have already been overexploited.

In addition to its impact on seedling establishment, population structure, and the foraging behavior of local animal populations, harvesting commercial quantities of fruits, nuts, and oilseeds can also affect the genetic composition of the tree population being exploited (Peters 1990). In this case, the important question is not so much how many fruits or seeds are harvested, but rather which ones. Tropical tree populations usually exhibit a high degree of genetic variability (Hamrick and Loveless 1986; O'Malley and others 1988; Bawa and Krugman 1991). A single population of forest fruit trees, for example, will invariably contain several individuals that produce large, succulent fruits, a great number of individuals that produce fruits of intermediate size or quality, and a few individuals that produce fruits that, from a commercial standpoint, are inferior because of their small size, bitter taste, or poor appearance. If this population is subjected to intensive fruit collection, the "inferior" trees will undoubtedly be the ones whose fruits and seeds are left in the forest to regenerate. Over time, the selective removal of only the best fruit genotypes will result in a population dominated by trees of marginal economic value. This process, although more subtle and occurring over a longer period of time, is identical to the "high-grading" or "creaming" of the best tropical timbers that occurs in many logging operations.

Given proper management and controlled harvesting, the inherent genetic variability characteristic of tropical tree populations can be manipulated by the resource manager to actually improve the genetic composition of the forest. Carefully adjusting harvest levels to conform to the regeneration and growth requirements of the species under exploitation can also minimize many of the negative demographic impacts of fruit, nut, and oilseed collection. Specific methodologies for achieving these objectives are elaborated in chapter 3. At this point, however, the critical caveat is simply that the uncontrolled collection of reproductive propagules from a tropical forest has a definite ecological impact. Under no circumstances can forest collectors harvest commercial quantities of these resources year after year and expect the forest to maintain a constant level of production. Extraction without some type of management will inevitably lead to overexploitation.

Plant Exudates

When properly conducted, the tapping of latex, resins, and gums does not disturb the forest canopy, kill the exploited tree, or remove its seeds from the site. In theory, this activity—out of all non-timber forest product extraction—probably comes the closest to conforming to the ideal of sustainable use. In actual practice, however, the exploitation of plant exudates can be quite destructive. As is illustrated by the following two examples from Southeast Asia, destructive harvesting appears to be especially prevalent in the case of resin extraction.

Several species of *Dipterocarpus* trees produce an oleo-resin or *damar*, which has long been valued as a source of varnish, caulking, and more recently, as a base for perfumes (Gianno 1981, 1986; de Beer and McDermott 1989). In many parts of Peninsula Malaysia, the standard method of tapping this resin is known as "boxing and firing." As described by Foxworthy (1922), Foston (1935), and Gianno (1990), this process involves first chopping a large, pyramidal hole or "box" into the trunk of a *Dipterocarpus* tree. This hole, which may extend inward one-third of the diameter of the tree, is carved concave at the bottom to collect the oleo-resin dripping from the injured stem tissue. The flow gradually stops after two to three days as the resin starts to build up and harden along the upper surface of the hole. To renew the flow, the old resin is melted away by building a fire within the hole. This sequence is usually repeated several times, and a very large tree may be boxed at two or three different places on the trunk. Although Gianno (1990) contends that trees subjected to this form of tapping "show no discernable signs of ill health," the boxing and tapping process undoubtedly severely weakens the tree and causes resources that might have been otherwise allocated to essential ecological functions such as fruit production and growth to be spent on resin production and the formation of callous tissue to heal over the wounds.

Another resinous forest product that is widely exploited in Malaysia, Borneo, and Indochina is *gharu* or aloes wood. This prized incense wood is produced by the fungal-infested heartwood of several species of *Aquilaria* trees (Jalaluddin 1977). *Aquilaria malaccensis* is the most widely distributed taxa, and it is this species which apparently produces the highest grade of aloes wood (Burkhill 1935; Gianno and Kochummen 1981). The blackened, diseased wood does not occur in every tree, and even when present the quantity is extremely variable. As there are no external signs to indicate whether a tree contains aloes wood, collectors frequently fell every *Aquilaria* tree they find.[6] Once an infected tree has been felled, collectors use axes and knives to hack out the blackened heartwood. The uncontrolled exploitation of aloes wood, together with the wasteful trial and error method of searching for it, has virtually eliminated this species from all but the most remote and inaccessible forests (Jessup and Peluso 1986).

It is important to point out that the destructive harvesting of plant exudates is not limited to resinous trees or to Southeast Asia. *Couma macrocarpa*, for example, is a valuable latex and fruit-producing tree that is widely distributed throughout Amazonia. The species produces copious amounts of creamy white latex used in the manufacture of chewing gum; the latex is also occasionally used as adulterant in Para rubber (*Hevea brasiliensis*). Although the species can be tapped repeatedly as easily as rubber and exploited every year for its fruits, opportunistic collectors have felled an incalculable number of *C. macrocarpa* trees to quickly drain them of their latex (Vazquez and Gentry 1989).

The exploitation of these three forest resources will probably never be sustainable given current harvesting practices. While the situation with *C. macrocarpa* could be remedied by simply using existing methods for tapping latex, innovative, less-destructive technologies are sorely needed for extracting resinous compounds. It might be possible, for example, to make a series of smaller cuts along the stem of *Dipterocarpus* trees to extract the oleo-resin. Although this practice would undoubtedly reduce the total yield of resin, it might significantly increase the tapping life span of the tree. Rather than felling every *Aquilaria* tree, a small increment borer, such as is commonly used to extract cores from temperate trees to determine their age, could be used to first check for the presence of aloes wood. Controlled experimentation and field trials of different harvest techniques would be extremely useful to ensure the continued existence of these forest resources.

Rubber, gutta percha, and jelutong (see box 2.1) are common examples of plant exudates that are tapped in a nondestructive fashion. It is tempting to assume that the exploitation of these species will be sustainable in the long term, and that there is therefore little reason to invest in management activities.[7] It should be remembered, however, that maintaining a continual supply of latex is contingent upon these species being able to replace themselves in the forest. There is currently a large number of tappable rubber trees growing in the lowland and upland forests of Amazonia. These trees will eventually die. Are any provisions being made to recruit a second and third generation of Hevea trees?

It is useful in this context to briefly examine the physiology of rubber production by *Hevea* trees. Rubber latex is manufactured in specialized vascular cells (modified sieve tubes produced by the cambium) using stored carbohydrates. In addition to rubber, the latex contains proteins, resins, sugars, glucosides, tannins, alkaloids, and mineral salts (Purseglove 1968). Although the exact biological function of this latex is unknown, biochemically it is quite expensive for the tree to produce. The large-scale production of rubber by *Hevea* trees is an abnormal response to injury: a tapped tree produces hundreds of times more latex than it would have formed had it not been tapped (Polhamus 1962). Commercial tapping regimes cause the tree to divert a considerable proportion of the resources normally used for basic metabolic functions (maintenance, growth and reproduction) to the production of rubber. This diversion of resources can cause a measurable reduction in the growth of *Hevea* trees subjected to tapping.

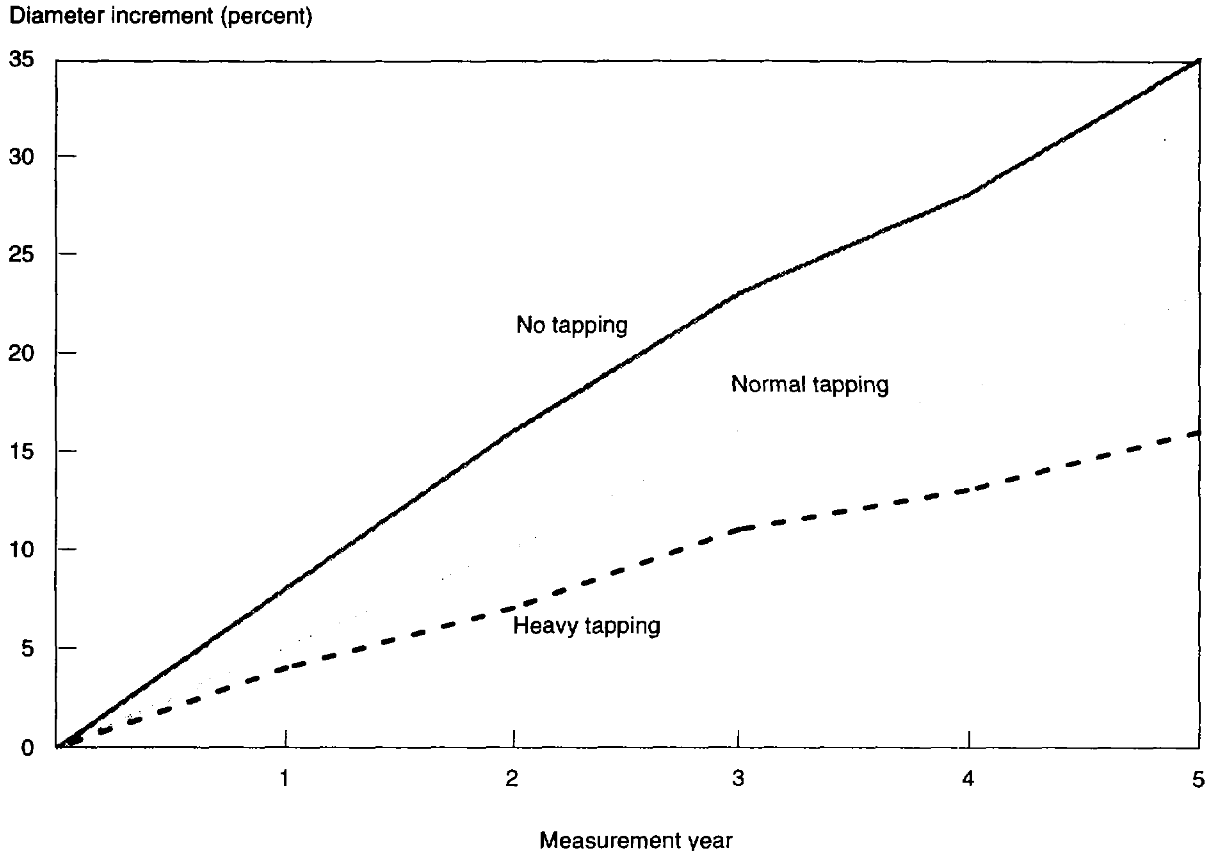
As is shown in figure 2.4, tapping reduced the diameter increment of plantation-grown rubber trees in Southeast Asia by as much as 50 percent over a five-year period. This growth reduction was significantly greater at higher tapping intensities. It should be noted that the sample trees were growing in a plantation with abundant light, water and soil nutrients and free from the competitive effects of other plants. The growth of wild *Hevea* trees in an Amazonian forest environment would undoubtedly be even more severely affected. It is very possible that this reduction in vegetative growth would also be accompanied by a reduction in fecundity. Several studies have shown that internal resource limitations produced by disease, seed predation, or herbivory can cause a reduction in the total fruit yield of a tree by increasing the rate of fruit abortion (Boucher and Sork 1979; Stephenson 1981; Heithaus, Stashko, and Anderson 1982). There is no reason to assume that repeated tapping will not produce a similar response. The most productive *Hevea* clones used in plantations, in fact, rarely set fruit at all. Polhamus (1962), for example, reports that fruit set percentages of only 2–4 percent are obtained in plantation stock even after controlled hand pollinations. The physiological demands of producing a continual supply of latex are clearly in conflict with the ecological imperative of producing seeds.

The preceding example of rubber physiology can, in a very general sense, be applied to almost every type of plant exudate. The limitations imposed by forcing a forest tree to allocate a large percentage of its internal resources to a basically nonmetabolic function presents a dilemma for resource managers. From an economic standpoint, the relatively low natural yields exhibited by wild latex and resin-producing trees would appear to warrant immediate silvicultural treatment (weeding, thinning of competitors, reducing canopy cover, and so forth) to stimulate their productivity. From an ecological standpoint, however, increasing exudate yields will almost certainly restrict the regenerative capacity of the tree populations being exploited, and hence may compromise the long-term sustainability of resource exploitation. Although there are probably a variety of management strategies that could be used to resolve this dilemma, periodic monitoring of population recruitment levels under different tapping intensities is probably the easiest and most direct method of finding an optimal balance between latex or resin yields and total ecological impact. It is somewhat surprising that after almost 150 years of exploiting Amazonian forest rubber this critical management information is still lacking.

Vegetative Structures

This category of non-timber forest resources contains a diverse assemblage of different plant tissues used for fibers, building materials, medicines, fish poisons, and foods (see box 2.1). The plant part exploited may be the

Figure 2.4 Percent Reduction in Diameter Increment Exhibited by Plantation-Grown *Hevea* Trees in Southeast Asia Subjected to Two Different Tapping Intensities



Note: Solid line indicates the untapped control trees.
Source: Adapted from Dijkman 1951.

root, stem, leaf, bark or apical bud. Although the origin and uses of these plant products are very different, their harvest produces a similar ecological impact. The plant species will either be killed during the collection process or, in a limited number of cases, will survive harvesting and later regenerate the vegetative structure removed. There are numerous examples of plant resources that are killed or fatally wounded by the harvest of vegetative structures. The current situation with rattan in Southeast Asia provides a particularly useful illustration of the deleterious effects of harvesting commercial quantities of stem fiber.

Rattans are climbing, spiny palms (Subfamily Calamoidae) that commonly occur in the mixed dipterocarp forests of Southeast Asia from sea level up to about 3,000 meters. The largest concentration of species occurs in Peninsula Malaysia and Borneo where at least 104 and 151 species, respectively, have been identified to date (Dransfield 1981). Over half of these species pertain to the genus *Calamus*; other important genera include *Daemonorops* (115 species) and *Korthalsia* (29 species). The stem fibers of about fifteen to twenty of these palms species are widely sought after as a source of cane for manufacturing furniture, woven mats, baskets, and other types of wickerwork. The most important commercial rattans are the large-diameter (up to 2.0 centimeters) furniture canes of *Calamus manan* and the smaller, pencil-size canes of C. *caesius* and C. *trachycoleus* (Menon 1980; Dransfield 1988). About 90 percent of the world's supply of rattan comes from Indonesia (Menon 1978), which exported about 144,000 tons of cane valued at over US$210 million in 1987 alone (Biro Pusat Statistik 1987). Malaysia, Thailand and the Philippines are also major producers of rattan (De Beer and McDermott 1989).

After locating a suitable specimen in the forest, rattan is harvested by cutting the plant at the base and then pulling the entire spiny stem and leaves out of the forest canopy by repeated strong tugs. Given that a large C. *manan* stem may be more than 100 meters long, this is a particularly arduous and time-consuming task. Once on the ground, the spiny leaves and sheath around the stem are removed with a knife, and the stem is bundled for transport out of the forest. The actual impact of harvesting depends on the specific growth form or type of rattan that was cut. Large cane rattans, including the valuable C. *manan*, possess a single stem that does not resprout after cutting. Harvesting kills these individuals. Smaller cane rattans, however, are typically acaulescent or multi-stemmed and can resprout after cutting if sufficient time is allowed between harvests. (Dransfield 1979; Manokaran 1985). It is not surprising that intensive and uncontrolled harvesting has drastically reduced the abundance of solitary rattans in many localities. Unfortunately, the rising demand for small-diameter canes has also caused the overexploitation of many multi-stemmed species, as collectors cut them too young or too close to the ground to permit resprouting.

Ave (1988) reports that the commercial collection of rattan by the Semai of West Malaysia has caused supplies of many valuable species to become severely threatened. Natural populations of C. *manan*, C. *peregrinus*, and C. *ornatus*, said to have been very common in the area at one time, are now virtually extinct. In response to this situation, local collectors turned to C. *diepenhorstii*, which is also being rapidly depleted. The excessive cutting of young plants was found to be the major cause of the resource depletion. Similar examples of overexploiting rattan have been documented in the Philippines (Conelly 1985; Siebert and Belsky 1985), East Kalimantan (Peluso 1983; Jessup and Peluso 1986), Sulawesi (Siebert 1986), Central Sumatra (Siebert 1988), and Sabah (Marsh and Gait 1988). The general pattern is usually one in which the excessive demand for selected rattans has exhausted local supplies, and collectors are forced to forage over increasing longer distances to find the desired species. On the island of Leyte in the Philippines, for example, all rattan harvesting prior to 1970 was conducted within a 6-kilometer radius of local villages. By 1985, collectors were forced to travel up to 12–14 kilometers along steep mountainsides to find merchantable rattan (Siebert and Belsky 1985). In Ulu Kinabatangan, Sabah, collection rates of over 100 pieces of rattan per day were common in 1980. By 1985, a collector was lucky if he could find even forty pieces per day (Marsh and Gait 1988). The relative magnitude of the overexploitation of rattan that is currently occurring can perhaps be best appreciated by a final example. In 1979, it was estimated that approximately 67,000 tons of rattan per year could be sustainably harvested from the forests of Indonesia (Menon 1980). Official government statistics show that over 102,000 tons of rattan were actually exported from Indonesia during that year (Biro Pusat Statistik 1979).

Rattan is an extremely valuable non-timber forest resource. It is also a resource that could be managed *in situ* on a sustained-yield basis, especially in the case of acaulescent forms that exhibit the ability to resprout after cutting. Most recent efforts to manage rattan, however, have focused exclusively on plantation establishment (Manokaran 1984, 1985; Shim and Tam 1984; Wong and Manokaran 1985), and little attention has been paid to the rehabilitation of wild populations. Unless harvest controls, enrichment plantings, and effective programs of forest management are rapidly initiated, the rattans of Southeast Asia may soon cease to be a forest product.

The commercial collection of other types of vegetative structures can also cause an ecological impact, although this impact is frequently less notable than that produced by the extraction of stem tissue. Harvesting leaf fibers, for example, may have a negligible impact on the structure and abundance of the plant populations being exploited if: individual plants are not killed in the process, a few healthy leaves are left on each plant to produce photosynthate, the reproductive structures and meristems are not damaged, and sufficient time is allowed between successive harvests for the plant to produce new leaves. In Peruvian Amazonia, the periodic collection of leaf fibers from the chambira palm (*Astrocaryum* spp.) for cordage and weaving materials has little effect on the vigor of exploited trees, and the species appears to be maintaining itself quite well in local forests (Kahn 1988; Peters, personal observation). Similarly, the collection of xate palm (*Chamaedorea* spp.) leaves in Central America for use in floral arrangements is also assumed to be sustainable under existing harvesting levels (Heinzman and Reining 1989). The fact that there is almost a 50 percent reduction in *Chamaedorea* stem density between harvested (2,478 stems per hectare) and unharvested (4,506 stems per hectare) sites, however, would seem to call in question the long-term viability of this practice (Cabrera-Madrid and others 1990).

Although very little information is available on the topic, the collection of roots and bark tissue undoubtedly weakens or fatality wounds the exploited tree species. The impact of this selective mortality can become quite severe under high levels of exploitation. In the early 1930s, for example, a significant export trade in barbasco (*Lonchocarpus* spp.) was developed in many parts of Amazonia (Padoch 1987). The roots of this leguminous plant contain rotenone, an extremely potent natural insecticide (Acevedo-Rodriguez 1990). Given the typical "boom and bust" history of the forest products trade in Amazonia, the subsequent cultivation of barbasco in the region (Villarejo 1979) was undoubtedly precipitated by commercial collectors digging up, and not replacing, a significant percentage of the *Lonchocarpus* plants found in the forest.

The large-scale collection of *amate* bark (*Ficus* spp.) for making bark paper handicrafts in Mexico has virtually eliminated these tree species from the forests surrounding San Pablito, Puebla where the paper is made (Peters, Rosenthal, and Urbina 1987). If given sufficient time, *Ficus* trees are able to regenerate new bark (technically periderm tissue) over a small portion of the stem. Unfortunately, faced with a rising demand for bark paper handicrafts, local collectors began to increase the intensity, as well as the frequency, of harvest and entire populations of *Ficus* trees died. Rather than attempt to regenerate these trees, bark tissue is currently hauled in by truck from the neighboring state of Veracruz. The harvesting of *Litsea* bark as currently practiced in many parts of Borneo will probably result in a similar process of resource depletion. The bark, which is used in the manufacture of mosquito repellant coils, is typically stripped from felled trees.

Apical buds are the final category of non-timber forest products harvested from vegetative structures, with palm hearts being the most important and well-known example. In Amazonia, two forest palm species, *Euterpe oleracea* and *Euterpe precatoria*, are the preferred source of this delicacy.[8] *Euterpe oleracea* is a slender, multi-stemmed palm that is widely distributed in the seasonally flooded forests of eastern Brazil (Anderson 1988). As was discussed in chapter 1, extensive oligarchic forests of this species occur along the floodplains of the Amazon estuary. *Euterpe precatoria* grows in a similar habitat in western Amazonia, but is a solitary palm (Kahn 1988). These differing growth forms play a major role in determining the overall ecological impact of harvesting.

In a single-stemmed palm species, harvesting the heart or apical meristem necessarily kills the tree. This is exactly what happens when palm hearts are extracted from *E. precatoria*. The establishment of a palm heart canning factory in Iquitos, Peru during the mid-1980s was sufficient impetus to destroy almost every population of this species in a wide radius around Iquitos. The factory was eventually forced to close due to a scarcity of raw materials (Peters, personal observation). The vast stands of *E. oleracea* found in eastern Amazonia are also exploited quite heavily for palm hearts. Official government sources report that almost 99,000 tons of palm hearts were extracted from these forests in 1982 alone (IBGE 1983). Most of this material was harvested in the state of Para, Brazil near the city of Belem. Fortunately, the acaulescent growth form of the *E. oleracea* enables the species to sprout back after cutting, and this ecological factor has greatly facilitated its continued survival in the region. In an exemplary demonstration of forest management capabilities, local collectors on Onças Island near Belem have developed an innovative system for harvesting palm hearts on a sustained-yield basis by using weeding and pruning techniques to take advantage of *E. oleracea*'s unique ability to sprout from the stump after cutting (Anderson and others 1985).

The initiative of the forest farmers on Onças Island in the Amazon estuary is an appropriate point of closure for this chapter. The exploitation of almost any type of non-timber forest resource produces a measurable impact on the structure and dynamics of tropical tree populations. There are typically two responses to this impact. One is to completely ignore that it is occurring, the other is to implement management activities that will minimize the intensity of this impact. The former course of action, or lack thereof, inevitably leads to forest degradation and resource deletion; the latter may ultimately produce a sustainable form of land-use.

The fact that many forms of non-timber resource exploitation kill the target species is, in itself, not an insurmountable problem. As long as there are other conspecific individuals available to replace this mortality, harvesting can theoretically be sustained almost indefinitely. For most forest species, however, securing this recruitment will require a concerted management effort. It will require meticulous selection of the species, resources, and habitats most suitable for sustainable forest extraction. It will require detailed inventories to determine the density and size-class distribution of the useful tree species found within the management area, and it will require yield studies to determine the size-specific production of each desired resource (for example, fruits, oilseeds, latex, stem tissue, leaves, bark, or roots). Finally, effective forest management will also require periodic regeneration surveys to monitor the demographic response of each population to differing harvest intensities and to serve as an ecological warning system in case of resource overexploitation.

Chapter Summary

1. Almost any type of resource extraction conducted in tropical forests will have an ecological impact. The magnitude of this impact depends on the floristic composition of the forest, the nature and intensity of harvesting, and the particular species or type of resource under exploitation.
2. The ecological impacts of selective logging are quite extensive, with forest structure, floristic composition, soil properties, site fertility, water relations and wildlife populations all being adversely effected. Harvesting less than 5 percent of the trees within a tropical forest can destroy up to 50 percent of the residual stand and seriously damage an additional 3–6 percent of the standing trees. The drastic canopy clearing involved irreparably modifies the species composition of the forest and makes it extremely susceptible to wildfire. The use of heavy equipment damages 15–50 percent of the soil surface, re-

duces the infiltration rate of soil water, and causes soil erosion. The rapid expansion of commercial logging in tropical forests has depleted the supply of several valuable timber species and has pushed many forest animals to the brink of extinction.

3. One of the most basic, and rarely questioned, assumptions underlying much of the current interest in extractive reserves is that the commercial exploitation of non-timber forest products has little or no ecological impact. This assumption is both incorrect and potentially dangerous. Every non-timber resource has a site-specific maximum sustainable level of harvest. If this harvest level is exceeded, the plant populations being exploited, as well as the community of animals that depend on them, will all be adversely effected.

4. Given that the initial impact of resource extraction is largely determined by the specific type of resource or plant tissue harvested, the enormous variety of non-timber resources produced by tropical forests can be grouped into three basic categories: reproductive propagules (fruits, nuts, and oilseeds), plant exudates (latex, gums, and resins), and vegetative structures (stem fibers, leaves, roots, barks, and apical buds).

5. Although unnecessary, felling the tree is a common method of harvesting many reproductive propagules. This practice has led to the serious depletion of several important fruit and oilseed-producing species. However, even in the absence of destructive harvesting, the continual collection of commercial quantities of fruits and seeds can cause notable changes in the structure and dynamics of a tree population. These changes are typically precipitated by a reduction in seedling establishment and population recruitment caused by overharvesting. If uncontrolled, this process can result in the gradual extinction of the population under exploitation.

6. When properly conducted, the extraction of plant exudates does not disturb the forest canopy, kill the exploited tree, or remove its seeds from the site. There are, however, several examples of exudate-producing trees that are harvested destructively, and even the nondestructive tapping of rubber can cause a reduction in the growth and reproductive output of wild *Hevea* trees.

7. The harvest of vegetative structure inevitably produces one of two different impacts. The plant species either will be killed in the collection process or, in a limited number of cases, will survive and later regenerate the vegetative structures removed. Rattan is a well-known example of the former scenario, and uncontrolled harvesting is rapidly depleting this resource in Southeast Asia. Leaf fibers and a few types of barks and apical buds are regenerated by the harvested tree and, therefore, may be sustainable resources over the long term.

8. There are typically two responses to the ecological impact caused by harvesting non-timber forest resources: one is to completely ignore that it is occurring, the other is to implement management activities that will minimize the intensity of this impact. The former course of action inevitably leads to forest degradation and resource depletion; the latter may ultimately produce a sustainable form of land-use.

Notes

1. This point is debatable. If "common" implies the total number of people involved, the harvest of non-timber forest products is probably a more common form of forest exploitation. Furthermore, it is unclear at this time whether the area of logging concessions is actually greater than that foraged over by rural people in their search for fruits, rattans, oilseeds and latex. There is no question that selective logging is the most visible, highly subsidized, and rapidly expanding form of forest exploitation in the humid tropics.

2. One of the most frequently reported (for example, Richards 1952; Longman and Jenik 1974; Jacobs 1988) characteristics of tropical forest ecosystems is that the great majority of inorganic nutrients are contained in the aboveground biomass (tree stems, branches, twigs, leaves, fruits, animals, and forest floor material). This pattern is quite different from

a temperate forest ecosystem in which most of the inorganic nutrients are in the soil (Likens and others 1977). Although several recent studies of nutrient cycling in the tropics have shown that these basic distinctions are actually not that clearly defined, tropical forests do appear to contain a relatively larger percentage of their total nutrient capital in plant tissues than do temperate forests (Jordan and Kline 1972; Golley and others 1975; Herrera and others 1978; Grubb and Edwards 1982). This general pattern accounts for the increased nutrient loss that occurs when the boles of large timber trees are felled and removed from a tropical forest.

3. This ubiquitous idea, or some variant of it, has appeared in books, scientific papers, conference proceedings, grant proposals, magazine articles, newspaper stories, on television and radio shows, in the annual reports of private companies, and even on the back of cereal boxes and ice cream cartons.

4. The first and second year rates of seedling mortality used in this example are entirely realistic. Fruit or seed production rates could be either much higher or lower depending on the tree species and the size of the population. Commercial harvest intensities are also extremely variable depending on the species, habitat, access and market price. For large, poorly dispersed, highly valued market fruits that are easily collected under the crowns of adult trees (for example, the Brazil nut or certain species of illipe nut), a 90 percent harvest intensity could be an underestimate.

5. Unlike tree felling, collecting fruit off the ground has little impact on the foraging of arboreal or flying frugivores. These animals (bats, birds, primates and squirrels) remove ripe fruits directly from the crown of a tree. Humans then collect from the fruits that have been left behind by the frugivores.

6. Gianno (1990) reports that Semelai collectors in Peninsula Malaysia have special techniques for determining whether a tree contains gharu wood without felling it. An infested tree is said to produce a cracking or bubbling sound when struck; other informants confided that they were able to smell the resinous aroma of the diseased heartwood.

7. The fact that rubber tapper families have exploited the same *seringal* or grove of rubber trees for over sixty years has been cited as evidence of the inherent sustainability of extracting plant exudates from a tropical forest (Schwartzman 1989). Sixty years, however, is considerably less than the life span of a wild *Hevea* tree; the abundance and quality of subsequent generations of rubber trees that occupy the site will be what ultimately determines the sustainability of this practice.

8. A third palm, *Bactris gasipaes*, is also an important source of palm hearts, but this western Amazonian species is completely domesticated and has never been encountered in the forest.

III

Management Strategies for Non-timber Tropical Forest Resources

> "Measure twice, cut once, wise man put it..."
>
> —*Gibson (1984)*

Regardless of existing markets or land tenure systems, maintaining a continual supply of harvestable resources from a tropical forest requires management. However, although the great potential for exploiting these forest resources sustainably has been frequently emphasized (see, for example, Myers 1983; de Beer and McDermott 1989; Fearnside 1989; Peters, Gentry and Mendelsohn 1989; Allegretti 1990; Peters 1990a), rarely, if ever, has this objective been achieved. In fact, the commercial extraction of non-timber tropical forest resources is currently plagued by destructive harvesting, overexploitation and a basic disregard for the functional ecology of tropical tree populations. This situation is largely caused by the lack of any concerted effort to manage the non-timber resources, ensure their regeneration in the forest, or even broadly define a sustainable level of harvest.

In spite of the importance of this topic, very little has been written about the management of non-timber tropical forest resources (Posey 1985; Denevan and Padoch 1987; Posey and Balée 1989; Anderson 1990). Foresters working in the tropics have traditionally viewed the production and harvesting of wood products as their primary objective. Not surprisingly, most of the voluminous literature on forest management has focused exclusively on timber species, cutting cycles, and silvicultural techniques for increasing merchantable volumes of wood. Tropical agronomists, on the other hand, have been primarily concerned with the propagation, tending, and breeding of cultivated species, and few have ventured into the domain of forest trees. Even plant ecologists have only rarely addressed the problem of managing non-timber tropical forest resources on a sustained-yield basis. This lack of information and neglect reflects, in large part, the "minor" forest product status generally afforded tropical fruits, nuts, latex and oilseeds and has made improving the current patterns of resource exploitation extremely difficult.

This chapter presents an overall strategy for managing non-timber tropical forest products on a sustained-yield basis. The specific procedures described are sufficiently general that they can be applied to almost any class of non-timber resource (reproductive propagules, plant exudates or vegetative tissues). Furthermore, they allow a high degree of flexibility so that management operations can be tailored to the specific ecological requirements of a particular site, species, or plant population. The operations may cover 100 hectares or 100,000 hectares. An important note, however, is that these guidelines do not comprise a single management technology or package that can be blindly applied without modification. Rather, the basic concept is to provide the resource manager with a constant flow of diagnostic information about the ecological response of a species or resource to varying degrees of exploitation. Sustainability is achieved through a continual process of reciprocal feedback: that is, the demographic reaction of the target species must result in a corresponding adjustment in harvest levels. The exact nature of this process of "fine-tuning" will depend on the site, the judgment of the resource manager, the precision of the diagnostic data collected, the effectiveness of harvest controls, and, perhaps most importantly, the ecological behavior of the plant populations selected for management.

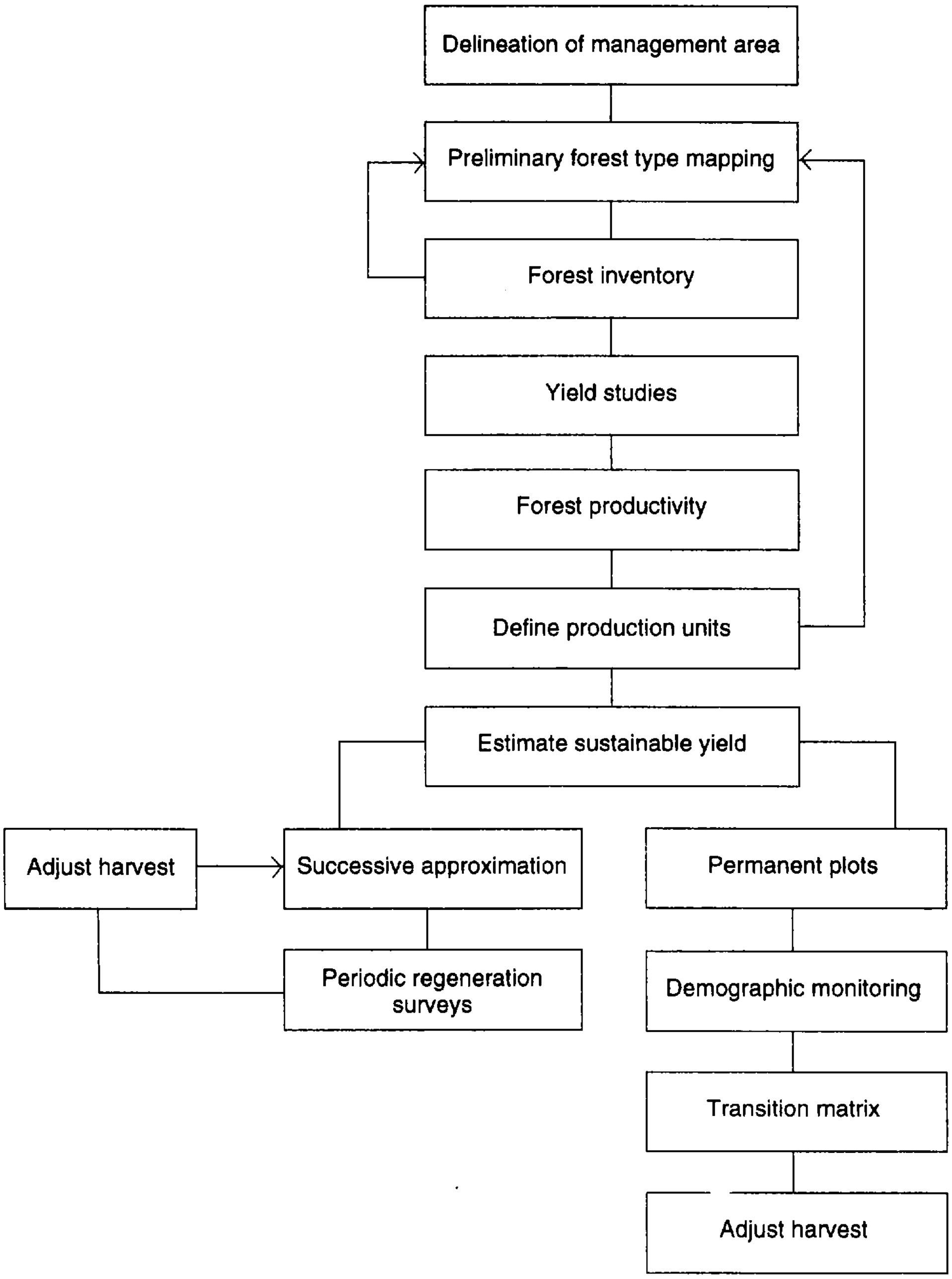
A schematic flow chart of the different management operations discussed in chapter 2 is presented in figure 3.1. The complete process is composed of five basic steps: initial planning, forest inventory, species selection, yield studies, and definition of sustainable yield. The initial planning phase involves the delineation and preliminary mapping of the forest types in the management area. A quantitative forest inventory is then conducted to describe the distribution and abundance of different plant resources within the management area. This inventory provides the initial data on population density and size-class structure needed for selecting the species or resource groups with the greatest management potential. Additional field studies are initiated at this point to document the natural yield characteristics of each species selected. Depending on the type of resource involved, these studies will focus on either size-specific fruit production, exudate yield, or the growth of particular vegetative tissues. The final phase of the process is basically an iterative procedure for estimating, and ultimately attaining, a sustainable level of resource extraction. Two methods of achieving this goal are outlined: periodic regeneration surveys and successive approximation, or demographic studies coupled with the use matrix models and computer simulations.

The guidelines outlined in this chapter have, in many cases, been adapted from the standard inventory, monitoring and management procedures developed by tropical foresters. However, given the obvious ecological and operational differences between periodic tree felling and the annual collection of fruit or latex, the present application of these procedures is somewhat different from that originally envisioned by the professional foresters who created them. A number of the analytical tools commonly used in plant population ecology (life tables, fecundity schedules and transition matrix models) have also been incorporated, together with the survey techniques of quantitative ethnobotany (Prance and others 1987). The net result is an interdisciplinary hybrid that may be a useful starting point for resource managers and policymakers striving to develop more-efficient systems for managing non-timber tropical forest resources.

Initial Planning Operations

Before beginning management activities, every attempt should be made to collect as much supporting information as possible about the forest area of interest. Examples of this type of information include large-scale topographic base maps (scale from 1:10,000 to 1:100,000), soil or geologic survey maps, climatological data, descriptive analyses of the vegetation, inventory data or forest type maps, standard aerial photographs (scale from 1:6,000 to 1:12,000; preferably as overlapping stereopairs) and multispectral satellite images. It is also useful to visit the nearest herbarium to compile a working list of all the plant species that may have been collected within the area. This list should be referenced by both scientific and local nomenclature and should include ethnobotani-

Figure 3.1 Flow Chart of the Basic Strategy for Managing Non-Timber Forest Resources on a Sustained-Yield Basis



Note: The complete process is composed of the five steps: (1) initial planning, (2) forest inventory, (3) species selection, (4) yield studies and (5) definition of sustainable harvest. See text for explanation of different management operations.

cal or use information whenever appropriate. Finally, literature about the area should be thoroughly reviewed, using both published and unpublished "grey" literature such as government documents, internal reports, memoranda, and draft maps. Usually, the local forestry department is a good place to start compiling this information.

In many parts of Amazonia, Southeast Asia, and other remote and poorly studied areas of the tropics, baseline information frequently is lacking. In these situations, a good set of large-scale aerial photographs is essential. If none are currently available, a special reconnaissance flight of the area will have to be commissioned. The timing of this flight should be scheduled during a period of low cloud coverage (often the dry season), and if possible it should coincide with a general flowering event in the forest to later facilitate species identifications and forest type mapping. If sufficient funds are available, overlapping vertical panchromatic prints should be requested so that the images can later be viewed stereoscopically.[1] Some engineering firms even prepare aerial photographs with overlays of topographic contour lines and polygons indicating the area on each photo (away from the central focal point) that has unacceptable distortions. In spite of the significant expense involved in procuring these images, aerial photographs are an indispensable management tool and their frequent utility will quickly repay the initial investment. They can be used to prepare preliminary forest typologies, to determine the distribution and area of different plant communities, to trace the lines of access into the management area, to locate adjacent villages and agricultural fields, and to orient inventory activities and the location of permanent study plots (Avery 1978).

Delineation of the Management Area

Needless to say, the first step in planning is to select and define the specific area within which management activities are to occur. This process can be more difficult than it sounds. The exact boundaries of most of the extractive reserves created in Brazil in 1990, for example, have yet to be fully demarcated. Regardless of the history, origin or size of the proposed management area—whether government-decreed reserve, community forest land, or private concession—the borders of the area must be delineated with a reasonable degree of precision. Without this basic information, it is virtually impossible to do detailed forest mapping, to conduct representative and meaningful inventories, to define discrete production units, or to estimate the total quantity of harvestable resources on the site. The absence of well-defined boundaries also invites land disputes. The current state of affairs within the nebulous boundaries of many logging concessions in tropical forests is an unfortunate illustration of these constraints. To use a mathematical analogy, efficient forest management is contingent upon a knowledge of the total size or area of the statistical population to be sampled.

If reliable coordinates for the management area are available, these should be plotted first on a large-scale base map (effective scale ranging from 1:10,000 to 1:50,000). In most situations, however, the boundaries of large, remote, forested tracts are defined in reference to notable topographic or physical features such as rivers or mountains, or only broadly described with respect to existing administrative or political divisions. In these cases, the borders of the management area should be tentatively sketched on a base map after a thorough review of all available information. If no maps at all are available, the proposed area should be delineated as best as possible directly on the aerial photographs, preferably while viewing them as pairs under a stereoscope.

Once a preliminary outline of the management area has been drawn on either a base map or a series of aerial photographs, the borders should be "ground-truthed" by spot checks in the field. The reason for this is to verify that the outline or legal description of the tract conforms to the general conditions encountered in the field, for example, that the boundary crosses a river or follows a mountain ridge when the base map or photo indicates that it should. Any discrepancies should be duly recorded and the boundaries modified on the base map. It should be noted that the process of field verification is especially problematic in flat, homogenous areas of forest with limited access such as are found in much of the lowlands of Amazonia. Given sufficient funds, the ideal solution would be to have the entire perimeter of the area surveyed by a qualified field crew using a theodolite. The precise boundaries of the area could then be permanently marked in the field with concrete or metal posts set at regular intervals.

The final operation involves determining the total area of forest contained within the boundaries of the site. If a survey has been conducted, this result can be calculated trigonometrically with a high degree of precision by using the bearings and distances recorded in the field. Alternatively, the total area of the site can also be determined planimetrically from the base map or aerial photos.[2]

Preliminary Forest Typology

Given the high species diversity and floristic patchiness of most tropical forests, the management area will inevitably contain a number of different forest types or plant communities. The composition, density, diameter distribution, canopy height, and dominance of each of these communities will be different. The availability of different nontimber plant resources will also vary from one forest type to the next. From a management perspective, it is extremely important to document the areal extent, community structure, and floristic composition of these different forest types. Such baseline information will later play a significant role in determining the actual pattern and intensity of forest exploitation.

Before going into the field, an attempt should be made to identify and delineate the major forest types in the management area. This task is accomplished by carefully examining the aerial photographs of the region under a stereoscope and paying particularly close attention to changes in the tone, texture, and pattern of the tree crowns visible in the forest canopy. In most cases, distinct canopy patterns will be related to physical aspects of the landscape such as changes in topography or orientation, proximity to rivers, or local soil conditions. Some plant species, such as palms or large emergent trees whose crowns are especially easy to distinguish on aerial photographs, may serve as indicator species of a particular forest type. For mapping purposes, specific forest types can be named in accordance with their topographic position (lowland, slope or montane forest), dominant species (*Nypa* swamp or mangrove forest) or, if detectable, their substrate (peat, white sand forest, and so forth). Numerical modifiers (for example, relative tree density or canopy height) can also be used to distinguish between different subclasses of the same forest type.[3]

Upon completion of the photogrammetric analysis, the plant communities detected on the aerial photographs are outlined, traced onto a transparent overlay, and then transferred to the base map. In most cases, an adjustment will have to be made to compensate for the larger scale of the aerial photographs. If no base map is available, additional photointerpretation should be conducted to construct one. Concurrent with the delineation of forest types, all roads, trails, rivers, streams and human settlements should also be traced from the aerial photographs. These features, together with the preliminary forest typology, should then be mapped at a relatively large-scale (1:50,000 or larger) on a high-quality paper stock. The final map should contain a clear scale and a linear grid to ease interpretation, as well as to orient subsequent inventory operations. The total area of each forest type can be estimated planimetrically using this map.

The forest types distinguished at this stage are only a first approximation of what may actually be encountered in the field. They are, in essence, a temporary planning tool for guiding a more detailed process of vegetation analysis. The initial typology of the forest will be continually modified when field operations begin, and the input of inventory data and repeated field observations should ultimately result in a more complex, finely grained, and realistic classification of local vegetation types.[4] Although the actual level of detail required for management purposes is considerably less than that collected in many ecological studies of tropical vegetation, refining estimates of the classification, description, and area of the plant communities found within the forest should be a constant priority. Different plant communities contain different resources that must be exploited and managed in different ways. The closer the final typology conforms to the reality of the forest, the easier it is to manage these resources.

Forest Inventory

The second phase of the management process involves extensive fieldwork and the counting and measuring of trees. The objective of these activities is to answer several basic questions about the nature and extent of the forest resource base. For example, what economic plant species are found within the management area? How abundant are they, and do they appear to be maintaining themselves in the forest? Which of these resources are restricted to a particular forest type, and which are more evenly distributed throughout the site? What plant resources have the highest potential for sustained-yield management? Addressing these questions requires the data from a quantitative forest inventory. Although time-consuming, somewhat costly, and extremely tedious to collect, inventory data is the core of all management operations.

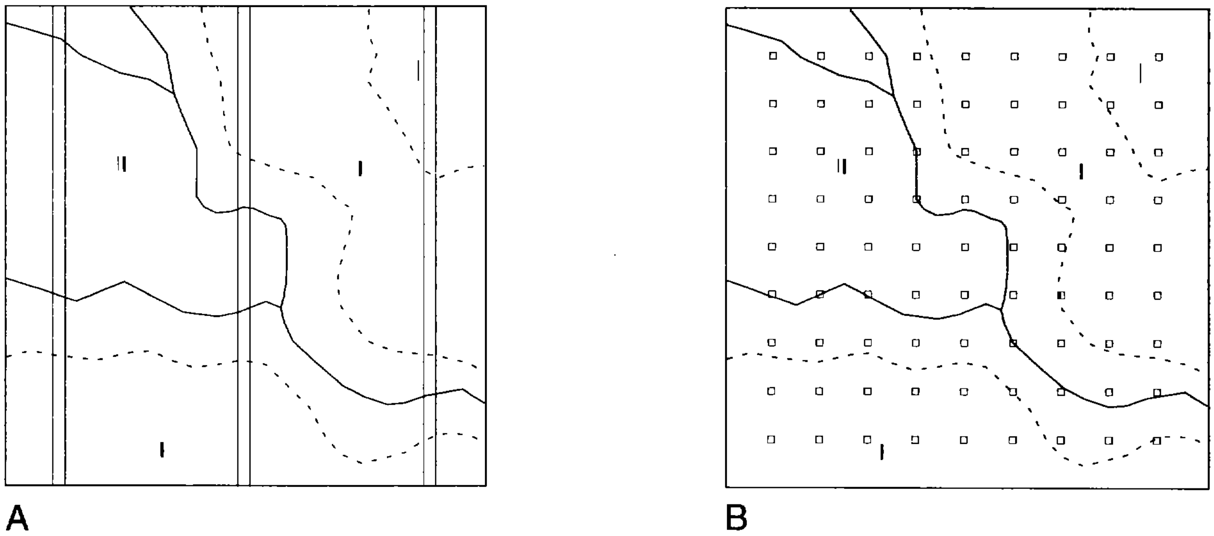
Foresters have a long history of counting and measuring tropical trees, and they have developed a wide variety of inventory techniques. These techniques are explained in detail in almost any basic forestry or mensuration textbook (Husch, Miller, and Beers 1972; Loetsch and Haller 1973; FAO 1981; Avery 1983; de Vries 1986). For the purpose of this discussion, however, forest inventory systems can be divided into two main groups based on the manner in which the samples are located in the field. The samples may be arranged in a systematic pattern at regular intervals throughout the forest. Or, conversely, the samples may be placed at random with every area of the forest having an equal probability of being represented. There are benefits and disadvantages to each of these sampling designs.

Sampling Methods

In systematic sampling, the sampling units are spaced at fixed intervals throughout the management area. The location of the first sampling unit is usually selected at random and all other samples positioned according to a strict pattern. The actual sampling units employed may be either fixed-width strips (transects) or plots of a square or circular configuration. The general layout of a systematic strip and plot sample is illustrated in figure 3.2. The square area shown is equivalent to a 100-hectare block of forest composed of three different forest types (I, II and III). The sample strips in figure 3.2(a) are 10 meters wide and 1,000 meters long. The interval between the strips is 300 meters, resulting in a total sample percentage of 3 percent.[5] As is indicated in this figure, it is preferable to orient the transects so that they bisect any topographic or drainage features at a right angle. Following this procedure, all soil types and environmental conditions from valley floor to ridge top are theoretically intersected to provide a more representative sample of the local vegetation.

The basic design of a systematic plot sample is shown in figure 3.2(b). As can be appreciated, the plots are uniformly spaced throughout the forest in a grid pattern along north-south and east-west compass bearings. The plots indicated in the figure are each 20 x 20 meter squares (400 square meters) arranged in 9 rows and columns (81 plots). The total sample area obtained by this design is 32,400 square meters (81 plots x 400 square meters per plot), resulting in sample intensity (3.24 percent) of similar magnitude to that of the transects. Given the even coverage provided by this design, the plots can be oriented without worrying about the topography or drainage of the site.

Figure 3.2 General Layout of Systematic Forest Inventory Design



Note: Square area shown equals 100 ha block composed of three different forest types. 1. Systematic strip sample. Strips are 10m wide, 1000m long and separated by 300m giving a total sample intensity of 3%. B. Systematic plot sample. Plots are 20 x 20 m (400 m^2) and arranged in nine rows and columns giving a total sample intensity of 3.24%.

Forest inventories based on systematic sampling present several distinct advantages relative to other designs. First, they provide a good estimate of population means and totals because the sample area is spread over the entire site. Second, they are faster and less expensive to conduct than designs based on probability sampling, because the location of sample units is based on fixed directional bearings and distances. Transect or plot location in the field, as well as the travel time between plots, therefore, is greatly facilitated. Third, because the entire site is traversed by field teams in a regular pattern, forest type information can be collected and easily mapped on the ground during inventory operations. Finally, systematic sampling does not require *a priori* knowledge of the total area of forest to be inventoried.

The major disadvantage of a systematic design is that there is no satisfactory way to estimate the precision or sampling error of the data collected. The fundamental reason for this is that statistical variance computations require a minimum of two randomly selected sample units (Husch, Miller, and Beers 1972; Grieg-Smith 1983). In systematic sampling, however, only the location of the first transect or plot is selected at random, the remaining sample units follow a predetermined and regular pattern. This would not be a problem if all of the trees within a tropical forest were distributed at random and exhibited no pattern of variation. Unfortunately, the individuals within a biological population are rarely, if ever, arranged independently of one another and there is a high degree of natural variability. It is, therefore, impossible in systematically collected data to separate the variability attributable to randomness from that naturally exhibited by the population. Although worthy of note, this limitation detracts very little from the overall utility of systematic sampling for management purposes. In practice, the lack of an estimable sample error means only that the inventory results from two different forests cannot be compared statistically.

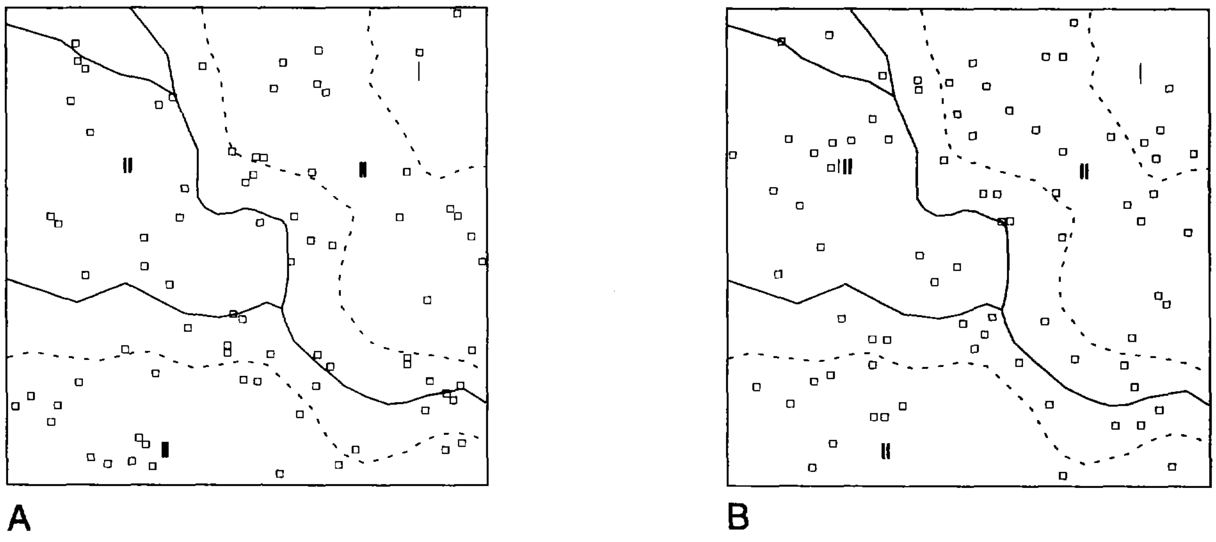
A random sampling design, on the other hand, provides not only mean and total values but also an estimate of the precision of these values. The calculation of the standard error of the mean (the standard deviation of the sample divided by the square root of the total number of sampling units) or confidence limits allows a statement to be made that, at any given probability level, the true value lies within a certain specified range (Greig-Smith 1983).[6] Two examples of different random inventory designs are illustrated in figure 3.3. As before, the total area shown is 100 hectares, there are 81 sample plots (each 20 x 20 meters), and the sample intensity is 3.24 percent. The first example, figure 3.3(a), represents simple random sampling, with all 81 plots randomly allocated throughout the site. A convenient method for determining the location of random plots is to place a transparent grid over the base map and to draw randomly generated pairs of Cartesian coordinates for each plot. After marking the location of all plots on the base map, compass bearing and distances from a central starting point are derived to describe their relative position in the field.

The example shown in figure 3.3(b) represents a stratified random sampling design. Although at first glance the pattern seems identical to that of simple random sampling, the important difference is that the plots have been "stratified" by forest type. The number of sampling units allocated to each forest type is determined by the percentage of the total area represented by each type, larger forest types containing a greater number of plots. Besides providing a more precise and efficient sample design, stratification also helps to avoid the uneven distribution or clumping of plots that frequently occurs with random sampling (Philip 1983; Adlard 1990). In figure 3.3(a), for example, a large area of type I forest remains unsampled. The same procedure used to locate plots for simple random sampling can also be used for stratified random sampling; random coordinates that place a plot within a forest type requiring no further sampling are simply rejected.

The clear advantage of a randomized system of forest inventory is its statistical rigor. Precise confidence limits can be assigned to all of the data, and given a knowledge of the inherent variability of the population being sampled, the exact number of sampling units required to obtain a given level of precision can also be calculated (see box 3.1). This calculation can save time and expense by indicating the minimal number of plots that need to be sampled to adequately describe the forest. There are, however, several disadvantages to a random sampling design. The plots can be exceedingly difficult to locate in the field, and much time is wasted traveling from one plot to the next. Furthermore, the random selection of plot location may leave significant areas of the forest unsampled. Perhaps the greatest limitation, however, is that random sampling does not allow the regular, grid-like observations necessary for detailed forest type mapping.

Notwithstanding the variety of different techniques available, the selection of an appropriate sampling scheme for a forest inventory ultimately depends on the capabilities and experience of local field workers, the conditions in the forest, and the personal preferences of the resource manager. Wood (1989) reports that out of thirty-six tropical countries surveyed, fixed-area plots have a higher frequency of use (44 percent) than transects (34 percent). Systematic sampling is the preferred design in Africa and Southeast Asia, while random sampling is more strongly favored in Latin America. Given the ease of field operations, the relatively low probability for errors in locating of the sample units, and the opportunity provided to map and refine the initial forest typology, systematic transects would seem to be the preferred inventory method for non-timber resources. Transect widths of either 10 or 20 meters are

Figure 3.3 General Layout of Random Forest Inventory Design



Note: Square area shown equals 100 ha block composed of three different forest types. All plots are 20 x 20m (400 m^2); plot location was based on random coordinates. 1. Simple random sample. Plots (N = 81) are allocated in a random fashion throughout the area. Note that forest type I (upper right corner of figure) is sampled by only two plots. 2. Stratified random sample. The number of plots allocated to each forest type based on the percentage of the total area represented by that type. Note that forest type I has been sampled with 5 plots.

recommendable in most situations, the smaller 10-meter transects being most appropriate in more homogeneous forests.

Two final aspects of inventory design that should be considered are the lower diameter limit of the trees to be measured and the overall sampling intensity. The minimum diameter limit for inclusion in an inventory defines the number of trees to be measured and can greatly influence the amount of time, effort and money invested in field operations. Most commercial forestry inventories in the tropics have employed a lower diameter limit of 40–60 centimeters diameter at breast height (DBH) (Heinsdijk and de Bastos 1965); a few more-recent surveys have used a cutoff point of 20 centimeters DBH (UNESCO 1978). These "industrial" standards, however, are clearly inappropriate for the assessment of non-timber resources. Many forest fruit trees, for example, are mid-canopy or understory species that may never reach these diameters. These resources would be completely missed by such an inventory.

Unfortunately, reducing the lower diameter limit of an inventory results in a drastic increase in the number of stems that have to be measured. This relationship is shown in figure 3.4 using data from a detailed 3.0 hectare forest inventory conducted at Rio Xingu in Brazilian Amazonia (Campbell and others 1986). The increase in the number of trees sampled is basically linear down to a diameter of about 20 centimeters DBH; further lowering of the diameter limit results in an exponential increase in the number of stems. This trend indicates an important trade-off. A smaller minimum diameter limit increases the amount of information obtained from an inventory, but it also increases the time and expense of fieldwork. Larger diameter cutoffs, on the other hand, facilitate field opera-

Box 3.1 Procedure for Achieving Desired Precision in Forest Inventories

Problem: To estimate the total number of sample units needed to achieve a standard error equal to 10 percent of the mean value using unrestricted random sampling.

Formula:

$$n = \frac{s^2}{D^2 x^2}$$

where,
n = the number of sample units
s^2 = the estimated population variance
D = the standard error to mean ratio
x = the estimated population mean value.

Solving this formula requires a pre-estimate of the mean and variance of the population to be inventoried. This estimate can be obtained by measuring a small preliminary sample of the population or by using the results from a previous inventory of the same forest. The first method is probably the most reliable as long as the expense of the preliminary sample can be justified. Given that the variance and mean of a statistical population are independent of the number of sample units used, both parameters can usually be estimated with a very small number of plots.

Data: From a preliminary sample of four 20 x 20 meter plots scattered randomly throughout a mixed dipterocarp forest in West Kalimantan, Indonesia, the following tree density estimates were obtained: 650 trees/ha, 900 trees/ha, 800 trees/ha, and 950 trees/ha. The mean (x) value calculated from these data = 825 trees/ha; the variance (s^2) = 17,500.

Calculation:

$$n = \frac{17.500}{(0.1)^2\,(825)^2}$$

$$n = \frac{17.500}{(0.01)\,(680.625)}$$

$n = 2.57$ sample units

Based on this result, a minimum sample of 2.5 plots per hectare, or operationally 5 plots every 2.0 hectares, will provide an estimate of the density of tree stems in this forest with a standard error of 10 percent of the actual mean value. Given that each plot covers 400 square meters, an overall sample intensity of approximately 10 percent is required to achieve this level of precision.

Note: These are the formulas and procedure for calculating the number of sample units required to achieve a given level of precision in random or stratified random forest inventories.
Source: Adapted from Philip 1983 and Avery and Burkhart 1983.

tions but may result in an unrepresentative sample of existing forest resources. As is advocated by Campbell (1989), a 10 centimeter limit is probably a good compromise in most situations. Whenever necessary, specific exceptions could be made to include acaulescent palms, lianas, or other small-stature forest resources of particular importance or value.

The overall sampling intensity required in a forest inventory is governed by the variation within the forest, allowable inventory costs, and the desired standard of precision (Avery 1983). Give unlimited time and money, all of the forest could be inventoried to give the ultimate degree of precision. This laborious procedure, in fact, is actually employed sometimes on small tracts of particularly valuable timber. Under most conditions, however, a 100 percent inventory is neither warranted nor economically feasible. The more typical situation is one in which the resource manager is forced by economic considerations to select the minimum sample intensity that will generate sufficiently reliable information about the forest. If a random inventory is planned, the formula outlined in box 3.1 can be used to calculate the exact number of plots needed to obtain a reasonable level of precision (for example, with a standard error of the estimate that is less than 5–10 percent of the mean). For systematic inventories, a more subjective process will have to be used to define the intensity of sampling. Although no hard and fast rules are available, sample percentages should probably not drop much below 3–5 percent of the total management area. Finally, it is also useful when using either systematic or random sampling to periodically construct a species-area curve from the data being collected in each forest type (McGuiness 1984). If this curve begins to approach an asymptote, there is a high probability that the current sample intensity is sufficient to encompass almost all of the species within the area.

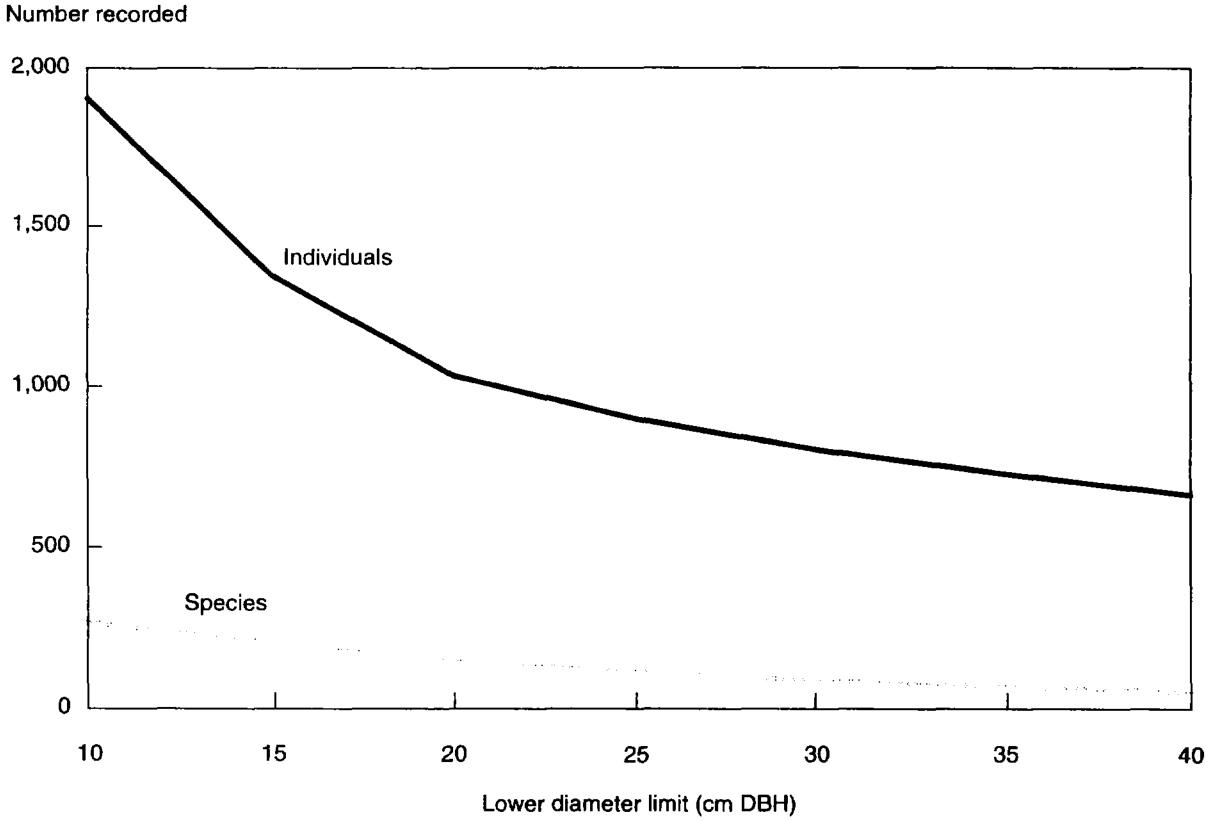
Field Procedures and Measurements

The location of all plots or transects should be clearly marked on the base map or aerial photographs, and exact bearings and distances to each sample unit should be calculated for use in the field. Referencing the starting point of the transect, or first plot, to some easily recognizable, permanent feature such as a river fork, road intersection, or large rock outcrop will greatly simplify the process of orientation. It can also help to minimize errors caused by incorrect placement of the sample units. Before starting the inventory, all of the field crews should be thoroughly briefed on the mechanics of locating, establishing, and measuring the transects or plots.

Individual crews comprised of three to four people are probably most effective for forest inventory work. One person should be solely occupied with running the compass line and stretching the meter tape; the other one or two field workers can lay out the plots or transects and identify and measure the sample trees. Ideally, one of these workers should be a trained botanist who is familiar with the local flora; another should be a local woodsman or *matero* who knows the common names and specific uses of the trees in the region. The final crew member, who can also serve as crew leader, is responsible for recording the data, separating the tallies by forest type, and doing the mapping. This person should be provided with clear, easily understandable tally sheets, a detailed, large-scale base map, and copies of all pertinent aerial photographs. The tally sheets should be formatted in such a manner that there are columns for the local name, scientific name, diameter and various uses of each sample tree. A separate column for miscellaneous observations (tree vigor, presence of flowers or fruits, resinous secretions, latex, and so forth) is also helpful. Every tally sheet should be labeled with the plot number (if appropriate), the date, and the names of all field personnel conducting the inventory. If sampling is based on transects, a different tally sheet should be used every 200–400 square meters, the exact linear distance along the transect of each sample block, as well as the transect number, being duly recorded on all the appropriate pages.

The field procedures on each plot or transect are essentially the same. After determining the precise location of each sample unit, its boundaries are first carefully measured with a meter tape.[7] If square plots are being used, it is a good idea to stake out the four corners and mark the perimeter with a rope, flagging or a plastic line. Although it is not

Figure 3.4 Relationship Between Lower Diameter Limit Used in Forest Inventorv and Total Number of Individuals and Species Recorded



Note: Data from a 3.0 ha inventory conducted at Rio Xingu, Brazilian Amazonia.
Source: Campbell *et al.*, 1986.

necessary to mark the entire boundary of a transect, the location of questionable border trees should always be checked with a tape. Once the borders have been established, all of the trees greater than or equal to the minimum diameter limit that have more than 50 percent of their trunk inside the sample unit are inventoried. Any trees located exactly on the boundary should be treated as alternating samples—the first border tree counted, the second tree not, and so on.

The first parameter to be determined for each sample tree is its taxonomic identity and local name. This can be quite a bit more difficult than it sounds. Although the field crew will probably be able to assign a local name to most sample trees, detailed botanical surveys based on the analysis of voucher specimens have shown that frequently a single vernacular name refers to several different taxa (Gentry 1988; Peters, unpublished data). The common practice of tallying trees exclusively by local name and then later consulting a list of scientific-vernacular name equivalents, therefore, is not recommended. Collecting herbarium specimens of each sample tree, on the other hand, is a laborious and time-consuming process that is difficult to justify during extensive forest inventories. Furthermore, unless the inventory was conducted during a period of peak flowering and fruiting, it is doubtful that the fertile specimens needed for positive taxonomic identification could even be obtained from very many tree species. A compromise between taxonomic rigor and the operational realities of forest inventory work is clearly needed. One potential solution might be to limit the collection of herbarium specimens to only the most abundant or economically important plant resources, but to record copious notes on bark, leaves, exudate, and form for all trees of questionable identity.

The second parameter to be recorded for each tree is ethnobotanical or use information. This information should be as detailed and specific as possible and should not be restricted to the primary or current commercial use of the resource. For example, perhaps the seeds of a tree contain a valuable oil and the bark is used medicinally. How exactly is the tonic prepared from the bark and for what illnesses is it employed? Does the species appear to regenerate its bark after harvesting? Is the fruit used in any manner? The answers to such questions provide an estimate of the overall resource "richness" of the forest and will later serve as baseline criteria for selecting the specific resources to be managed. Given the obvious utility of this data, it is somewhat surprising that ethnobotanical analyses have only recently become a component of quantitative forest inventory (see Prance 1972; Prance and others 1987; Balée 1986, 1987; Pinedo-Vazquez and others 1990).

The third and final parameter to be recorded is tree size. The most common and easily measured expression of this is diameter at breast height (approximately 1.4 meters above the ground). All measurements should be made with a diameter tape and care should be taken to insure that the tape is maintained level, pulled taut and not twisted or looped around a liana or epiphyte root. Cleaning every bole of debris prior to measurement is a good standard procedure to minimize errors. In cases where extreme buttress formation, wounds or forked boles preclude the measurement of DBH, a section of clear trunk immediately above the problem area should be measured and a note to this effect included in the observations column of the tally sheet. Unlike commercial forestry inventories in which the volume of wood or number of logs per tree is a critical variable, the measurement of tree height is not essential in an inventory of non-timber forest products. This time-consuming procedure would only be justified for selected vegetative tissues of extreme commercial value such as rattan. Additional measurements apart from tree diameter may be necessary depending on the nature of the resource being sampled. Bark thickness, for example, would be a useful measurement for medang trees (*Litsea* spp.), and increment cores could be extracted to check for the presence of gharu wood in *Aquilaria* trees (see box 2.1).

When moving between plots or along the transect, the crew chief should watch for notable changes in floristic composition, forest structure, or tree stature that may indicate a transition between forest types. The exact location of this transition should be pinpointed using the measured transect length or the distance traveled between plots and then compared to the preliminary forest type boundaries delineated on the base map. Any inconsistencies or additions should be noted on the map. A similar procedure should be used to locate the position of all rivers, streams, roads, and trails crossed during the inventory. In case there is ever a need to reinventory the site, all transect lines and plots should be permanently marked with paint or brightly colored tags to facilitate finding them again.

Although necessarily brief, the preceding discussion has touched on some of the major problem areas encountered in the planning and execution of quantitative forest inventories. However, beyond the general advice to always double-check the location and boundaries of the sample unit, to make meticulous measurements, to be sure before assigning a name to a tree, and to write down all observations, there is really no single "recipe" for successful inventory work. The final precision of the sample will ultimately depend on the field crews and the conditions within the forest.[8]

Data Analysis

The data collected during the inventory can be analyzed on several different levels. The first phase in this process is to define the final forest typology, and to this end a general meeting of all of the field personnel should be called to review the base map and aerial photographs of the site. The input of new observations and corrections made in the field will inevitably modify the initial typology and, in most cases, will require the creation of new forest type categories or the subdivision of existing types. A new base map should be drawn using this final classification system.

Once the typology is completed, the plot or transect tally sheets should be grouped by forest type and phytosociological analyses performed on each data set. The objective of these analyses is to describe the floristic composition (or resource abundance) of each forest type and to determine the relative dominance or importance of each species within the forest community. The overall ecological importance of a species depends on more than just its numerical abundance. A species with high abundance (a large number of stems) may in fact be less important than a species with fewer individuals if the latter trees are of greater size or more even distribution. To account for these factors, a derived index known as "importance value" (*sensu* Cain and Castro 1959) is frequently used in ecological studies to rank species. This index is based on relativized density, frequency and basal area (square meters) values taken from the plot or transect tallies. The calculation of this index is shown in box 3.2 using plot data collected in Peruvian Amazonia. In a very general sense, the higher the importance value of a species, the more successful it is in that particular habitat. Floristic lists showing the density, basal area, and importance value of each species and resource should be compiled for each forest type. These data provide a quantitative description of each forest type, and they will later be used to select the species with the highest management potential. They will also form the basis for locating and delineating specific production units within the management area.[9]

After collecting inventory data on forest communities, the analysis shifts to a population-level focus. With the transect or plot results still sorted into forest type groups, the number of individuals per diameter class (DBH) should be recorded for different species. As it is unnecessary to inventory all the tree species, a preliminary selection of the most abundant or potentially important plant resources in each forest type should be made. Each of the species selected should be represented by at least fifteen individuals (Bongers and others 1988). A standardized size-class interval of either 5 or 10 centimeters DBH can be employed depending on the species and range of diameters encountered. The tallies for each species should then be compiled into size-structure histograms showing the $\log_{10}$ number of individuals plotted against diameter class. As was discussed in chapter 1, these histograms will typically be one of three different types; species or resources exhibiting similar size-class distributions should be grouped and indexed according to the forest types within which they occur.

Selection of Species and Resources

The final selection of the particular resource to be managed undoubtedly will be based largely on economic criteria. Those resources possessing the highest current market price, or the greatest potential for future market expansion, will obviously be the most desired. Social factors can also come into play here. Some forest resources, for example, may have a long history of extraction and traditional use in the region, and there may be a

Box 3.2 Calculation of Importance Value Index

Problem: To rank the different species recorded during a forest inventory in terms of their ecological importance within the community.

Data: The following density, frequency and basal area data were compiled by sampling twenty-five 20 × 20 meter plots (total area = 1.0 hectares) located within a lowland tropical forest of Peruvian Amazonia. Frequency values represent the total number of plots within which a species was encountered; basal area is equal to the cross-sectional area of the trunk at DBH expressed in square meters.

	Density		*Basal Area*
Species No.	*(Trees/ha)*	*Frequency*	*m^2/ha*
1	106	24	1.45
2	71	21	1.80
3	31	17	4.75
4	73	24	1.20
5	21	13	4.31
.	.	.	.
.	.	.	.
.	.	.	.
160	1	1	0.01
Total	868	481	55.82

Procedure: The density and basal area of each species are relativized by dividing them by the total value of each parameter (summed over all species). The total frequency value is equal to the total number of plots within which all species appeared. As shown below, summing the relative density, relative frequency, and relative basal area of a species and then multiplying this result by 100 yields the importance value (IV).

Species No.	*Rel Density*	*Rel. Frequency*	*Rel. Basal Area*	*IV*
1	0.122	0.050	0.0259	19.79
2	0.082	0.044	0.0322	15.82
3	0.036	0.035	0.0851	15.61
4	0.084	0.051	0.0215	15.55
5	0.024	0.027	0.0772	12.82
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.
160	0.001	0.002	0.0002	0.32

strong cultural bias toward continuing to exploit these resources. Conversely, other resources such as medicinals or plants of ceremonial importance may be subject to certain taboos that prohibit commercial exploitation.

In addition to economic and social factors, however, a third set of criteria should also be considered: the overall ecological potential of the resource to be managed on a sustained-yield basis. Because of their reproductive biology, regeneration and growth strategies, or population structure, some species are inherently better able to withstand the continual perturbations caused by resource extraction. This fact seems to have been overlooked by many resource managers. Although the importance of economic and social factors cannot be denied, the low success rate of non-timber forest resource extraction in the tropics suggests that greater attention to ecology is needed during the selection process.

Four basic pieces of information are needed to select a species for exploitation: life cycle characteristics, multiplicity of uses and types of resources produced, abundance in different forest types, and size-class distribution of populations. For simplicity, different expressions of these ecological parameters have been summarized in table 3.1 and ranked according to their management potential. The main categories and subdivisions in this table have been synthesized from the topics discussed in chapters 1 and 2. There are admittedly a variety of combinations and intermediate stages of the three possibilities listed (for example, some species may use both biotic and abiotic seed dispersal, populations of the same species may exhibit a type I size-class structure in some habitats and a type III in others, and some individuals within a single population may be annual fruiters while others are unpredictable in their phenology). These shortcomings notwithstanding, the information shown in table 3.1 is provided as an ecological framework for comparing different forest resources that have been preselected using economic and social criteria.

The life cycle characteristics of a species can either facilitate or severely complicate management operations. The unpredictably fruiting dioecious species serviced by specialized animal vectors for pollination and seed dispersal probably are the most difficult to manage. An optimal proportion of female to male trees must be maintained within the population, only about half of the individuals will produce fruit, and the obligate plant-animal interactions exhibited by these species increase their susceptibility to pollinator or disperser shortages. Conversely, an annually fruiting hermaphroditic species pollinated by a common, generalist vector such as small insects or bees is much easier to work with. In terms of regeneration guilds, primary forest species adapted for growth and regeneration under a closed canopy will, in most cases, be preferable over fast-growing, early pioneers that require large canopy gaps.

The type of resources produced by particular species can also have a major influence on its potential for sustainable exploitation and management. The harvest of bark, stem tissue, and roots almost invariably kill the individual, and as is the case with logging, sustainability can only be achieved by insuring that the death of every adult tree is replaced by growth of another conspecific. Unfortunately, maintaining the continual recruitment of a desirable species when the seed-producers in the population are being routinely eliminated can be an extremely difficult and expensive proposition. The harvest of latexs, fruits, oil seeds and leaf tissues, on the other hand, do not necessarily kill the adult tree or alter the initial size-class distribution of the population, and although this harvesting has ecological impacts (see chapter 2), avoiding or correcting them is not so difficult as in other types of resource exploitation. Finally, there are certain benefits afforded by the exploitation and management of multipurpose trees such as certain species of *Shorea* in Southeast Asia that produce both oil seeds and a valuable oleo-resin or numerous palm species in Amazonia that produce edible fruit and also leaves that are useful for cordage or thatch. Management activities focusing on a single multiple-use species can generate two sources of revenue without the expense of monitoring the regeneration and population dynamics of two separate plant populations. It is important, however, that the physiological trade-offs of multiple resource harvesting from a single tree be assessed before beginning such a program. Tapping oleo-resin or cutting leaves will

Table 3.1 Management Potential of Various Non-Timber Forest Resources

	Management Potential		
Indicator	*Low*	*Medium*	*High*
Resource Group:	Bark, stem tissue, and roots	Some resins, fruits, and seeds	Latex, fruits, and leaf tissue
Yield/tree:	Low	Medium	High
Species Characteristics:			
Flowers	Few, large	Intermediate	Small, many
Fruits	Few, large; single-seeded	Intermediate	Small, many; multi-seeded
Seed germination	Recalcitrant; low viability	Intermediate	Orthodox; high viability
Sprouting capability	None	Low	High
Population Structure:			
Size-class distribution	Type III curve	Type II curve	Type I curve
Tree density/hectare	0–5 adults	5–10 adults	10+ adults
Tree frequency	Low	Medium	High
Community Dominance:			
Relative Importance Value	Low	Medium	High
Regeneration Guild:	Early Pioneer	Late Secondary	Primary
Flower/Fruit Phonology:	Unpredictable	Supra-annual	Annual
Reproductive Biology:			
Pollination	Biotic, with specific vector	Biotic, with generalist vector	Abiotic
Pollinator Abundance	Rare (bats and hummingbirds)	Intermediate (beetles and moths)	Common (small insects)
Breeding System	Dioecious	Monoecious	Hermaphrodictic
Outcrossing	Obligate	Intermediate	Facultative
Seed Dispersal	Biotic, with specialized vector	Biotic, with generalist vector	Abiotic
Disperser Abundance	Rare (large birds and mammals)	Intermediate (small mammals)	Common (bats and small birds)

Note: The overall managment potential of the various non-timber forest resources is based on their botanical characteristics, life cycle, productivity and population structure.

undoubtedly have some effect on the production of fruit by individual trees.

A third key criteria for species selection is the current density and distribution of resources within the management area. Abundant species that are obviously regenerating themselves in the forest are considerably easier to manage than low-density, scattered populations. High-density populations will also produce a greater resource yield per unit area, are less susceptible to overexploitation, and require a shorter travel time between conspecific trees during harvest operations. The forest type(s) within which a species occurs must also be considered. A resource may be extremely abundant in one forest type and completely absent in others. If this particular type of forest occupies only a very small percentage of the total area, the yield per unit management cost from the resource is likely to be quite low. Furthermore, given the apparent habitat specificity of the species, the potential for increasing its distribution within other areas of the forest is probably very limited. To more fully account for the relative density and distribution of different resources, the importance value indices derived from the inventory data should be used as ranking parameters during the selection process.

Even more important than the overall abundance of a plant resource, however, is the size-class distribution of individuals within existing populations. A species may be the most abundant in the forest in terms of number of stems, but if all of these stems are of a similar intermediate diameter class or if the population is characterized by a preponderance of large adult trees and exhibits no regeneration, sustainable resource exploitation can still be exceedingly difficult to achieve. As was discussed in chapter 1, tree species with type II and type III size-class structures are characterized by discontinuous population recruitment, seedling establishment usually being keyed to the occurrence of canopy gaps of varying size. The management of these resources will therefore require that gaps of the appropriate size and location be maintained continually in the forest, that an adequate quantity of seedlings already exists in the understory, and that these seedlings are physiologically able to outcompete every other species that tries to colonize the gap environment. This is quite a bit more complex than working with species that are adapted for regeneration and growth under a closed canopy. The major requirement for managing populations with a type I size-class distribution is that the abiotic (irradiance levels, moisture and nutrient regimes) and biotic (seedling densities, pollinator and disperser populations) environment be maintained as closely as possible to that found in undisturbed forest.

Relative to other forest resources, the exploitation of species with type I population structures presents several advantages. Initial management costs are lower because the population already displays an adequate level of regeneration and no preharvest treatment is required. In most cases, harvest controls and monitoring are all that are needed to insure the sustainable exploitation of these species. Additionally, the fact that population recruitment does not depend on the creation of large canopy gaps means that very little tree felling is required. Forest structure is preserved intact, nutrient and hydrological cycles remain essentially unaltered, and pollinator and disperser populations within the forest are little disturbed. In essence, the controlled exploitation of non-timber forest resources possessing a type I population structure represents a unique opportunity to truly integrate the use and conservation of tropical forests. If at all compatible with the economic and social criteria employed, the selection of species with this type of population structure is strongly recommended.

Yield Studies

The fourth step in the management process involves the measurement of productivity. Given an understanding of the density and size-class distribution of selected plant populations, the resource manager must inevitably address the question of "how much of the desired product do these populations actually produce?" Foresters routinely collect this type of information by monitoring the radial increment of timber trees, and there is a large and detailed literature on the growth and yield characteristics of commercial timber species (for a good overview of this research, see UNESCO 1978; Alder 1980; Razali, Chan, and Appanah 1989; and Adlard 1990). Unfortunately, the situation is quite different for non-timber forest resources. Virtually nothing is known about the fruit, oil seed, latex or resin yield of tropical forest trees, even for the most valuable and widely exploited market species. For example, how much rattan does wild *Calamus* produce every year? How many illipe nuts are produced by a *Shorea* tree growing in the upper canopy of a mixed dipterocarp forest? What is the rubber yield from a large *Hevea* tree in the lowland forests of Amazonia? To date, these questions remain essentially unanswered.[10]

Yield studies are a prerequisite to economic planning and forest valuation. They are also the key to defining a sustainable level of resource extraction. Just as foresters use growth data to avoid cutting timber at a faster rate than that at which it is produced by the forest, the sustained-yield management of non-timber resources also requires a knowledge of the productive capacity of the species being exploited. That this knowledge is frequently lacking sheds some doubt on the long-term viability of many current efforts to promote the increased utilization of non-timber resources. The systematic collection of production data is unquestionably one of the most important, yet routinely ignored, of all forest management activities.

Selection of Sample Trees

The basic objective of a yield study is to provide a reasonable estimate of the quantity of resource produced by a given species growing in a particular habitat. As it is rarely feasible, or even warranted, to monitor all of the individuals of a selected species, data collection will necessarily be focused on a subsample of trees. If at all possible, the selection of these sample trees should be stratified by two main variables—diameter, or some other size parameter, and site condition. There are several good reasons for conducting a stratified sample of this type. Regardless of the type of resource, tree size exerts a major influence on yield and larger trees are usually more productive than smaller ones due to their improved canopy position, increased leaf area and root mass, and greater availability of internal resources. The real parameter of interest, therefore, is not simply mean production, but rather the size-specific production rate of a particular species. As will be shown later in this section, the exact nature of the statistical relationship between tree size and yield is an important tool for deriving an estimate of total population productivity. Although diameter (DBH) is the most convenient expression of tree size to measure, for some species (rattans, shrubs, or herbaceous plants of value, for instance) other measurements such as basal diameter or height to apical bud should be employed.

The productivity of forest trees will also vary with respect to certain site characteristics. Even after accounting for the effect of size, most species will probably exhibit a higher yield in some habitats than others, and the resource manager should try to identify these habitats. As a first approximation, population density within a given forest type is a useful second parameter for stratifying the sample trees. Depending on the range of different densities encountered, the individuals selected for measurements could, for example, be grouped into high, medium and low density classes. Other site parameters that potentially could affect tree yields are soil depth and fertility, soil moisture, relative slope, canopy cover, and the total basal area of associated or competitor tree species. Although any of these variables would be appropriate for stratifying the sample trees, it should be noted that the population density and basal area data for each forest type are readily available from the inventory of the area. The use of soils, slope or canopy cover criteria would require additional fieldwork and expense.

There are no hard and fast rules to determine the number of sample trees that should be selected from each species. This decision will ultimately be determined by the relative abundance of each species in different forest types, the size-class distribution of the population and the number of individuals available in each class, and the overall time and expense involved in conducting the yield studies. Obviously, the greater the number of individuals that can be sampled, the higher the precision of the measurement. Using the sorted results from the inventory as a guide, individuals from different diameter classes and forest types should be selected at random. If possible, the number of sample trees selected from each diameter class should be the same in each forest type, habitat or density class. Ideally, every diameter class should be represented by at least three individuals so that some index of variability (such as standard error) can be calculated. Diameter classes can sometimes be lumped together to achieve this objective if fewer than three individuals per class are available. To ensure a reasonable level of precision, the total number of samples selected per habitat class should fall within the range of 25–30 trees (5–6 trees in each of five size-classes).

After selecting the sample trees to be measured in each forest type, these individuals should be located in the field, permanently labelled with paint or highly visible tags, and their diameters checked to make sure that they conform with those indicated on the field sheets.[11] The location of these trees should also be plotted as accurately as possible on the base map of the area. If sufficient time and funding are available, additional information such as tree height, crown area, canopy cover, and distance to and basal area of nearest-neighbor trees can also be collected at this time. These data can later be grouped into classes and compared statistically to provide a more detailed and rigorous analysis of size-specific productivity.

Methodology and Data Collection

The exact sampling procedures used in the yield studies will necessarily vary with the type of resource being measured. For ease of discussion, these resources can be divided into three main groups based on the origin of the plant tissue or compound of value: reproductive propagules, plant exudates, and vegetative tissues (see box 2.1). Although fruit, nuts and oil seeds are different commodities, their production by individual trees can be measured using a similar methodology.

Reproductive Propagules. The production of these resources is measured at discrete intervals throughout the fruiting season using either direct counts or a random sample of the area under the crown of adult trees. For small trees that produce few fruits of large size (for instance, certain palms and cauliflorous trees) direct counts can be employed with reasonable precision. To avoid errors caused by counting the same fruit twice, the fruits recorded during each sampling period should be marked with a small spot of paint or harvested. If nuts or seeds are actually the resource of interest and the fruits are multi-seeded, a large number of mature fruits should be opened (N = 50 to 100) and the seeds counted to determine the average number of seeds per fruit. Direct counts can also be used with species that produce multiple fruits in racemes or infructescences by harvesting these structures when mature and carefully counting the fruits. An alternative strategy is to first record the total number of infructescences produced by the tree and then to harvest a small subsample for counting individual fruits. Given the ease of direct counts, it is tempting to use this procedure on large-fruited canopy trees by scanning the crown with binoculars. This technique, however, should be avoided as there is no way to mark the fruits that have already been counted, and it is extremely difficult to survey the entire crown of a large tree without some degree of overlap or repetition.[12]

Tall forest trees that produce more fruit than can be counted individually must be sampled using small plots or specially constructed fruit traps. A critical assumption involved in using this method is that a large percentage of the fruits will fall directly under the crown of the adult tree. For most commercial fruits, nuts and oil seeds, that are relatively large and heavy, this assumption is probably valid. However, sampling under the crown of a tree will not account for the fruits and seeds that are eaten or dispersed by animals, and the data collected will not represent the total number of fruits produced. Notwithstanding this limitation, the use of fruit traps or plots does provide a reasonable estimate of "harvestable" yield, which is actually a more important and useful measurement for management.

The first step in this process is to determine the exact area in the vertical projection of the crown of each sample tree. This is accomplished by measuring out from the trunk of each tree to the outermost branches of the crown along at least four radii. Based on these measurements, the vertical projection of the crown is sketched on graph paper and its area calculated using the appropriate formula for that configuration (for example, circle or ellipse). A stratified random design is then used to allocate the sample plots or traps within this area. The crown area is divided into four quadrants of similar area, the boundaries of these quadrants being determined by four perpendicular radii extending out from the trunk. Random coordinates are then chosen to position the samples within each quadrant. The reason for this stratification is that fruits rarely fall in a symmetrical pattern under a tree: prevailing winds and the position of fruit-laden branches usually cause more fruits to fall on one side of the crown than the other. Dividing the crown projection into four areas ensures that regions of both high and low fruit density are sampled.

There are two different options for determining the number of sample plots or traps to be used under each tree. A constant percentage of the crown area can be sampled (Howe 1980; Howe and Vande Kerckhove 1981) or, alternatively, a constant number of traps can be used irrespective of crown area (Howe 1977; Peters 1990b, 1992; Peters and Hammond 1990). The former method requires that a greater number of samples be located under large trees than small ones, and certain statistical tests may be complicated because of the unequal sample sizes (Sokal and Rohlf 1981). The latter method samples smaller trees more intensively than large ones. If a fixed sampling percentage is desired, a sufficient number of traps should be used to sample about 10 percent of the total crown area. If a constant number of sample units is desired, a total of 12–16 traps or plots (3–4 per quadrant) should be used under each tree.

Although fruit traps may have a slight advantage over plots in that propagules cannot roll out of the sample unit, the ultimate decision about which to use will be based largely on the time and funds available. In some cases, however, fruit size can also be an important consideration.[13] The most common plot size employed in fruit production studies is a 1 x 1 meter square. After being located under the tree, the plots should be numbered sequentially, the corners staked, and the boundaries clearly marked with plastic string or flagging. Fruit traps can be either 0.5 square meters or 1.0 square meters and square or round in shape; the smaller traps are somewhat more stable and easier to transport to the field. Square traps are constructed by first making a box frame out of 1 x 4 centimeters wooden battens and then stretching a piece of 2 millimeter nylon netting tightly over the bottom and affixing it with tacks or staples. Circular traps can be made out of either stiff wire or plastic tubing. A 79.8 centimeter diameter circle has an area of 0.5 square meters; a 112.8 centimeter diameter circle provides a 1 square meter sample area. Nylon screening is used to make a loose, concave net (approximately 30 centimeters deep) that is tied or clipped to the circular frame. Both square and circular fruit traps should be elevated about 50 centimeters off the ground using wooden stakes treated with preservative.

Fallen fruits start to decompose quite rapidly, and there is also the possibility that some will be eaten by animals between sampling periods. This can even be a problem with traps, which are easily climbed by squirrels and other forest rodents. To avoid these potential sources of error, the traps or plots should be reviewed as frequently as possible, preferably at biweekly intervals. At each sampling period, the number of immature and mature fruits in each plot or trap should be carefully counted and recorded; screens, stakes, and plot boundaries should also be checked at this time and repaired if necessary. The results from each plot should be tallied separately. Biweekly sampling of each tree should be continued until at least two consecutive fruit counts give null results.

Plant Exudates. The measurement of plant exudate yield requires some *a priori* knowledge of the traditional tapping techniques used with a particular species. Of special importance is information concerning the frequency with which the trees are usually tapped. Through a continual process of trial and error over the years, experienced collectors have undoubtedly determined the tapping method and harvest schedule that produces the greatest amount of latex, resin or gum. The objective here is to actually quantify this yield. Perhaps the easiest way to obtain these data is by careful participant observation: that is, hire an experienced local assistant and follow him around as he taps the sample trees. The exudate obtained from each tree is measured (by weight or liquid volume depending on the resource) and recorded in the field, and with the help of the local assistant, an initial estimate is made of the frequency with which the tree can be tapped. Several sequential tappings should be measured to obtain some idea of the variability in yield, as well as to observe the tree's response to the damage caused by harvesting. Based on the particular tapping regime employed, daily, weekly, or monthly production rates are then calculated for each sample tree and exudate type under study.

Vegetative Tissues. The variety of different vegetative structures exploited from tropical forests (stems, leaves, bark, roots, and apical buds) can be divided into two groups based on the physiological response of a plant species to harvesting: the species regenerates the tissue extracted or is killed by harvesting. The former group includes leaves, bark, and apical buds of certain species; the latter group includes most types of stem tissue, roots and bark. Different sampling methodologies are required to estimate the productivity of these two groups.

For species that exhibit regrowth or sprouting, the basic idea is to first quantify the existing stock of harvestable resource and then to monitor the rate at which these resources are replenished by the tree. The periodic collection of palm leaves provides a useful example to illustrate this concept. Working together with experienced collectors, the average number of leaves harvested from the crown of each sample tree is recorded together with data on the total number of leaves per crown. The residual leaves on each tree should be marked with paint or tags to differentiate them from the new leaves that are later produced. After allowing an adequate period of time for the new leaves to fully elongate, the tree is re-harvested and leaf numbers are again determined. This procedure should be followed through at least two cycles of harvest and new leaf production to get some idea of whether leaf production decreases in response to repeated harvested. The mean yield figure for each tree represents the total number of new leaves harvested throughout the sample period. The final result should be adjusted to a yearly production rate.

Given the type of "hidden" resources usually involved, the procedure for collecting yield data for species that are killed by harvesting is a bit more complicated. Measuring root growth, the production of bark tissue (as separate from stem growth) or the spread of fungal tissue within the heartwood of a gharu tree (*Aquilaria* spp.) are plagued with methodological difficulties.[14] To avoid these problems, a two-step sampling scheme involving allometric analyses and growth studies is recommended. During the first phase of this process, the preselected sample plants are felled, dissected, and carefully measured to obtain an estimate of the size-specific bark, heartwood or root volume for that species. Regression analyses are then used to derive a predictive equation relating plant size to the quantity of resource present. The slope of this line can eventually be used to predict yield.

The problem, however, is that there is, as yet, no time dimension or rate associated with this production. What is lacking is information about the rate at which these plants grow from one size class to the next. To collect this information, a second subsample of plants representing a range of different sizes and habitats is selected and their growth monitored periodically for at least a year. Diameter (DBH) growth is probably the best parameter to measure for most species. Combining the two data sets provides a reasonable estimate of the productivity of these resources. For example, if the root biomass of a 20 centimeters DBH tree is 3.0 kilograms and the root biomass of a 25 centimeters DBH tree is 3.5 kilograms, a 20 centimeters DBH tree growing at 0.5 centimeters per year would produce approximately 50 grams of root tissue a year. If necessary, the order of the allometric and growth studies can be reversed, the growth studies being conducted first and these same sample trees later being harvested and analyzed. This strategy, which requires only one group of sample trees, may be warranted for species represented by a relatively small number of individuals.

Solitary rattans are a final and especially difficult subject for yield studies. In many respects, the harvest of these resources is identical to logging in that entire stems are removed and there is no re-sprouting. The problem is that there is no easily measurable indicator of growth, such as diameter (DBH), as is used by foresters to estimate productivity. Rattan, like all palms, has no secondary meristems and exhibits no radial growth. It produces new stem tissue (cane) solely by extension growth. For small and intermediate-sized individuals, height growth can be measured directly to obtain an estimate of cane yield. Measuring the height increment of the larger, more valuable canes, some of which may be 40–50 meters long, however, is an extremely challenging exercise that requires tree climbing.

There is no easy solution to this problem. Basing yield figures solely on the extension rate of smaller, and undoubtedly faster-growing, individuals will lead to an overestimate of productivity. Periodic controlled harvests can be used to estimate growing stock, but this procedure ignores the critical issue of size-specific yield. Perhaps the only recommendation that can be made is to attempt the measurement of at least a few large-sized canes. To achieve this objective, tree-climbing must be used to locate the apical bud or growing point of the individual in question. A point on the stem immediately behind the bud should then be permanently marked with paint and tied with flagging to facilitate re-location. After a period of six to twelve months, the climber should enter the canopy again and measure the distance from the paint mark to the end of the apical bud. The average growth rate taken from several stems could then be applied to all large-sized, canopy individuals.

Estimating Total Population Productivity

The results from the fieldwork described thus far can be integrated to estimate the total quantity of harvestable resource produced by different plant populations within the management area. Two pieces of information are needed for this analysis: size-specific production data (described in the previous section), and the size-class distribution of the populations in question (obtained from the inventory data). Although the following discussion contains examples specifically related to fruits, the basic procedure for estimating population yield is essentially the same for all types of non-timber forest resources,

The size-specific production data collected in the yield studies are first grouped by habitat or site class, and then regression analyses are performed to derive a predictive equation describing the relationship between plant size and productivity. In some cases, the functional relationship between these two variables will not be linear and the data may require some type of transformation (conversion to logarithms, for example) before they are analyzed. It is also possible that after inspection the data could be best described using curvilinear or polynomial regression techniques.[15] Whatever degree of analysis is used, however, the objective is to produce a result that is both biologically meaningful and statistically significant. Two examples of the form that this relationship might take are shown in figure 3.5. The data were collected in yield studies of natural populations of fruit trees growing in the lowland forests of Peruvian Amazonia (Peters and Hammond 1990).

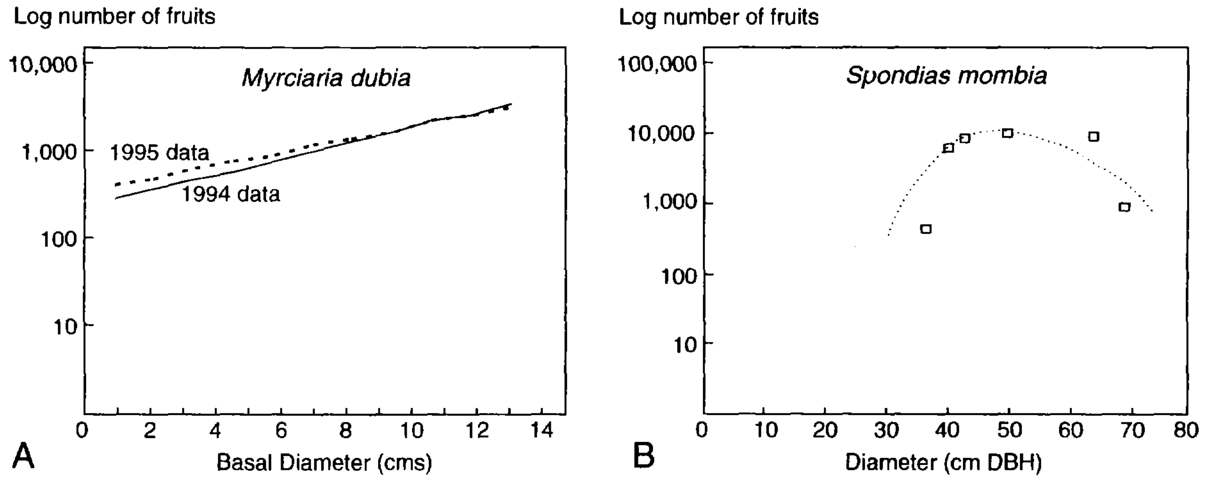
In the case of *Myrciaria dubia*, a small riparian shrub, an increase in basal diameter results in an exponential increase in the number of fruits produced (figure 3.5(a). A similar pattern of fecundity has been reported for other tropical trees (Melampy and Howe 1977; Hubbell 1980; Bullock and Bawa 1981; Peters 1989, 1990a). The regression lines for the 1984 and 1985 fruiting seasons appear linear because the fruit production data is graphed on logarithmic scale. The high coefficient of determination calculated for each line (1984 data $r^2 = 0.97$, P 0.01; 1985 data $r^2 = 0.99$, P 0.001) suggests that there is a strong predictive relationship between size and fruit production for *M. dubia*, although the exact nature of this relationship may vary somewhat from year to year.

The curve for *S. mombin* shown in figure 3.5(b) illustrates a completely different pattern. Annual fruit production by this upper canopy tree seems to increase exponentially up to a diameter of about 50 centimeters DBH and then stabilize at a rate of approximately 30,000 fruits per year. Further increases in diameter have little effect on fruit production up to about 65 centimeters DBH; beyond this size production begins to decrease notably. This reduction in reproductive activity may represent the onset of senescence as was reported by Enright and Ogden (1979) for *Araucaria cunninghami* in Papua New Guinea, or may simply reflect the natural variability inherent in such a small sample size (N = 6 trees). In any case, it is clear that the production of fruits by *S. mombin* is not a linear function of size. In response to this pattern, polynomial regression was used to fit a curve through the data points. A cubic function gave results of sufficiently high significance (r^2=0.94, P 0.01) to allow the use of diameter as a predictor variable.

The final equations obtained from the yield studies are used to estimate the collective productivity of each of the appropriate size classes (those containing individuals of reproductive or merchantable size) within the population of interest. These estimates are calculated by substituting the midpoint of each size class as the dependent or "y" variable in the yield equation. The average yield value for each class is then multiplied by the actual number of individuals within that class taken from the inventory data) to obtain a class total. Summing these totals over all size classes provides an estimate of total population yield. Care should be taken to include only productive trees in these calculations—for instance, the male trees of dioecious species should obviously be omitted from an analysis of fruit production.

To illustrate this procedure, inventory and fruit production data for a 1.0 hectare population of *M. dubia* are presented in table 3.2. The specific yield estimates for each size class were calculated using the regression equations reported in figure 3.5(a). As the table shows, total population fruit yield is a function of both tree density and individual fecundity. The least productive individuals in the population (2.1–3.0 centimeters size-class) account for over 40 percent of the total population fruit yield because of their great abundance. The largest and most fecund individuals, on the other hand, are represented by only ten trees per hectare and produce only 2 percent of the total quantity of fruit. This pattern, which is probably common for many populations and types of resources, has significant implications for management. Enhancing the continual recruitment of individuals into the smaller size classes will have a much greater effect on future yields of non-timber resources than trying to increase the productivity of large adult trees through intensive silvicultural treatment such as liberation thinning or weeding.

Figure 3.5 Fruit Production as Related to Tree Diameter for *Myrciaria dubia* and *Spondias mombim*



Note: Production data are shown on log scale for both species. A. Regression line for *M. dubia* based on general linear model, i.e. log fruit production = a + b (diameter); parameter values and coefficient of determination are as follows: 1984 data, $a = 2.17$, $b = 0.11$, $r^2 = 0.97$, $P < 0.01$; 1985 data, $a = 2.38$, $b = 0.09$, $r^2 = 0.99$, $P < 0.001$. B. Regression line for *S. mombin* fitted using a cubic polynomial; parameter values and coefficient of determination are: $a = -89095.57$, $b = 2150.05$, $c = 33.67$, $d = -8.65$, $r^2 = 0.94$, $P < 0.01$.

Source: Peters and Hammond 1990.

Delineation of Production Areas

Assuming that the yield studies were, in fact, stratified by forest type or habitat class, the estimates of total population productivity obtained from different sites can be used to subdivide the management area into distinct production units.[16] The selection of these areas should be based on *a posteriori* statistical comparisons of the density and yield data both between habitats (for a single species) and between species within a single habitat. A relatively easy and effective method for accomplishing this task is to compare the slopes of the regression lines fitted to the size-specific production data and then to rank them in descending order. Significant differences between regression coefficients can then be calculated using the GT-2 or Tukey-Kramer methods (Sokal and Rohlf 1981). Simple analysis of variance (ANOVA) can be used to test for habitat differences in the mean density of a single species; nested ANOVA can be used to compare the density response of different species across habitat classes.

The basic reason for these analyses is to factor out those species, or combination of species, that are the most productive in a particular habitat or forest type. It makes little sense to invest time, energy and expense in trying to manage a low-density or marginally yielding resource when a more abundant or high-yielding product occurs in the same forest type. A more ecological, as well as economical, approach is to take advantage of any competitive or productive "edge" that a species may have in a given forest type. It is much easier to manage a population that can probably maintain itself in the forest without assistance; there is also less risk of overexploitation. Given these considerations, those areas containing the most productive populations of the species selected for management should be located and outlined on the forest type map of the area. Some forest types may contain several of these "class I" populations, more adverse sites may be the preferred habitat of only a single species or none at all. After blocking out these areas, the habitats containing the second (class II) or third (class III) most productive populations of the desired species should also be demarcated. This procedure will, in effect, generate a second forest type map of the management area. Whereas the first typology was based on floristic composition, the second is defined by the productivity of specific resources. The finished map is an important document that will serve as the basis for all subsequent management planning on the area.

Defining a Sustainable Harvest

Sustainability is a tricky word. Although there appears to be a general consensus that the exploitation and management of tropical forests should be sustainable, there is considerable confusion about what the word actually means (Turner 1988; MacNeil 1989; Pearce, Barbier, and Markandya 1989). For this discussion, sustainability is defined in a very restricted, ecological sense. From an ecological or management perspective, a truly sustainable system for exploiting non-timber resources is one in which fruits, nuts, latexes, gums, and other plant products can be harvested indefinitely from a limited area of forest with negligible impact on the structure and function of the plant populations being exploited. Two different procedures for obtaining this objective are available to the resource manager. The first—a conceptually simple, inexpensive, and straightforward process—monitors the population impact of exploitation and sequentially adjusts harvest levels over time to obtain a sustainable yield. The population being exploited is, in effect, viewed as a "black box" with certain inputs (recruitment) and outputs (harvestable yield). The second procedure opens this box to examine the details of why the population responds as it does. By collecting and analyzing demographic data on the growth, mortality and reproduction of different individuals within the population, certain predictions can be made about the impact of harvesting before the resources are actually extracted from the forest. The elegance of this technique is that overexploitation occurs first in a computer simulation, not fifty or sixty years later in the field when it may already be too late to remedy the situation.

Successive Approximation

The first signal that a plant population is being subjected to an overly intensive level of resource extraction is usually manifested in the size-class distribution of that population. In most cases, the effects of overexploitation are most clearly visible in the seedling and small sapling classes. Harvesting may kill a large number of adults (rattan, gharuwood, or palm hearts), may lower individual tree vigor to the point that reproduction is affected (leaf or bark extraction, or the tapping of plant exudates), or may remove an excessive number of reproductive propagules from the site. The net effect of these activities is to reduce to varying degrees the natural rate of recruitment into a population. This demographic impact, however, can be detected and avoided by periodic monitoring of the densities of seedlings and saplings in different production units.

In a typical management scheme, it is very likely that a 10 centimeters DBH minimum diameter limit was used in the initial inventory of the management area, and that, as a result, little or no information was collected on the density of the individuals in smaller-size classes. Given this lack of information, a

Table 3.2 Sample Calculation of Total Annual Fruit Production

Basal Diameter Class (centimeters)	*N*	*Average Fruit Production*	*Class Total*
2.1–3.0	1,800	3,406	12,000
3.1–4.0	600	427	256,200
4.1–5.0	310	535	165,850
5.1–6.0	150	672	100,800
6.1–7.0	50	844	42,200
7.1–8.0	40	1,061	42,440
8.1–9.0	20	1,334	26,680
9.0–10.0	30	1,679	50,370
10.1–11.0	30	2,113	63,390
11.1–12.0	10	2,661	26,610
12.1–13.0	10	3,353	33,530
Total Fruit Yield per Hectare		1,420,070	

Note: The calculation was made for a 1.0 hectare population of *Myrciaria dubia*. *N* is equal to the number of adult trees per size-class; the class total represents fruit yield per size-class per year.

Source: Data from Peters and Hammond 1990.

network of permanent regeneration plots should be established throughout the area. These plots should be of a relatively small size, either 5 x 5 meters or 10 x 10 meters (Wyatt-Smith 1963; Hutchinson 1988; Adlard 1990). Although a systematic re-sampling of a small proportion of the original inventory transects would also give good results, a stratified random design is probably the preferred sampling method. Regardless of whether plots or transects are used, the samples should be stratified by production unit with the total number of samples being adjusted to reflect the area embodied by each unit. Plots should be selected using random coordinates and their exact position marked as accurately as possible on the production unit map. After locating the plots in the field, they should be permanently marked using metal stakes or PVC pipe; the plot number should be clearly painted on the corner stakes. Within each plot, the total number of seedlings and saplings less than 10 centimeters DBH of the species to be exploited in that production unit are counted and recorded. For ease of data collection, the sample individuals can simply be tallied into size classes and only individuals of questionable size (those bordering on two classes) need be measured. The use of four 50 centimeter height classes (0–50, 50–100, 100–150, and 150–200 centimeters) and one 1–10 centimeter diameter class is appropriate for most tree species.

The final plot totals should be grouped by production unit, and mean densities and standard errors calculated for each size class and plant species. These data are then combined with the size-class distributions constructed from the inventory results to give a more complete representation of population structure from seedlings to large adult trees.[17] The existing density of seedlings and saplings in each population are held as "threshold" values against which the effects of harvesting are compared. The regeneration plots should be inventoried every five years, preferably at the same time of the year as the initial survey, to monitor the fluctuation in the number of seedlings and saplings recruited into each population.[18] As long as densities remain above the threshold value, there is a high probability that the current level of exploitation can be sustained. If, however, seedling and sapling densities are found to drop below this value, immediate steps should be taken to reduce the intensity of harvest. The effectiveness of this harvest reduction will be verified during the next inventory of the regeneration plots. Further decreases in harvestable yield may be warranted if seedling and sapling densities fail to stabilize, or drop even lower, during the five-year period.

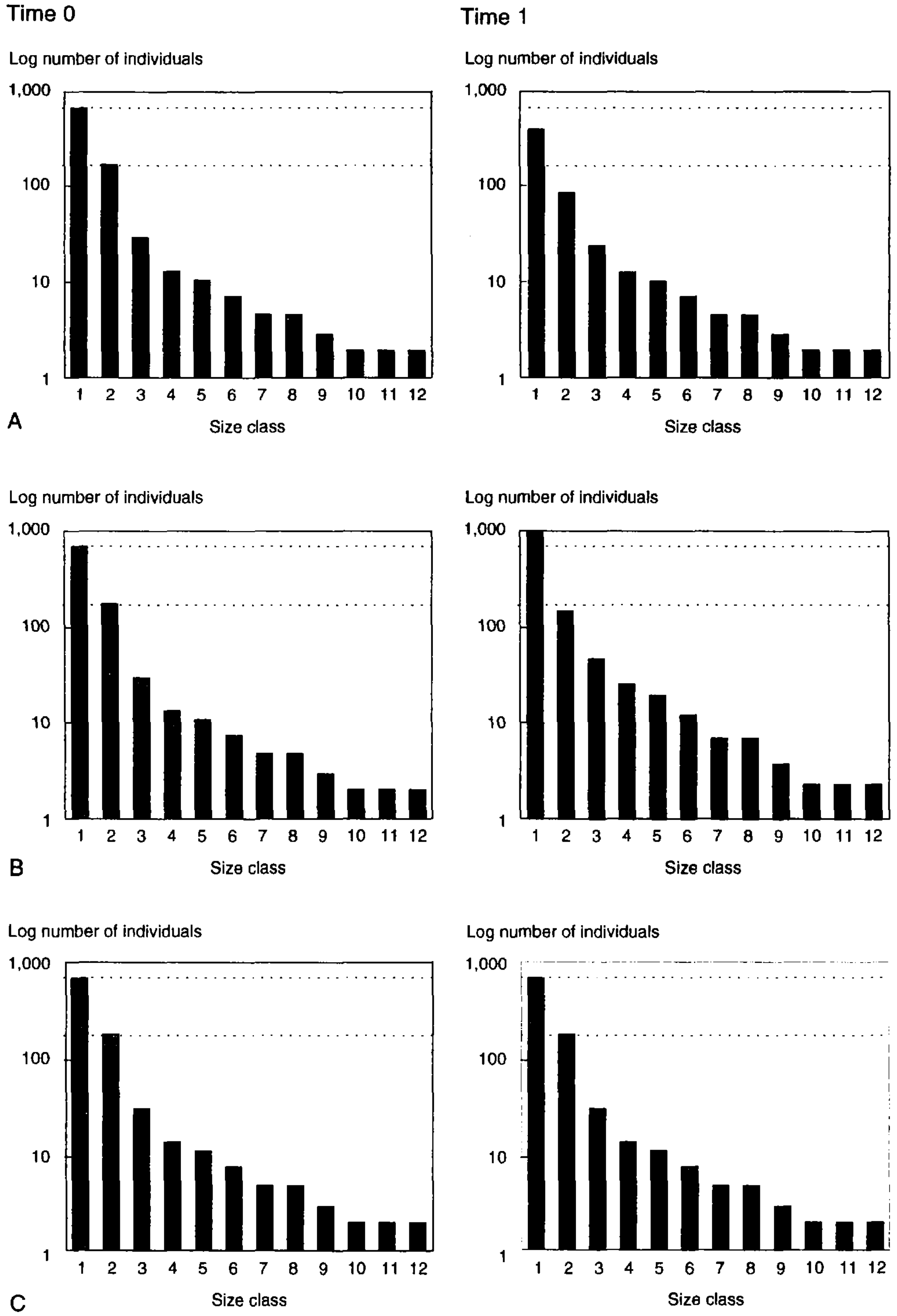
The mechanics of this process of successive approximation are shown graphically in figure 3.6. The left side of the figure depicts the initial size-class distribution of the population at Time 0, immediately following the first inventory of the regeneration plots; the right side shows the structure of the population five years later at Time 1. The threshold values for seedlings and saplings are shown as dotted, horizontal lines. The first four numbered size classes shown in each histogram are 50 centimeter height classes, the remainder are 10 centimeter DBH diameter classes. Note that the y-axis is graphed on a logarithmic (base10) scale. The uppermost histogram, figure 3.6(a), illustrates the incipient stage of resource overexploitation. By Time 1, seedling and sapling densities have both dropped well below their threshold values. Harvest levels in this population should, as a result, be immediately decreased before the reduction in numbers exhibited by the smaller size-classes is passed on to the intermediate and larger size-classes. Figure 3.6(b), on the other hand, depicts a hypothetical example of underexploitation. The population in question has actually increased its level of recruitment in response to harvesting, a behavior that suggests that additional quantities of resource could probably be extracted from the production unit. That exploitation might, in fact, enhance recruitment is not an entirely unrealistic scenario. Seed collections could reduce density-dependent mortality among seedlings (see chapter 2) or limit food supplies to the point that potential seed predators were driven from the site. The reduction in canopy cover caused by the harvest of vegetative tissues might also improve light conditions in the understory for seedling establishment. Whatever the ultimate cause, an increase in seedling and sapling densities over a five-year period is a good indication that the population can withstand an increased intensity of exploitation. The final histogram in figure 3.6 illustrates a steady-state or sustainable harvest level, the existing level of resource extraction having little effect on the number of seedlings and saplings recruited into the population.

In practice, achieving a sustainable yield through successive approximation will probably involve a considerable number of harvest adjustments. There is frequently a lag time in the demographic response of a population to perturbation, and after several cycles of apparently stable results from the regeneration plots, the population may exhibit a drastic fluctuation in seedling and sapling densities. The important thing, however, is that these fluctuations do not go unnoticed. By gradually lowering, or even raising in some cases, the intensity of resource extraction, the level of recruitment should eventually approximate the threshold value established for each population. If seedling densities drop dangerously low in spite of successive harvest adjustments, the exploitation of that population ideally should be suspended for a five year period to allow recruitment levels to recuperate. If seedling densities continue to drop in the absence of harvesting, some type of remedial treatment should be initiated as soon as possible (see chapter 4).

Plant Demography, Matrix Models and Computer Simulations

Despite the relative simplicity and ease of data collection of the successive approximation technique, a major limitation is that the resource manager is forced to respond blindly to fluctuations in population recruitment level with little understanding of the actual origin or cause of these fluctuations. This is not a problem so long as harvest adjustments produce the desired result. In some instances, however, a greater understanding of the workings of a plant popula-

Figure 3.6 Diagrammatic Effect of Harvest Intensity on Size-Class Distribution to Illustrate Process of Successive Approximation



Note: Time 0 represents size-class distribution immediately following inventory of regeneration plots; time 1 shows population structure 5 years later after annual harvesting. Note log scale on y axis. A. Incipient stages of over-exploitation with decrease in seedling and sapling numbers below threshold value (shown as dotted, horizontal lines). B. Under-exploitation of resource base. C. Sustained-yield harvesting.

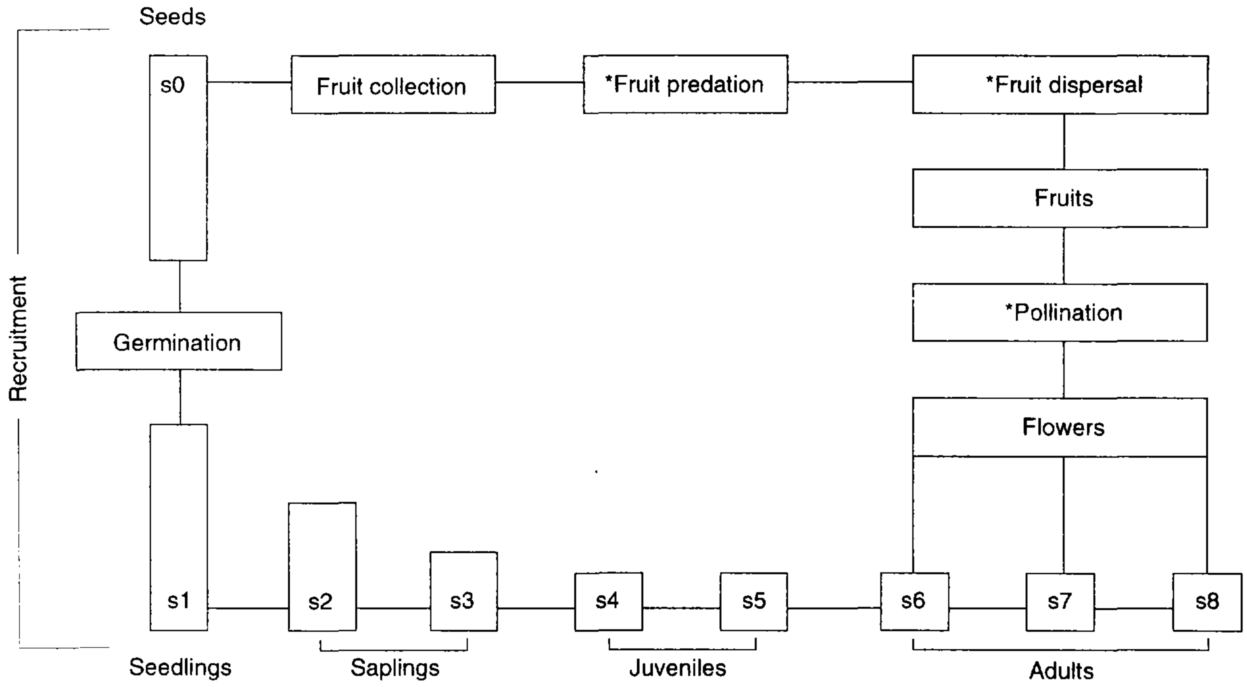
tion can be extremely useful. Some populations, for example, may not respond to harvest controls; others may be characterized by a recruitment problem that could be easily corrected given sufficient information about seedling and sapling dynamics. Given that the removal of an ecological barrier to regeneration can effectively lower the threshold value for the population and cause an increase in sustainable yields, the rationale for studying the intricacies of population function goes well beyond that of purely academic interest.

The quantitative study of how tree populations work is known as plant demography (Harper and White 1974). Several of the analytical tools from this discipline can be used to good advantage in the management of non-timber forest resources. The use of these tools, however, requires that supplementary information be collected about the size-specific behavior of the individuals within a population. Perhaps the easiest way to explain the additional parameters that need to be measured is by referring to the generalized life cycle model presented in figure 3.7. The population illustrated is composed of nine life cycle stages (s_0 to s_9) and an intermediate reproduction and recruitment phase linking the three adult stages (s_6 to s_9) to that of established seedlings (s_1). For optimal results, all of the stages and fluxes in this model must be quantified.[19] Some of these data have already been collected. The number of individuals contained in each size class is available from the inventory results and initial regeneration survey; the yield studies, at least for the fruit, nut and oil seed species, compiled data on the size-specific fecundity of adult trees. What remains to be done, therefore, is to quantify the fluxes between the vegetative stages of the model (the transition from seeds to seedlings, from seedlings to saplings, and so forth). During the lapse of a year, one of three things can happen to an individual within a given size class. It can grow to the next size class, it can remain in the same size class, or it can die. These fluxes can be approximated by collecting data on the size-specific growth and mortality of selected individuals. It is important to emphasize that the collection of demographic data is both tedious and time-consuming. The procedures described below, therefore, can be best applied as a supplement to the regeneration surveys and serial harvest adjustments, especially in the case of extremely valuable resources or species plagued by limited or unpredictable recruitment during the early stages of their life cycle.

Data Collection. The collection of reliable growth and mortality data requires the periodic observation and measurement of marked individuals. These data can be most easily obtained by establishing permanent demography plots within the production units for a given species. The total area of each plot is not so important. What is important, however, is the total number of conspecific individuals contained in each plot. As a general rule, an area big enough to include at least three or four adult trees per 10 centimeter DBH class will probably contain a sufficient number of seedlings, saplings and juveniles to provide a meaningful sample. Depending on the actual density of the species in the forest, a demography plot may range in area from 1.0 to 5.0 hectares. Only the individuals of the target species need be monitored within these plots. All of the large saplings (2.0–3.0 meters tall), juveniles, and adult trees of the species should be located and permanently labelled with a plastic or aluminum tag. The number of seedlings and small saplings in some populations may be too numerous for all to be labelled, and a subsample of these individuals will have to be selected. Given the magnitude and rapidity of the demographic change that occurs in these size classes, the subsample should be as large as time and available funds allow. If possible, several hundred seedlings and small saplings should be individually tagged for observation. The fate of seeds can be quantified by monitoring the percent germination of replicated samples (50–100 seeds each) randomly located on the forest floor.

Growth data is obtained through the periodic measurement of these individuals. Growth in height is monitored for seedlings and saplings less than 2.0 meters tall; diameter (DBH) growth is recorded for all remaining individuals. Height growth is a relatively difficult measurement to make with precision, and care should be taken to ensure that the tape or range pole is completely vertical at all times and that the same point along the plant axis is measured each time. Diameter growth can be measured in several different ways. The easiest and least expensive way is to paint a ring around each sample tree at DBH and to carefully place the diameter tape along this line at each measurement period. This procedure has been used with good results in a number of forest surveys and ecological studies of tropical tree growth (Lang and Knight 1983; Primack and others 1985; Manokaran and Kochummen 1987). The most precise way to measure small changes in radial increment, however, is through the use of dial-gauge or vernier band dendrometers. The first instrument records growth at a single radius of the trunk; the second measures changes in circumference. The relative advantages and disadvantages of each type of dendrometer are discussed in detail by Bormann and Kozlowski (1962) and Breitsprecher and Hughes (1975). The overall benefit of using dendrometers relative to periodic measurement by tapes is that diameter increments as small as 1–2 millimeters can be detected. If growth measurements are to be continued for only two or three years, the use of dendrometers is highly recom-

Figure 3.7 Generalized Life Cycle Diagram of a Plant Population



Note: Height of size-class boxes indicates the relative abundance of individuals at each stage. Reproductive processes in which animals play an important role are marked with an asterisk.

mended. Liming (1957) outlines a simple technique for making vernier tree bands out of stainless steel strapping which has proven quite effective for use in tropical forests (Murphy 1970; Daubenmire 1972; Lieberman and others 1985; Peters 1989).

Information about size-specific mortality rates is obtained through periodic observation of the individuals tagged within the demography plot. Short observation periods (one or two years) will probably be sufficient to gain a meaningful estimate of seedling and sapling mortality; longer periods of time will be required for large adult trees. In addition to simply recording the number of deaths in different size classes, the specific source of individual mortality (herbivory, falling debris, desiccation, or fungal attack) should also be noted whenever possible. In many situations, the frequent and repeated sampling required to obtain this level of detail may not be warranted. The minimum data required for demographic analysis is a simple average of the number of individuals per size class dying within a year divided by the total number of individuals within that size class.

Life Table Analysis. Life tables represent a convenient format for organizing the demographic data collected from each study population. Although life tables have been traditionally used by demographers (and insurance agents) to analyze solely the age-specific probability of death (Krebs 1985; Pianka 1988), the recent increase in the number of studies concerning the population biology of long-lived plants has somewhat modified the utility of this actuarial technique. For the study of tree populations, a life table contains not only death rates, but also birth rates and the rates at which individuals advance from one size class to another (Harcombe 1987). These three pieces of data encapsulate the demographic mechanisms controlling the dynamics of a population of trees. The population grows when the recruitment of new individuals exceeds the number of deaths, and diminishes in size when mortality is greater than the number of births. Stability is achieved when birth and growth rates are exactly balanced by mortality. Given a knowledge of the initial size of a population, the data contained in a life table can later be used to predict future changes in the structure and size of the population with a reasonable degree of precision.

To illustrate the basic construction of a life table, demographic data for *Grias peruviana*, a common lower-canopy fruit species from Peruvian Amazonia, is presented in table 3.3. For simplicity, the population has been grouped into nine life cycle stages (s_0 to s_8). The pre-reproductive phase of the life cycle is represented by seeds (s_0), seedlings (s_1), saplings (s_2 and s_3), and juveniles (s_4); adults are stratified into four different size classes (s_5 to s_8). The first column of the table shows the number of individuals per hectare (N) at each stage, while columns two and three describe the annual growth and mortality of each stage. The proportion of individuals moving from or remaining in a given size-class after one year is calculated using annual growth rates and the actual height and diameter class interval. For example, small saplings (stage s_2) grow 12 centimeters per year in height. Given a class interval of 50 centimeters, 4.2 years would be required to move all of these individuals to the next stage (s_3). Assuming a homogenous size distribution within this class, 24.0 percent of the small saplings would advance to stage s_3 each year, and 76.0 percent would remain in stage s_2 until some future time period. The fecundity values shown in the final column represent the average number of fruits produced by the adults trees in each reproductive size class. A total of 715 individuals were monitored for sixteen months to obtain the demographic data shown in this table (Peters 1990a).

The general format of a life table can be modified to accomodate a variety of different species and life cycles. The number of size classes and the width of each class should be chosen in such a way that each class contains at least eight to ten individuals; it is not necessary that all class intervals be equivalent.

Table 3.3 Life Table Data for *G. peruviana*

Size-class	*Stage*	*Number per hectare*	*Survival (%)*	*Growth (cm/yr)*	*Moving (%)*	*Remaining (%)*	*Fecundity*
Seeds	s0	8,581	0.525	n.a.	1.000	0.000	n.a.
Seedlings (0–50 cm tall)	s1	997	0.124	7.9	0.158	0.842	n.a.
Small saplings (50–100 cm tall)	s2	463	0.682	12.0	0.240	0.760	n.a.
Large saplings (100–150 cm tall)	s3	167	0.877	17.2	0.344	0.656	n.a.
Juveniles (1–5 cm DBH)	s4	132	0.965	0.21	0.052	0.948	n.a.
Adults (5–10 cm DBH)	s5	118	0.978	0.26	0.053	0.947	16
Adults (10–15 cm DBH)	s6	82	0.978	0.15	0.031	0.969	34
Adults (15–20 cm DBH)	s7	35	0.978	0.19	0.038	0.962	59
Adults (20+ cm DBH)	s8	13	0.978	0.18	0.000	1.000	97

n.a. Not applicable.

Note: Data are for *G. peruviana* growing at Rio Ucayali, Peruvian Amazonia. All rates are expressed on a yearly basis. Growth rates for height and diameter classes are measured in the respective unit for that class. (See the text for sources and calculations of all coefficients.)

Source: Adapted from Peters 1990a.

Vandemeer (1978) presents a useful formula for calculating the statistically optimal class interval to use in life tables and demographic modelling based on the observed size-structure of the population. A more precise estimation of the proportion of individuals moving out of a given size class during one year can also be calculated using mean growth rates and the actual size distribution of the individuals within that class. For example, given a 1.0 centimeter diameter increment per year and a 10 centimeters class interval, the assumption of a homogenous size distribution would predict that 10 percent of the trees (those 9.0 centimeters DBH) grow into the next class in the span of one year. It is extremely doubtful, however, that exactly 10 percent of the individuals in this class are 9.0–10 centimeters in size. Grouping the individuals in each size class into 1.0 centimeter intervals is a quick way to correct this potential source of error. If a life table is being prepared for a dioecious species, only the number of female trees should be included in the adult classes; the exclusive use of growth and mortality data collected from pistillate trees is also recommended.[20]

Matrix Models of Population Growth. Given basic life table data about a population, some means of tabulating and manipulating the information is needed before future changes in the population can be predicted. Matrix methods are particularly useful in this context and have been used in several demographic studies of plant populations (Sarukhan and Gadgil 1974; Hartshorn 1975; Van Valen 1975; Enright and Ogden 1979; Bullock 1980; Piqero, Martinez-Ramos, and Sarukhan 1984). The basic model was initially developed by Leslie (1945) to predict the structure and growth rate of populations grouped into age classes. In view of the difficulty of accurately determining the age of many organisms (for example, tropical trees), this model was subsequently modified by Lefkovitch (1965) to utilize size-class data. The classes do not necessarily have to be of equal size, and even broad life stages such as seedlings, saplings, and adults may be used. This modification has greatly enhanced the utility of the model for studies of tree populations.

The basic structure of the model as expressed in matrix notation is:

$$nt+1 = M_{nt}$$

where nt is a column vector containing s life cycle stages that represent the structure of the population at a given moment in time. The transition matrix, M, contains transfer rates from one stage to the next, and mortality and fecundity data for each life cycle stage. Multiplying the transition matrix by the column vector yields the size and stage structure of the population at one time interval in the future. In a similar fashion, the model can be used to predict the stable size-class distribution of a population (the state at which the proportion of individuals in each size-class remains constant through time) even though the absolute size of the population may continue to change. Further details about the properties and uses of the Lefkovitch matrix model are outlined in box 3.3.

Given that M is a square matrix with s rows and columns, multiplying the transition matrix repeatedly by a column vector will eventually produce the dominant latent root, or λ, of the matrix. As Leslie (1945), Lefkovitch (1965), Usher (1972) and other workers have shown, the dominant latent root of a transition matrix is equal to e^r, or the finite rate of increase of a population.[21] This is a very important parameter because it can be used to assess the stability, growth or decline of a study population. For example, a λ greater than 1.0 indicates that the population is increasing in size, while a λ less than 1.0 shows that the population is decreasing in size. A λ equal to 1.0 indicates that birth and death rates are exactly balanced so that the population remains stable.

Despite its utility and widespread use, a basic limitation to the model should be noted. The Lefkovitch model assumes exponential growth, and the transition probabilities calculated from the growth, mortality and fecundity rates do not change with increasing population density. As a result, model prediction soon depart from reality when values are greatly different from unity (Enright and Ogden 1979; Lorimer and Frelich 1984). Viewed in this context, the value of matrix models can be seen to result more from the general trends that they depict and the questions that they raise than from the precision of the numerical predictions that they generate (Peters 1989).[22]

Model Simulations. To proceed with the determination of a sustainable yield using matrix analyses, the life table data collected from the demography plots need to be arranged within a matrix format. An example of this procedure is presented in table 3.4 using the demographic data previously presented for *G. peruviana*. As indicated in this table, the top row of the transition matrix lists the size-specific fecundity values for adult trees. The principal diagonal gives the proportion of individuals that remain in a given stage. This element takes into account both mortality and growth and is equal to the proportion of individuals that remain in a given stage multiplied by the survivorship (the reciprocal of mortality) of that stage. Similarly, the subdiagonal lists the proportion of individuals that move into the next stage.

Exponentiation is used to determine the dominant latent root of the transition matrix derived for each species. The matrix should be sequentially exponentiated to the *k*th power of 2 until a constant value of λ is obtained; stable values are usually obtained at a *k* of about 256. A constant latent vector, *n*, will also result from the matrix after exponentiation, this set of values representing the stable size-class distribution of the population. A variety of different statistical packages and commercial computer programs are currently available for manipulating matrices; BASIC programs specifically developed for calculating population growth rates from demographic data can also be obtained (Enright and Ogden 1979; Harcombe and Marks 1978; Ferson 1991).

Following this procedure, a dominant latent root of 1.018 was calculated for the *G. peruviana* population. Although this is reasonably close to the theoretical value of 1.0 expected for a stable population, the slight departure from unity indicates that the density of *G. peruviana* in the forest should increase slightly over time. In the absence of exogenous disturbance, the population consistently maintains a level of recruitment that is more than sufficient to compensate for

Box 3.3 The Lefkovitch Matrix Model

The general format of the transition matrix (M) and column vector (n) is illustrated by:

$$\begin{array}{llllll} & r0+f0 & f1 & f2 & f3......fs & n0 \\ & m0 & r1 & 0 & 0.....0 & n1 \\ M = & 0 & m1 & r2 & 0.....0 & n = n2 \\ & 0 & 0 & m2 & r3....0 & n3 \\ & 0 & 0 & 0 & m3....rs & n4 \end{array}$$

In most cases, only the top row, *f*, the principal diagonal, *r*, and the subdiagonal, *m*, need be considered; all other elements will be zero. The *f* values represent the average size-specific fecundity of an individual. This parameter will be zero for all pre-reproductive stages of the life cycle. The *r* values of the principal diagonal give the proportion of individuals remaining in a given stage after one time interval. This element takes into account both mortality and growth and represents the product of the proportion of individuals remaining in a given stage times the survivorship of that stage. The subdiagonal elements, *m*, give the proportion of individuals in a given stage that grow into the next stage. The *m* values, therefore, represent the product of the proportion of individuals that move into the next stage times the survivorship of the preceding stage.

It should be noted that the upper right half of the transition matrix could potentially have non-zero values if the individuals of a given stage contribute to a lower stage other than through the production of seeds. This may occur, for example, in a species that exhibits vegetative reproduction. Similarly, the lower left half of the matrix could also contain non-zero values if individuals move more than one stage during a unit time period.

To give a specific example, consider a hypothetical population of forest trees that is divided into four size-classes: seedlings (s0), juveniles (s1), small adults (s3) and large adults (s4). Size-specific fecundities and m and *r* coefficients for the population are as indicated in the transition matrix below; the initial size-class distribution of the population is shown in the column vector (n).

$$\begin{array}{cccccccc} & M & & & & N & & Mt+1 \\ 0 & 0 & 2 & 4 & & 40 & & 44 \\ 0.5 & 0.3 & 0 & 0 & & 30 & & 29 \\ & & & & \times & & = & \\ 0 & 0.3 & 0.2 & 0 & & 10 & & 11 \\ 0 & 0 & 0.5 & 0.5 & & 6 & & 8 \end{array}$$

Multiplying the transition matrix by the column vector yields the size and stage structure of the population at Nt+1, or one unit time period into the future.

Note: The Lefkovitch matrix model is used for simulating the population dynamics of organisms grouped into size, rather than age, classes.

mortality in the larger size classes. Taken by itself, the dominant latent root provides the resource manager with important information about the ecological behavior of the species being analyzed, as well as an indication of the potential investment required to sustain its exploitation. A λ value greater than or equal to 1.0 is a good indication that a species will be able to maintain itself in the forest under varying degrees of exploitation with only minimal management inputs. Species that exhibit a λ value less than 1.0 will re-

Table 3.4 Transition Matrix for *Grias peruviana*

				Stage				
s0	*s1*	*s2*	*s3*	*s4*	*s5*	*s6*	*s7*	*s8*
0	0	0	0	0	16	34	59	97
0.52	0.10	0	0	0	0	0	0	0
0	0.02	0.52	0	0	0	0	0	0
0	0	0.16	0.57	0	0	0	0	0
0	0	0	0.30	0.91	0	0	0	0
0	0	0	0	0.05	0.93	0	0	0
0	0	0	0	0	0.05	0.95	0	0
0	0	0	0	0	0	0.03	0.94	0
0	0	0	0	0	0	0	0.04	0.98

Note: The top row gives fecundity values for adults; the principal diagonal lists proportion of individuals staying in a stage; the subdiagonal lists proportion of individuals moving from one stage to the next. The transition probabilities have been rounded to two digits. See text for explanation of parameter estimation.

Source: Peters 1990a.

quire a greater intensity of management to ensure the long-term sustainability of harvesting.

Given that the dominant latent root derived from a transition matrix yields an estimate of population stability, this parameter can also be used to gauge the relative resilience of a population to different patterns and intensities of exploitation. By selectively varying the coefficients in the transition matrix and assessing the resultant change in , the demographic effects of these perturbations can be simulated prior to their implementation in the field. Coefficient changes that reduce the value below unity can be assumed to be detrimental to the long-term stability of the population, that is, they are not sustainable. Sensitivity analyses of this type have been used in several ecological studies to assess the demographic impact of seed predation (Hartshorn 1972), survival rates (Caswell 1978; Piqero, Maritnez-Ramos, and Sarukhan 1984), and vegetative vs. sexual reproduction (Bullock 1980). Although rarely applied to non-timber forest resources, these analyses can also be used to evaluate the population effects of collecting fruits, nuts, or oil seeds (Peters 1989, 1990a), tapping plant exudates, or harvesting different vegetative structures such as leaves, roots, stem tissue or bark (Usher 1966).

The specific manner in which the matrix is modified will depend on the type of resource to be exploited. Annual fruit collections, for example, can be modelled by reducing the fecundity coefficients of all adult classes. This alteration effectively lowers the number of seeds that are available for germination each year and, therefore, provides a realistic analog to commercial fruit harvests. The tapping of plant exudates can be simulated by either lowering the annual growth rates and fecundity values for the merchantable size classes (to reflect a reduction in individual vigor) or by raising the mortality rates of certain classes (to reflect that the tree is killed by harvesting). Similarly, the impact of harvesting vegetative tissues can be simulated through a reduction in growth and reproduction or through increased mortality depending on the nature and final outcome of resource exploitation. Different parameters can be combined and adjusted in such a manner that almost any type of resource or harvest practice can be simulated with meaningful precision.

As an example of the utility of sensitivity analyses, the fecundity coefficients in the G.

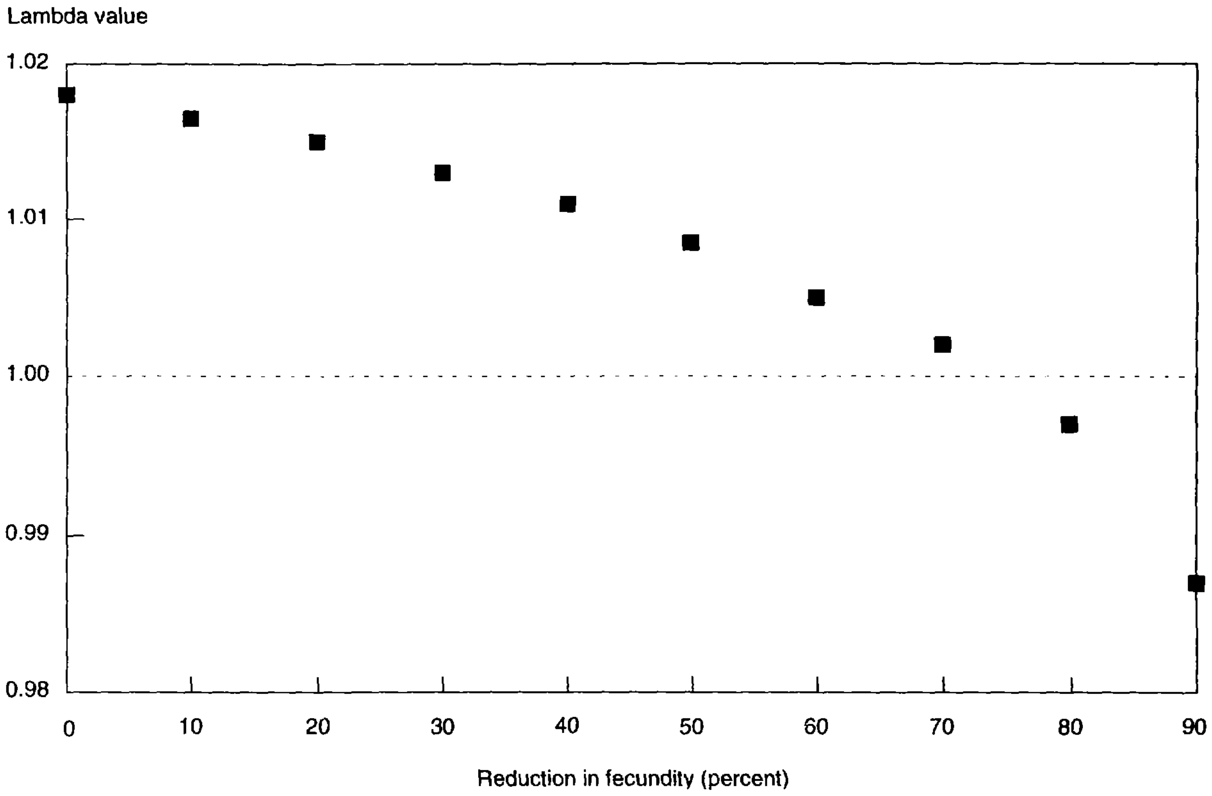
peruviana transition matrix were reduced in a stepwise fashion for all adult classes to simulate the effects of varying intensities of fruit collection. Dominant latent roots were then calculated for each new matrix to determine the harvest intensity necessary to drive the λ value below 1.0. The results from this analysis are presented in figure 3.8, which shows the dominant latent roots derived from matrices in which fruit production parameters have been reduced in a stepwise fashion from 10 to 90 percent. The dotted, horizontal line at 1.0 represents the value of a stable population. As indicated in the figure, latent roots greater than 1.0 are maintained under all harvest intensities up to 80 percent. If more than 80 percent of the fruit produced each year is harvested, however, λ values drop below 1.0 indicating that the existing level of regeneration is insufficient to balance natural mortality rates. Based on these results, there is strong quantitative evidence to suggest that natural populations of *G. peruviana* can be exploited on a sustained-yield basis if at least 20 percent of the fruit crop produced each year is left in the forest to regenerate.

A similar process can be followed to estimate the sustainable yield of any resource extracted from natural populations. Although it is unlikely that permissible harvest levels will always be as high as that calculated for the *G. peruviana* population (but see Peters 1989, 1990b), there is some evidence to suggest that plant populations can inherently withstand a large reduction in reproductive output. Apparently, population growth rates are not very sensitive to changes in reproduction (Caswell 1978). Hartshorn (1975), Enright and Ogden (1979), Enright (1982), Bullock (1980) and Piqero, Martinez-Ramos, and Sarukhan (1984), for example, have all reported that population growth rates are less sensitive to changes in fecundity than to the mortality rate of sapling and juvenile trees. In these same studies, even the mortality of adult trees was less important to population stability than that of the intermediate size-class. These pre-reproductive individuals are rarely of interest to commercial collectors of resin, bark, or stem tissue, and further field studies may indicate that natural populations of these resources are also extremely resilient to the effects of exploitation.

After defining the sustainable harvest level from a particular population, some means of controlling the intensity of resource extraction is needed to ensure that this level is not exceeded. To achieve this objective, harvests can be controlled by regulating either the number or size of the trees exploited or the total area from which the resources are extracted. In the case of *G. peruviana*, for example, adult trees greater than 20 centimeters DBH (stage s_8) produce approximately 30 percent of the total fruit crop each year (table 3.3). The individuals in this class, however, represent only 5 percent of the total number of adults. Marking these trees and leaving them unharvested would ensure that an adequate amount of fruit is left in the forest. A second approach would be to divide the production unit into five parcels, each parcel containing more or less the same number of adult trees. Only four of these parcels would be harvested in a given year, the fifth being left fallow to permit seedling recruitment. Especially vigorous or productive individuals could also be left to regenerate for several years to enhance the genetic composition of the population.

The results from the present chapter suggest that non-timber forest resources can, in fact, be managed on a sustained-yield basis. The essential ingredient of such management programs is information. Information about the density and distribution of resources within the forest, the population structure and productivity of the resources to be managed, and the ecological or demographic impact of resource harvest. The combination of inventories, yield studies, and demographic monitoring can provide the resource manager with these data. In many cases, simply defining an effective compromise between harvest intensity and population recruitment

Figure 3.8 Demographic Impact of Annual Fruit Collection on the Population Dynamics of G. *Peruviana*



Note: Lambda values calculated using transition matrices in which fecundity coefficients were reduced from 10 to 50 percent.

is sufficient to ensure the long-term sustainability of resource extraction. Some species, however, may not be so easy to exploit. They may occur at low densities in the forest, exhibit marginal productivity, or be extremely sensitive to the effects of harvesting. In addition to controlled harvesting, the sustainable management of these "recalcitrant" species will require some form of direct silvicultural manipulation. Foresters working in the tropics have developed a diverse array of different tools or controlled interventions to stimulate the abundance, productivity, and regeneration of forest trees, and these practices are examined in chapter 4.

Chapter Summary

1. The commercial extraction of non-timber tropical forest resources is currently plagued by destructive harvesting, overexploitation and a basic disregard for the functional ecology of tropical tree populations. Rarely has any concerted effort been made to manage these resources on a sustained-yield basis, and tropical foresters, agronomists and plant ecologists have contributed little in the way of concrete solutions to remedy this situation.

2. An overall strategy for managing non-timber tropical forest resources on a sus-

tained-yield basis is presented. The complete process is composed of five basic steps: initial planning, forest inventory, species selection, yield studies, and defining a sustainable harvest. The specific procedures described can be applied to almost any class of non-timber resource on a scale of 100—100,000 hectares. The guidelines do not comprise a single management technology or package that can be blindly applied without modification. Rather, the basic concept is to provide the resource manager with a constant flow of diagnostic information about the ecological response of the target species to exploitation. Sustainability is achieved through a continual process of reciprocal feedback: the observed reaction of the plant population must result in a corresponding adjustment in harvest levels.

3. Initial planning operations involve collecting background information (maps, climatological data, existing surveys, and so forth) about the management area, delineating the boundaries of the site, performing a preliminary typology of the forest using aerial photographs, and constructing a base map for use in subsequent management operation.

4. Detailed forest inventories are conducted to document the distribution and abundance of different resources within the management area. Of the variety of different inventory techniques available, a systematic sample of fixed-width transects is recommended. The advantages of systematic sampling are: it provides a good estimate of population means and totals; it is faster and less expensive than probability sampling; forest type information can be easily collected and mapped; and it requires no *a priori* knowledge of the total forest area. A lower diameter limit of 10 centimeters DBH is suggested for the inventory, with certain exceptions made for acaulescent palms, lianas, or shrubs; sample intensities should not drop below 3–5 percent of the total management area.

5. Species selection will undoubtedly be based largely on economic and social criteria. However, the overall potential of a species to be managed on a sustained-yield basis (based on life cycle characteristics, multiplicity and types of resources produced, abundance in different forest types, and population structure) should also be an important selection criteria. Although the fact is frequently overlooked by many resource managers, some forest species are inherently better able to withstand the continual perturbations caused by resource extraction.

6. The fourth step in the management process involves the measurement of productivity. The objective of these yield studies is to provide a reasonable estimate of the quantity of resource produced by a given species within a particular habitat. The selection of sample trees should be stratified by diameter, or some other size parameter, and by site condition. Sampling methodologies are described for determining the size-specific yield of reproductive propagules, plant exudates, and vegetative tissues. A simple expansion technique is used to convert the individual yield data into an estimate of total population productivity.

7. Yield estimates are then used to divide the management area into distinct production units. The goal of this partitioning is to identify those species, or combination of species, that are the most productive in a particular forest type or habitat. All subsequent resource extraction and management will be concentrated in these areas.

8. Two methods of defining a sustainable harvest are outlined. The first, a conceptually simple, inexpensive and straightforward process called "successive approximation," monitors the population impact of exploitation and sequentially adjusts harvest levels over time to obtain a sustainable yield. The population being exploited is, in effect, viewed as a "black box" with certain inputs and outputs. The second procedure opens this box to examine the details of why the population responds as it does. The collection of demographic data on the growth, mortality and reproduction of different individuals within the population allows certain predictions to

be made about the impact of harvesting before the resources are actually removed from the forest. The elegance of this technique is that overexploitation occurs first in a computer simulation, not fifty or sixty years later in the field when it may already be too late to do anything about it.

9. Successive approximation requires the establishment of permanent regeneration plots that are monitored at five year intervals. The increase or decrease in population recruitment observed in these plots allows a "fine-tuning" of harvest levels that should slowly approach a sustainable threshold value.

10. Plant demography, matrix models and computer simulations provide a more quantitative, yet time-consuming, method of approaching a sustainable harvest intensity. This procedure requires the collection of size-specific growth and mortality data from a subsample of marked individuals within permanent demography plots; plot size will vary according to the density of the species under study. The growth and mortality data are compiled into a life table for the species together with information on seed production (from yield studies) and population structure (from initial forest inventory). A modified Lefkovitch transition matrix is then used to manipulate these life table data and assess the current stability (or growth or decrease) of the population. Selective alterations of the coefficients in the matrix model can be used to simulate the demographic effects of different harvest scenarios. This type of sensitivity analyses provides a meaningful estimate of the maximum quantity of harvestable resource that can be extracted from the forest without damaging the long-term regeneration of the population under exploitation.

11. From an technological standpoint, there is no reason that non-timber forest resources cannot be managed on a sustained-yield basis. All that is required is information—and the commitment to invest the time, energy, and capital to collect and apply it.

Notes

1. Readers unfamiliar with photogrammetry and the use of aerial photographs in forestry and other types of resource management should consult the excellent textbooks of Spurr (1960), Wolf (1974), Paine (1978) or Avery (1978, 1985) for additional information.

2. Useful discussions of the different methodologies of calculating land areas from large-scale maps or aerial photographs can be found in Spurr (1960), Wolf (1974) and Avery (1983).

3. Vegetation mapping by aerial photogrammetry is a common and well-established procedure. A more thorough review of this subject can be found in a variety of articles (for example, Francis and Wood 1955; Lee 1966; Goldsmith, Harrison, and Morton 1986) and textbooks (Thompson 1966; Kochler 1967; Howard 1970; Paine 1978; Avery 1978, 1985).

4. Interested readers are referred to Cain and Castro (1959), Fosberg (1961), Mueller-Dumbois and Ellenberg (1974) and Goldsmith (1974) for additional information about the theory and methodology of plant community classification.

5. The percent sampling intensity of a systematic strip sample is calculated simply by dividing the strip width (10 meters) by the distance between strips (300 meters) and then multiplying by 100. This feature is extremely useful in cases where the boundaries of forested tract are known but the total area has not been determined (Avery 1983). In the present example, a total of 3,000 meters of transect or 30,000 square meters were sampled. Given a sample percentage of 3 percent, the total area of the tract, if unknown, could have been calculated by multiplying the reciprocal of the sampling percentage (33.3) by the total sample area (30,000 square meters) to given a result of 999,999.99 square meters, or approximately 100 hectares. If the sample strips are tallied by forest type, a similar procedure can be used to provide an estimate of the areal extent of each type.

6. Readers unfamiliar with the principles of elementary statistics are advised to consult a basic textbook on this topic. Sokal and Rohlf (1981) provide a particularly readable treatment of statistics for the biological sciences.

7. The tape should be pulled very taut during all measurements and should be maintained horizontal as much as possible. Measuring along the slope in steep terrain can result in a significant underestimation of sample area; a slack meter tape causes a similar result.

8. Readers desiring more detailed information about forest inventory procedures are referred to the specialized texts of Loetsch and Haller (1973), Synnott (1979), FAO (1981), Philip (1983) or Adlard (1990).

9. If a more detailed analysis of forest types is desired, several methods of quantitative community classification can be employed: for example, association analysis (Goodall 1953; Williams and Lambert 1959), cluster analysis (Lance and Williams 1968), or principal components analysis (Goodall 1954; Austin and Orloci (1966). Although a discussion of these multivariate techniques is outside the scope of the present chapter, extensive reviews are provided by Pielou (1977), Orloci (1978), Whittaker (1978a, 1978b) and Gauch (1982). The textbooks of Vandemeer (1981) and Ludwig and Reynolds (1988) provide a good introduction for readers unfamiliar with these topics. It should be noted, however, that rarely will this level of statistical detail be required for routine management operations.

10. The pioneering work of Manokaran (1983, 1984, 1985) on rattan growth has focused primarily on cultivated plants; Siebert (1988) provides some useful yield information for wild C. *exilis* growing in Sumatra. Peters (1992) has recently reported quantitative data on illipe nut production from one forest population of *Shorea* in West Kalimantan. Almost all of the voluminous literature on *Hevea* yield is based on the performance of clonal stock grown in plantations (for example, Polhamus 1962; Purseglove 1968).

11. In the previous section on forest inventory, it was recommended that all tally sheets be separated by plot number or transect length, and that the plots or transects be permanently marked with flagging or paint to facilitate re-location. Strict adherence to these procedures will make it considerably easier for field personnel to locate the sample trees selected for yield measurements.

12. Direct counts have been used successfully to estimate fruit production in a number of ecological studies (Piqero and Sarukhan 1982; Anderson 1983; Anderson and others 1985; Peters and Vazquez 1987; Sork 1987; Peters and Hammond 1990), and these studies should be consulted for additional information on methodology.

13. To give an extreme example, it is doubtful that any amount of structural engineering could design a sample trap strong enough to withstand the impact of a durian or brazil nut fruit falling from a height of over 40 meters. Obviously, plots would be the most appropriate sample units for these large-fruited species.

14. The fungal-infested heartwood of *Aquilaria* trees is technically a plant exudate because of its high resin content (see chapter 2). This resource has been included in the present section, however, because of the obvious difficulties involved in estimating yield, and because harvesting removes a large quantity of stem tissue and inevitably kills the tree.

15. Detailed discussions of the theory and application of regression analysis are available in any basic statistics textbook. Steel and Torrie (1960), Snedecor and Cochran (1967) and Sokal and Rohlf (1981) are particularly good references to consult on this topic.

16. The determination and mapping of production areas is a routine part of management operations on large timber estates. This procedure, however, has rarely, if ever, been employed at any scale in the management of non-timber resources. The practices that most closely conform to this logic are probably the delineation of different *estradas* by the rubber tappers in Brazil (Schwartzman 1989), or the qualitative division of community forest reserves or *tanah adat* by the Dayaks of Indonesian Borneo (Peters, personal observation). Both of these groups use resource abundance as a criteria for subdividing the forests.

17. The initial size-structure histograms constructed for selected species were based on populations stratified by forest type. The subsequent subdivision of the management area into production units may warrant a re-analysis of the size-class data for some populations. Dividing one forest type into several production units, for example, may cause a reduction in the apparent size of a population.

18. It is important to sample the regeneration plots at approximately the same time every year, or

at least at a similar interval following peak seedfall. Surveys conducted one month after seedfall in one year and six months after seedfall in another will obviously yield completely different results, even assuming that fruit production was constant in both years.

19. Most detailed demographic studies pay special attention to the animal-mediated fluxes (see figure 3.7) between reproductive phases. For management purposes, however, the transition from flowers to fruits by pollination or the transition from mature fruit on the tree to mature fruit on the ground by dispersal can be overlooked. The most important parameter for the resource manager is the total number of viable seeds that finally arrive to stage s_0 and are available for germination.

20. A more detailed discussion of the construction and use of life tables in population analysis can be found in Begon and Mortimer (1981), Silvertown (1982), Moore and Chapman (1986), Crawley (1986), Pianka (1988) and a variety of other general ecology textbooks.

21. The coefficient *r* represents the intrinsic rate of natural increase of the Lotka (1922) population growth equation; also used to refer to a particular type of selective pressure in evolutionary biology, for example, *r* and *K* selection.

22. Readers desiring a more detailed treatment of the theory, derivation and application of matrix models are advised to consult the texts of Keyfitz (1968), Pollard (1973), Luenberger (1979), Hoppensteadt (1982), and Nisbet and Gurney (1982); Getz and Haight (1989) provide a particularly indepth discussion on the utility of demographic models in the management of natural resources.

IV
Silvicultural Treatment of Non-Timber Tropical Forest Resources

> "Each established silvicultural system for tropical forests reflects its time and place of origin. There is much to be learned from these systems, but it is dangerous to apply them without modification to forests about which little is known. Instead, it is preferable to begin by testing the forest's reaction to individual silvicultural operations and simple improvement treatments. This approach will rapidly provide reliable information upon which to develop a suitable silvicultural system."
>
> —*Hutchinson (1988)*

As outlined in the previous chapter, controlled harvesting and periodic regeneration surveys alone can frequently provide a simple and effective method of achieving a sustainable harvest of non-timber forest products. This inherently "passive" form of management has the added benefits of preserving forest structure and function to a high degree, being relatively inexpensive to apply, and permitting the simultaneous exploitation of a diverse array of different species and resources groups. The hallmark of this approach is that the intensity of human intervention is adjusted to the ecological dynamics of the targeted plant populations—instead of the other way around.

In some situations, however, a more intensive or "active" form of resource management may be warranted. Regeneration surveys, for example, may indicate that a particular species is being overexploited and that even drastic reductions in harvest intensity are ineffective in promoting adequate population recruitment. Conversely, resource managers may want to increase the density or sustainable yield of certain species or genotypes in response to improved market conditions. Both of these situations, the former remedial and the latter enhancement, require some form of conscientious silvicultural treatment.

Professional foresters have been testing, developing and refining silvicultural techniques for managing tropical forests for over one hundred years.[1] Given the appropriate site, species and funding, some of these efforts have been quite successful. Unfortunately, almost all of these techniques have been specifically designed to maximize the production of timber. Silvicultural systems for fruit or latex-producing trees that can be harvested nondestructively have received much less attention. This is not to say that such systems do not exist. Innumerable indigenous communities in the tropics have developed their own form of silviculture for managing non-timber tropical forest resources. Many of these systems are quite sophisticated and, not surprisingly, are comprised of many of the same operations that are routinely employed by trained silviculturalists. The major difference, however, is that the basic tenets of these indigenous systems have yet to be formally codified or even accepted as operationally valid.

Within the present context, both conventional and indigenous forms of forest management can provide useful insights into the appropriate silvicultural treatment of non-timber tropical forest resources. The purpose of this final chapter, therefore, is to provide a brief, yet comprehensive, review of the different silvicultural interventions currently in use, to describe their application, and to assess their overall effectiveness in procuring the regeneration and growth of desirable species.

The first section of this chapter focuses largely on the silviculture of commercial timber estates. Special attention is given to the individual operations or tools that are used to manipulate the floristic composition and structure of the forest. Selected examples of common silvicultural systems (the Selection System, the Malaysian Uniform System and the Tropical Shelterwood System) are then presented to illustrate how different combinations of these operations can be selected and scheduled to attain a particular management objective. The second section provides an overview of indigenous silvicultural practice as specifically related to the exploitation and management of non-timber resources. Specific examples from Amazonia and Southeast Asia are described in detail. The third section attempts to integrate these two management philosophies by proposing a general sequence of silvicultural operations for enhancing the regeneration, growth and productivity of a variety of different non-timber forest resources. Careful field trials and monitoring of these operations should ultimately lead to the development of an effective silvicultural system that is easy to apply, economically viable, and, most importantly, produces the desired changes in forest composition and structure.

The Components and Application of Tropical Silviculture

The primary objective of any silvicultural intervention is to modify the biotic or abiotic environment found within a tropical forest to favor the regeneration and growth of selected tree species (Smith 1962). This may be accomplished by opening the canopy to varying degrees, cleaning the understory, removing competitors, or in some cases, artificially increasing the density of desirable seedlings through planting. By definition, a successful silvicultural treatment is one in which the resultant forest environment encourages the production of some species (the desired resources), while depressing the establishment and growth of others (weeds, lianas, or tree species of marginal economic value). A detailed understanding of the shade tolerance, growth response and competitive potential of the seedlings and juveniles of the desired species is an obvious prerequisite to effective treatment. It is a waste of time, money and manpower to attempt extensive silvicultural intervention without having some knowledge of the ecological reaction of the principal species involved. If this information is lacking, which may frequently be the case, small-scale field trials involving any of the appropriate operations discussed below should first be conducted and monitored over time (Tang 1987; Hutchinson 1988).

Silvicultural Operations

Every silvicultural system is composed of individual operations or components that contribute to the overall management objective. Although the details may vary from system to system, the most common silvicultural operations applied in tropical forests may be divided into seven basic groups: harvesting, refinement, thinning, liberation, selective weeding, diagnostic sampling, and enrichment planting. The specific purpose and impact of each operation is quite distinct.

Harvesting. Harvesting is the most fundamental and, unfortunately in many cases the only, silvicultural operation in commercial forest management. While the primary purpose of this intervention is clearly the extraction of merchantable timber, tree felling can also play an important role in stimulating the regeneration and growth of certain species. It should be noted, however, that these supplementary benefits are not automatic, but rather are largely determined by the intensity of harvest, the shade tolerance and regeneration strategy of the desired species (see chapter 1), and the overall extent to which the forest is damaged by logging. This was illustrated by a comparative study of nine logging concessions in East Kalimantan (Soekotjo and Dickman 1978). On four concessions, the after-harvest density of established commercial seedlings was two to three times higher than that in undisturbed forest. The remaining five concessions, on the other hand, displayed a notable reduction in the density of desirable seedlings. The post-harvest growth response of poles and juvenile trees appears to be equally unpredictable. In Sabah and Sarawak, for example, the annual diameter increment of undamaged trees larger than 10 centimeters DBH has been found to both increase (Nicholson 1965; Fox 1972) and decrease (Nicholson 1958; Lee 1981) following logging. Additional components of this operation that usually occur prior to felling include the selection and marking of crop trees, the removal of woody climbers, and the design and placement of logging roads and skid trails.

In spite of the notable ecological impact of harvesting,[2] it is not unreasonable to assume that a low intensity of tree felling could also be extremely useful in the regeneration and management of certain non-timber forest resources. This would seem to be especially the case for many multiple-use tropical forest resources such as illipe nut (*Shorea* spp.), Brazil nut (*Betholletia excelsa*), and almendro (*Caryocar* spp.), all of which produce valuable seeds as well as commercial timber, or balata (*Manilkara bidentata*) and jelutung (*Dyera costula*), which produce both timber and latex.[3] Given sufficiently detailed information about the size-specific yields of these species, controlled, selective harvesting could be employed to replace those individuals that have passed their productive maxima. The timber would have a high marginal value at this point and would probably be of better quality than if harvesting were delayed until the tree began to senesce and completely stopped producing fruit or latex. Felling will also be an unavoidable component in the silvicultural treatment of resources such as gharu wood (*Alquilaria* spp.), rattan, and palm heart for which there is no alternative to destructive harvesting.

Refinement. Given the high species-richness of most tropical forests and the low density of merchantable timber, refinement operations are frequently employed to simplify the floristic composition of the stand. By removing stems that are old, defective or of no commercial value, the goal of refinement is to provide more utilization of the site by desirable tree species (Dawkins 1958). Girdling, injection with arboricide (such as a 5 percent 2,4,5-T solution in diesel oil), or felling are used to remove the unwanted stems. The enhanced irradiance and reduced interspecific competition resulting from refinement operations frequently causes a favorable response in the residual stand, and increases in growth of up to 50 percent have been reported from Central Africa (Wilkinson 1960) and Southeast Asia (Nicholson 1965, 1979). This common silvicultural practice has been applied for more than a century in Southeast Asia, and thousands of hectares of forest in West Africa have also been subjected to refinement (Wadsworth 1987).

The effectiveness of refinement, however, is contingent upon there being an adequate supply of desirable saplings and poles to fill the "ecological void" created by treatment. If such advance regeneration does not exist, refinement can actually worsen the current situation. There are additional ecological, as well as economic, reasons for minimizing the intensity of refinement. The selective removal of noncommercial species does not take into account the role that these species may play in pollination, seed dispersal, or nutrient cycling in the forest community, nor does it consider their potential importance as a source of shade to inhibit the growth of weeds and woody climbers. Furthermore, no provisions are made for subsequent changes in market conditions that could easily turn a currently useless species into a potentially valuable one.

Thinning. Thinning involves the selective removal of pole-sized stems of commercial species to favor the growth of the residual stand. This operation is frequently conducted in situations where there is an overabundance of individuals of intermediate size, not all of which can possibly survive until maturity. Rather than letting these individuals die from competition and suppression, they .are removed while they have at least some economic value. In marking these stems, special care is taken to leave those individuals with the best form, most rapid increment or highest productivity. By eliminating inferior trees from the forest, thinning functions in some respects as a type of refinement treatment. The importance difference, however, is that the products from thinning also provide the resource manager with an intermediate, and frequently substantial, source of revenue.

Liberation. Liberation is used to promote the growth of valuable understory trees through the elimination of less desirable neighboring competitors. After first selecting the most promising trees for future harvest based on species, size or form, unwanted stems are poisoned or girdled in small patches or "wells" around the desired individuals (Hutchinson 1987). As was succinctly described by Smith (1962), "liberation is logically indicated in any situation where a young crop of potentially good trees is overtopped by older, distinctly less desirable species. If the overtopped trees will respond vigorously and speedily to form a new stand of good quality, there is no quicker and cheaper silvicultural means of making a silk purse out of a sow's ear." This operation increases the illumination directly available to selected crop trees, yet maintains a generally shady and humid understory environment to inhibit the growth of pioneer species and woody climbers (Chaplin 1985). First developed for use in the neotropics (Wadsworth 1969), liberation is currently an integral component of silvicultural practice in the dipterocarp forests of Southeast Asia (Vincent 1961; Hutchinson 1975; Lee 1981; FAO 1989a).

Given that liberation involves the selective treatment of individual trees and therefore can be quite expensive, the reliability of the growth response following application is an important management consideration. A review of the existing literature suggests that this operation almost always promotes a significant increase in the growth and survivorship of target individuals. Primack and others (1989), for example, found increases in diameter increment of 60–120 percent within four treated forests in Sarawak; Nicholson (1980), Bryan (1981) and Hutchinson (1987) present similar data. In terms of the height growth of smaller size classes, Soerianegara, Alrasjid, and Hadisaputro (1976) report that liberation operations stimulated the average annual growth of commercial seedlings and saplings in East Kalimantan concessions by 26.7 centimeters and 45.6 centimeters, respectively. Based on these findings, liberation would seem to be a particularly promising tool for the treatment of non-timber forest resources. Canopy disturbance and stem removal are minimized by focusing attention solely on those individuals that are overtopped, crowded or otherwise merit release; the overall species composition of the forest remains essentially unchanged.[4]

Selective Weeding. Also known as "cleaning" or "underbrushing," this operation decreases competition in the understory by removing the saplings, shrubs and seedlings of undesirable species. Illumination at the ground level may also be increased somewhat following treatment. Although selective weeding of entire stands is occasionally conducted, this procedure is costly and subject to error due to the difficulty of identifying species in the smaller size classes. A more effective application is to selectively weed below the crowns of a limited number of commercially important adult trees prior to seedfall to specifically enhance the seed germination and seedling establishment of those species. As emphasized by the Food and Agricultural Organization of the United Nations (FAO) (1989a), selective weeding offers the multiple benefits of creating a reasonably uniform seedling distribution, ensuring a wide margin for the seedling mortality that will ultimately occur, and providing a considerable degree of choice in the selection of individuals for subsequent silvicultural activity. Selective weeding has been found to be especially successful in the mixed dipterocarp forests of East Kalimantan (Soerianegara, Alrasjid, and Hadisaputro 1976; Alrasyid, Soerianegara, and Warsopranoto 1978).

Diagnostic Sampling. Diagnostic sampling provides the quantitative information on seedling abundance and survival, tree growth, and available merchantable volume required for prescribing or assessing the impact of every type of silvicultural operation. Forest inventories and regeneration surveys, as discussed in chapter 3, are common examples of diagnostic sampling. Although the exact timing of these operations is extremely variable, they are an inevitable component of every commercial forest management system. As routinely practiced, diagnostic sampling is conducted before logging (to assess the standing stock and harvestable volume), immediately following logging (to assess the abundance and distribution of desirable seedlings and to prescribe appropriate silvicultural treatment), and at periodic intervals thereafter until the second harvest (to verify the success of silvicultural treatment). Different sample designs and intensities are employed depending on the structure and composition of the local forest; nested or "staged" linear sampling (as in Wyatt-Smith 1963) appears to be a particularly common procedure in Southeast Asia.

Enrichment Planting. Many of the previous silvicultural operations are designed to procure or enhance the natural regeneration of desirable species within the management area. In some environments, however, adequate regeneration may be lacking or be extremely difficult to establish, even with intensive silvicultural treatment. In such cases, enrichment planting or "artificial regeneration" is frequently employed. The intensity of this operation may range from a total dependence on artificial regeneration (as in plantations) to extensive planting within forests regarded as unsuitable for natural regeneration operations to selective enrichment of isolated patches of forest to supplement existing populations of seedlings and saplings (Baur 1964). The latter two types, known as "extensive" and "intensive" enrichment planting, respectively, are the most relevant to the present discussion.

Extensive enrichment planting has been frequently employed in the tropical forests of Africa (Aubreville 1953; Foury 1956). As usually practiced, planting lines are first opened in the forest at a spacing of 10–20 meters. As much as possible, these lines should be oriented east-west to maximize the incident radiation. At the start of the rainy season, nursery-grown seedlings are then planted every 3–5 meters within the lines (Aubreville 1957). The major constraints on this type of enrichment are the relatively high costs, poor survivorship exhibited by the seedlings, and necessity for frequent and intensive tending (weeding, liberation or thinning) of the planting stock. Given these limitations, extensive enrichment planting should only be applied with caution and should never be regarded as a sure or foolproof method of regenerating large areas of tropical forest (Dawkins 1959).

Intensive enrichment planting, on the other hand, has met with greater success and is currently used in Sabah (Chai 1975), Papua

New Guinea (White 1976), Peninsular Malaysia (Tang and Wadley 1876), Indonesia (MOF 1985) and other parts of Southeast Asia. The obvious benefit of this operation is that planting is only used in those areas that are notably deficient in regeneration (for instance, logging roads, skid trails and landings). Experience in East Kalimantan has shown that the survivorship of seedling transplants is generally satisfactory (70–80 percent), although there is much variability depending on the species and site conditions (FAO 1989b). Seedlings are easily raised in simple forest nurseries at a modest cost and can usually be transported to and planted in the desired area with little difficulty (GTZ 1989). Because of the apparent effectiveness of selective enrichment planting in supplementing the regeneration of mixed Dipterocarp forest, there is a large body of literature about seed storage and the propagation and transplant of seedlings of different commercial species (for example, Tang 1971; Sasaki 1980; Halle and Kamil 1981; Maury-Lechon, Hassan, and Bravo 1981; Srivasrava and Manggil 1981; Indrawan, Setiadi, and Manan 1982; Smits 1987).

The Development of Silvicultural Systems

Once the consequences of individuals operations are known with sufficient precision to allow prediction, different combinations of treatment can be pieced together to form a workable silvicultural system. It should be noted that the development of such a system reflects a long history of experimentation coupled with in-depth understanding of the ecological, economic and administrative framework within which the system is to be applied (Wyatt-Smith 1987). Successful silvicultural systems are not developed overnight.

There has been a great deal of experience with the silvicultural treatment of tropical forests in Asia and Africa (Schmidt 1987). Such experience is sorely lacking in Amazonia, where it has been recently estimated that less than 14,000 hectares of forest are subjected to any type of management at all (Lanly 1982; but also see De Graaf 1986). In view of this notable imbalance of existing information, the following discussion draws heavily on examples from Southeast Asia. It is important to emphasize, however, that the basic principles and operations outlined are equally applicable to many situations encountered in the neotropics (Wadsworth 1987).[5]

The silvicultural systems that have been developed for tropical forests can be divided into two groups: polycyclic and monocyclic systems. Polycyclic systems are those in which commercial trees are harvested repeatedly in a continual series of felling cycles. The length of these felling cycles is usually about half of the time required for a particular species to reach merchantable size. Monocyclic systems, on the other hand, harvest all of the merchantable volume in a single felling operation, with the length of the cycle being more or less equal to the rotation age of the species under exploitation. An additional difference of importance between these two types of silviculture is that polycyclic systems rely on the existing crop of seedlings, saplings and poles in the forest to produce the harvestable crop for the next felling cycle. Monocyclic systems ignore the accumulated growth of these smaller size classes and rely almost entirely on newly recruited seedlings to produce the next crop of trees. The Selective Felling System, as officially practiced in Indonesia, is a useful example of a polycyclic silvicultural system. The Malaysian Uniform System and the Tropical Shelterwood System are both common examples of monocyclic systems.

Selective Felling System. The Selective Felling System was first implemented in Indonesia in 1966 by government decree. The adoption of this system, based largely on its success in Malaysia and the Philippines, was precipitated by several factors (FAO 1989a). First, there was a strong desire on the part of the government to increase the existing production of commercial timber from local forests, but to do so in such a way that future wood supplies would not be severely diminished. Second, there was a growing appreciation of the important environmental benefits provided by intact forests (for example, soil, water and biodiversity conservation) and the need to safeguard these functions whenever possible. Third, the limited number of trained personnel and the enormous expanse of forest required that management activities be extensive rather than intensive in nature and of relatively simple application. Finally, the local dipterocarp forests were stocked with valuable *meranti* species (*Shorea* spp.) which were known to produce abundant, albeit periodic, crops of natural regeneration.

The basic sequence of operations in the Indonesian Selective Felling System is listed in table 4.1; following standard convention, the timing of each activity is referenced to the felling cycle. The system is composed of diagnostic sampling, harvesting, weeding, and enrichment planting operations. At least two years prior to harvest, the management area is inventoried and both the trees to be felled and the residual crop or "core" trees are marked. Harvesting is limited to trees larger than 50 centimeters DBH, and is contingent upon the existence of at least 25 core trees per hectare (greater than 35 centimeters DBH) of the desired species. Immediately after felling, weeding operations are initiated to enhance the growth of seedlings and saplings that have survived logging. Regeneration surveys are also conducted at this time, and any areas found to be deficient are enriched through planting. A second weeding is conducted five years later, and additional enrichment planting is employed as necessary to replenish existing seedling stocks. The continued growth of the core trees is expected to produce the harvestable volume for the next cutting cycle. Assuming an average annual increment of 0.5–1.0 centimeters, the length of this cutting cycle was fixed at thirty-five years. The overall goal of the system is to produce a sustainable yield of timber on a 70-year rotation using two felling cyclings and a base of natural regeneration that is occasionally supplemented by enrichment planting.

Besides in Indonesia, the selection system has been applied with slight modification in a number of other regions including Nepal, Pakistan, Burma, Viet Nam, Sri Lanka, India, Malaysia and the Philippines (Lanly 1982). It has met with varying degrees of success. In many regions, the damage resulting from repeated, and perhaps overly intensive, logging has greatly exceeded that originally predicted, and much of the advance regeneration upon which the system depends is destroyed (Hamzah 1978; Abdulhadi, Mirmanto, and Kartawinata 1987). Growth studies have also shown that the response of saplings and poles to release is notably less than anticipated, with the result that future yields may be difficult to maintain under a fixed-length, 30–40 year felling cycle (Tang 1976, 1987; Lee 1981). Lack of compliance with enrichment planting and weeding prescriptions is an additional and frequently chronic problem in those areas where available staff limitations preclude rigorous enforcement (Masson 1983). In spite of these limitations, however, selection systems still represent the most cost-effective and efficient alternative for integrating the often conflicting goals of sustained timber production and forest protection.

Malaysian Uniform System. The Malaysian Uniform System is perhaps the most classic example of a monocyclic silvicultural system. The epithet "uniform" refers to the single canopy opening that is used to procure regeneration, as well as to the even-aged condition of the young crop so produced (Whitmore 1984). This system, developed shortly after World War II for use in lowland dipterocarp forests, is based on the presence of an adequate stocking of seedling regeneration that can respond favorably to the heavy canopy opening created by logging (Walton 1954; Wyatt-Smith 1963). The system was developed in response to two

Table 4.1 Basic Silvicultural Operations and Sequence of Application in Indonesian Selective Felling System

Year	*Operation*
F–2	Pre-harvest sampling of regeneration/harvest of trees
F–1	Selection and marking of harvest trees
F	Felling
F + 0	Weeding and climber cutting
F + 0	Post-harvest inventory; enrichment planting (as required)
F + 5	Weeding; enrichment planting (as required); thinning of regeneration

Note: All operations are referenced to the time of felling (F).
Source: Adapted from Soerianegara and Kartawinata 1985; Wadsworth 1987; and FAO 1989a,b.

main factors: the increasing mechanization of logging and milling technologies that favor the use of a single, intensive harvest; and the observation that many areas exploited without any silvicultural treatment during the Japanese occupation displayed an abundance of spontaneous regeneration (Strugnell 1947; Walton 1948).

The silvicultural operations comprising the Malaysian Uniform System include diagnostic sampling, harvesting, refinement, weeding and thinning (table 4.2). Logging is preceded by regeneration sampling and the inventory and marking of harvest trees; harvesting is deferred if an insufficient seedling crop is encountered. The following year, felling and extraction of the harvest trees is conducted in a single operation, followed immediately by the poisoning of all noncommercial species down to a minimum diameter of 5–15 centimeters DBH. These operations usually produce a notable and rapid growth response from the advance regeneration. Three years later, linear strip sampling (Barnard 1950) is used to assess the need for weeding, refinement, or climber cutting to maintain an adequate growth rate in the newly developed crop of saplings and poles. Another sampling is made in the tenth year and additional treatment is applied as necessary. Light thinnings are conducted at twenty and forty years and the next harvest occurs at seventy years. If treatment is successful, the harvested stand should exhibit a mean diameter of 58 centimeters DBH and contain two to three times the merchantable volume of the initial forest (Wyatt-Smith 1963).

Local variants of the Malaysian Uniform System have been applied in Sabah, India and Pakistan (Wadsworth 1987). Although the system appears to be quite successful in the appropriate habitat (Burgess 1970; FAO 1974), its use in Peninsular Malaysia, where it was originally developed, has been largely discontinued due to a drastic reduction in the availability of such habitats. Many of the lowland forests for which the system was specifically designed have been converted to agriculture or plantations. Attempts to transplant the Malaysian Uniform System into the surrounding hill forests have been met with severe difficulties (Tang 1987). The steep terrain drastically increases the cost of operations, causes heavy mortality of young trees during logging, and creates an unacceptable degree of soil erosion. The most critical constraint, however, has been the low stocking and relative lack of natural regeneration of commercially desirable species, a condition that violates the basic premise of this form of silvicultural treatment. In an effort to resolve these difficulties, foresters in Malaysia have opted for a selection or polycyclic form of

Table 4.2 Basic Silvicultural Operations and Sequence of Application in Malaysian Uniform System

Year	*Operation*
F–1	Pre-harvest sampling of regeneration/harvest trees
F	Felling; poison girdling of unwanted trees
F + 3	Diagnostic sampling; weeding; climber cutting poison girdling
F + 5	Diagnostic sampling; weeding; climber cutting poison girdling
F + 10	Tending (as required)
F + 20	Tending (as required)
F + 40	Tending (as required)

Note: All operations are referenced to the time of felling (F).
Source: Adapted from Wyatt-Smith 1973; Burgess 1970; Thang 1987; and FAO 1989a.

management that requires more intensive tending of regeneration prior to harvest (Tang 1974; Griffen and Caprata 1977). The relevant lesson to be gained from this experience is the need for flexibility in the design and implementation of silvicultural systems, as well as a greater acceptance of the fact that no one system will ever be equally successful for all forest types and management objectives.

Tropical Shelterwood System. During the Second World War, a number of foresters with experience in Southeast Asia formulated a silvicultural system for use in the tropical forests of Nigeria. Similar in many respects to the older and somewhat outdated Malayan Regeneration Improvement Fellings (Taylor 1962), this new set of management procedures came to be known as the Tropical Shelterwood System. In contrast to both of the systems previously discussed, the Tropical Shelterwood System does not require an abundant crop of advance regeneration. Rather, a series of operations are initiated several years before the main harvest to gradually open the canopy, liberate the understory, and create conditions for the optimal establishment and growth of commercially desirable species. The newly recruited seedlings are "sheltered" for several years beneath a high canopy before being released through harvesting. The products of these preharvest refinements are sold as poles or firewood, providing an additional source of revenue for the system.

As is shown in table 4.3, the Tropical Shelterwood System is composed of diagnostic sampling, refinement, weeding, harvesting and thinning operations. Approximately six years prior to harvest, the management area is surveyed for potential harvest trees and existing regeneration. Based on the results from these surveys, refinement treatments are conducted to removed all undesirable stems from the lower canopy and understory; the cutting of woody vines is also initiated at this time. Only in the case of valuable pole species is tree felling employed, most of the stems being girdled to minimize damage to the residual stand and to provide a more gradual increase of illumination to the forest floor. An additional diagnostic sampling is performed four years before harvest to assess the effectiveness of refinement operations. A second felling is

Table 4.3 Basic Silvicultural Operations and Sequence of Application in Tropical Shelterwood System

Year	*Operation*
F–6	Sampling of regeneration/harvest trees
F–5	Climber cutting; poison girdling/felling of poles; formation of high shelterwood
F–4	Diagnostic sampling
F–3	Weeding; climber cutting; felling of middle canopy
F	Final felling; weeding
F + 2	Weeding; climber cutting
F + 10	Thinning (as required)
F + 20	Thinning (as required)

Note: All operations are referenced to the time of felling (F).
Source: Adapted from Haig, Huberman, and Aung Din 1958; Taylor 1962; Baur 1964; and Synnott 1979.

then conducted to remove stems from the middle canopy, followed by the final harvesting of upper canopy trees three years later. Weedings are performed between these two harvests as necessary to guide the development of the seedling and sapling crop. Finally, fifteen years after the initial treatment, thinnings are scheduled to groom the potential crop trees for the next rotation.

Although somewhat complicated in its application, the Tropical Shelterwood System has been employed with varying degrees of success in Ghana, Trinidad, and the Ivory Coast (Neil 1981). The system has been repeatedly modified in Nigeria to reduce treatment costs and to gain a greater degree of control over the regrowth that had started to swamp the sites after refinement. In actual practice, refinement operations were overly severe and frequently removed up to 65–80 percent of the total basal area of the site (Lowe 1978). As described by Baur (1964), the net result was a tangle of woody vines and shrubs that "spread like a cancerous growth under the canopy openings." These disappointing results can be largely attributed to the fact that, for administrative ease, prescriptions were routinely standardized from one forest to the next. The actual species composition and environment of each site, however, were extremely variable (Kio 1979). A final important factor hastening the demise of the Tropical Shelterwood System in Nigeria was the rapid conversion of local forests to plantations of oil palm and cocoa.

Although specifically related to the commercial production of timber, the preceding discussion has highlighted several considerations concerning the silvicultural treatment of tropical forests in general. First, effective techniques do exist for manipulating forest structure and composition in such a manner as to favor the abundance of desirable resources. The ultimate success of these techniques, however, is largely dependent on the particular species and site being managed. There is no single silvicultural system or package that can be blindly applied in every forest. Second, periodic sampling of the response of the forest to individual treatments is essential for guiding and refining subsequent operations. The most successful silvicultural systems are information-rich, and the greater the understanding of the ecological behavior of the species being managed, the easier it is to develop a viable system of silvicultural operations. Finally, the overall effectiveness of silvicultural activity is never dependent on technical elegance alone. Perhaps of greater importance in the long run is the ability of the resource manager to actually implement these activities, to change the prescriptions as necessary, and to be able to withstand the pressure and encroachment from conflicting forms of land use that will inevitably occur. Many of the failures of silviculture in the tropics are directly attributable to social and economic, rather than technical, constraints (Buschbacher 1990).

Indigenous Systems of Forest Management

Although the fact is seldom mentioned in forestry literature, native ethnic groups in the tropics have also developed effective systems for manipulating the distribution and abundance of important forest resources. Many of these systems are monocyclic and involve intensive management of the regrowth or secondary vegetation occurring after forest clearing for agriculture. This type of agroforesty activity is a common, albeit frequently overlooked, component of shifting cultivation in the tropics, and a growing body of research from both Southeast Asia (Conklin 1957; Pelzer 1978; Weinstock 1983; Dove 1985; Michon 1985) and Amazonia (Eden 1980; Posey 1982; Denevan and others 1984; Padoch and others 1985; Denevan and Padoch 1988) has documented its many forms and applications. Of perhaps greater interest to the present discussion, however, are the low-intensity, polycyclic systems that are used by indigenous communities to manage and conserve the limited areas of primary forest under their control.

Not surprisingly, very little information is available concerning the traditional management of intact tropical forest by native peoples. This lack of study is largely the result of the "invisibility" of these practices, that is, the forest, from a western perspective, does not look managed. There are few stumps, no neat lines of newly planted seedlings, and few visible means of access. A few researchers, however, have managed to document these procedures (for example, Chin 1985; Gomez-Pompa, Flores, and Sosa 1987; Posey and Balee 1989; Anderson 1990). The results from this work suggest that indigenous silvicultural practice is efficient, productive, and in all probability quite common in tropical forest environments. As such, these local management systems provide an interesting and potentially useful window into the sustainable management of non-timber tropical forest resources.

Based on existing reports and the author's personal observations, indigenous systems of forest management appear to exhibit several common characteristics. First, they are usually focused on the management of a large variety of different species and resource groups. Fruits, latex, resins and, in some cases, timber species are all managed simultaneously. This pattern is undoubtedly due, in part, to some basic cultural propensity toward resource diversity. For example, rather than managing for only the most commercial species of illipe nut (*Shorea macrophylla*), certain Dayak groups in West Kalimantan will selectively favor the regeneration and growth of nine different illipe nut species in their community forests (Padoch and Peters 1993). An additional benefit of this management strategy, however, is that it provides some security against sudden fluctuations in local market conditions. If the current prices for a particular resource are exceptionally low, others are always available for harvest. The former resource can simply be left in the forest that year to continue growing—and reproducing itself.

A second characteristic of indigenous silvicultural practice is that it rarely involves any type of drastic canopy opening. Tree felling, if employed at all, is usually of a low-intensity, selective nature. One of the obvious reasons for this is that most of the species being managed are non-timber resources which can be harvested non-destructively. The fact that many of these species are shade-tolerant, primary forest species (see chapter 1) that require only minimal canopy openings for establishment and growth is also undoubtedly important. As discussed in the previous section, canopy opening and liberation activities are a fundamental component of conventional silviculture, because they generally produce a notable growth response and can therefore significantly reduce the long interval between felling cycles. This shortening of rotation length is a major objective in commercial timber operations where more frequent harvests are directly translatable into higher economic returns. Growth enhancement and rotation length are relatively less important in the management of non-timber forest resources because these products continually provide a low level of economic return. The manipulation of light level and canopy closure involves a trade-off in these systems. Some degree of intervention may be desirable to stimulate the yield of a certain resource; more intensive treatment would require more work and might actually shorten the productive life span of the species.

A final characteristic of many traditional systems of forest management is the seemingly haphazard or casual manner in which they are applied. Management activities are usually conducted extemporaneously as part of harvesting or collection operations, or they are simply "squeezed in" between any of the innumerable work obligations (tending of agricultural fields, hunting or fishing) that characterize the lives of a rural farmers in the tropics. Many of these indigenous foresters would not even consider what they do as management (a tendency that, unfortunately, makes these operations additionally hard to document). The salient point, however, is that these systems appear to work quite well with minimum capital and labor investment.

In view of the apparent benefits afforded by a more traditional or indigenous approach to forest management, it is perhaps useful to examine in greater detail the specific procedures or sequence of operations that are employed in different habitats. For the purpose of this discussion, two representative examples or case studies have been selected. The first example concerns the treatment of hill dipterocarp forest in West Kalimantan and outlines the techniques used by local Dayaks to create *tembawang* or mixed forest orchards. The second example focuses on the management of floodplain (*varzea*) forest by rural communities living in the Amazon estuary. As will later become apparent, there are distinct silvicultural differences between these two systems.

Managed Forest Orchards in West Kalimantan

Although similar techniques are applied by a variety of different Dayak groups throughout Borneo, the current system of interest was developed by the Daret of Balai for use within the Sanggau subdistrict of West Kalimantan. This area is characterized by low hills of intermediate to steep topography, fertile valleys and numerous small rivers and streams. The natural vegetation is hill dipterocarp forest (Whitmore 1984). The following description is based largely on Padoch (1992), Padoch and Peters (1993) and extensive personal observations.

The managed forests (*tembawang*) that cover the upper slopes of the region contain a variety of useful plant resources including illipe nuts (*Shorea* spp.), rattan (*Calamus* spp.), sugar palms (*Arenga pinnata*), construction woods (for example, *Eusideroxylon zwagerii*) and bamboo. Edible fruits, including durian (*Durio zibethinus*), rambutan (*Nephelium* spp.), langsat (*Lansium domesticum*) and mangosteen (*Garcinia mangostana*) are especially common. The distribution and abundance of all of these resources, both wild and introduced, have been consciously enhanced by the Daret of Balai. The essential components of their management strategy are selective weeding, enrichment planting, and occasional, low-intensity harvesting of poles for house construction.

Much of the selective weeding occurs around durian and illipe nut trees during harvest season to facilitate the location and collection of fruits. The seedlings and saplings of particularly valuable species are spared during these operations, while less desirable species or even useful species that already occur in adequate abundance in the forest are eliminated. Daret informants cite the most casual and unintentional of planting techniques as important in the formation of tembawang. For example, they report that many trees are recruited from seeds discarded by people eating fruit as they walk through the forest. Other species, such as rattan, construction timbers and medicinal plants are carefully transplanted. Given the mixture of spontaneous and planted vegetation in these forests, it is extremely difficult to distinguish between wild trees, intentionally planted trees, and trees that became established as volunteers and were later spared during weeding operations. The Daret claim to have planted over seventy species of fruit trees, and they can identify over one hundred different species of edible fruits in their managed forests. The planting of durian trees to commemorate the dead is a particularly common practice.

The light canopy openings needed to drive the system are provided by natural treefalls and occasional selective fellings. Given that over thirty species of valuable timber trees were identified in one *tembawang*, periodic fellings to procure materials for house construction are probably sufficiently frequent to avoid excessive mortality or suppression among seedling populations. Qualitative observations in tembawang suggest that the canopy cover is continuous, yet relatively shallow and high.

Although most of the innumerable resources produced in *tembawang* are destined for household or subsistence use, important commercial species such as durian and illipe nut are collected and sold to local traders whenever available. The marketing of durian fruits has become an especially important economic activity within the last ten years. For instance, in 1991 during peak fruit production, more than 10,000 durian fruits were transported from four Daret villages in a single day. Even at a minimal price of about US$0.15 per fruit, the collective income earned throughout the month-long season was substantial. It should be noted that there is usually one major durian season every year.

Varzea Silviculture in the Amazon Estuary

A unique ecological feature of many of the floodplain forests of eastern Amazonia is the pronounced dominance of the açai palm (*Euterpe oleracea*).[6] These oligarchic tropical forests are particularly well suited to resource exploitation (Peters and others 1989), and it is therefore not surprising that local communities have developed sophisticated systems for doing so on a continual and sustainable basis. The present example details the management techniques used on Ilha das Onças (Jaquar Island) near the city of Belem in Brazil. The discussion is based almost exclusively on the extensive studies of Anderson and others (1985), Anderson and Marta Ioris (1989) and Anderson (1988, 1990).

The silviculture practiced on Ilha das Onças is used to maintain a variety of different fruit, latex and timber-producing species, but special attention is given to the *açai* palm because of its high commercial value. The system is composed of four basic operations: selective weeding, enrichment planting, liberation thinning, and periodic selective harvesting of important timber species such as *andiroba* (*Carapa guianensis*) and *ucuuba* (*Virola* spp.).

Occasional selective weeding is used to favor the regeneration of desirable species, to maintain good access to the site and to remove the troublesome spines produced by *Astrocaryum* palms. Species frequently spared in these weeding operations include *tapereba* (*Spondias mombin*), *inga* (*Inga* spp.), and *miriti* (*Mauritia flexuosa*), all of which produce edible fruit and also attract game, and *seringueira* or rubber (*Hevea brasiliensis*). Commercial fruit species such as *cacao* (*Theobroma cacao*), *cupuaçu* (*Theobroma grandiflorum*) and coconut (*Cocos nucifera*) are especially protected during these thinnings, sometimes by constructing temporary fences of palms leaves around the seedlings and saplings.

Enrichment planting can be either deliberate or unintentional. *Açai*, mango (*Mangifera indica*), inga and *annatto* (*Bixa orellana*), for example, are frequently propagated by unconscious human dispersal of seeds into the management area. Transplanted seedlings or cuttings, on the other hand, are used to specifically increase the regeneration of cacao, cupuaçu, coconut, mango and *genipap* (*Genipa americana*). Several varieties of banana are also introduced. Organic material (usually decaying leaves and inflorescences of the açai palm) is occasionally piled at the base of these transplants to provide an additional source of nutrients.

Liberation thinnings are employed to stimulate the growth of desired species, as well as to refine the floristic composition of the stand. Woody vines and tree species used specifically for timber or firewood are frequent targets in these operations. Large canopy trees with little value for timber are girdled rather than felled to reduce damage to the residual trees. Given the economic importance of açai palms, trees that branch at about 8–15 meters and therefore interfere with the mature crowns of this species, are especially prone to elimination. The products from these liberation thinnings provide an important source of firewood for household use. A final procedure employed in the system is the regular pruning of açai palms to harvest palm hearts. Besides providing an economic return, local residents report that this horticultural practice also enhances fruit production by the remaining stems.

The silvicultural operations applied at Ilha das Onças have a notable effect on the structure and composition of the local varzea forest. Relative to undisturbed habitats, the managed forests possess a lower total biomass, especially in the lower and middle canopies, and a lower species diversity (twenty-five species as compared to fifty-two species per 0.25 hectare). Apparently, liberation thinnings remove about 25 percent of the basal area and 50 percent of the tree species. The net result, however, is a marked increase in the concentration or abundance of economic species within the managed forest. From a silvicultural standpoint, the treatment has been extremely successful.

The economic returns provided by the system are also favorable. The results from a controlled field experiment (Anderson and Jardim 1989) revealed that the liberation, weeding, and pruning of *açai* increased fruit yields from 1,158 kilograms to 1,854 kilograms per hectare, resulting in a 58 percent increase in gross annual earnings. After discounting the estimated costs of management, net annual returns from the system were on the order of US$100 per hectare. It should be noted that this analysis does not take into account the value of other products (for example, palm heart and timber) extracted during pruning and liberation operations. Furthermore, the study was conducted only during the first year of management activities when treatment costs are somewhat elevated. In subsequent years, these costs will invariably drop while system outputs should continue at their present level.

There are notable differences between the Kalimantan and Amazonian systems of silvicultural treatment. Some of these differences reflect the nature of the forest within which each system is applied, the *varzea* forest containing a high initial density of useful resources and a smaller complement of associated tree species. Ilha das Onças is also located quite close to a major market center. Both of these factors have led to the development of a system that is more intensive and market-oriented than that observed in West Kalimantan. The Daret of Balai, on the other hand, employ a more casual approach to selectively manage a larger number of resources, most of which are destined for subsistence use. In their own way each system is surprisingly well adapted to existing forest and market conditions.

The successful application of selective weeding and enrichment planting is also an interesting feature of both of these indigenous management systems. By focusing specifically on the seedling and sapling stages, the coordinated use of these two operations provides a subtle degree of control over floristic composition with only minimal disturbance to forest structure. Although the selective removal of woody shrubs and vines with a machete can be quite labor intensive, it does eliminate the frequent need (and expenditure) for that quintessential instrument of forestry practice, the chain saw. Floristic changes are precipitated gradually through enrichment, not abruptly through refinement. In the Amazonian example, liberation treatments are judiciously employed to provide a larger degree of control over the development of particularly valuable growing stock.

Perhaps the most notable feature of both examples of traditional forest management, however, is their inherent simplicity. Each form of treatment has been stripped down to the minimum number of operations required to get the job done; they are both minimalistic, yet extremely flexible silvicultural systems. This level of accomplishment is, in large part, the result of the intimate knowledge possessed by Dayaks and rural Amazonians about the ecological behavior of different forest resources and a long history of continual, trial-and-error experimentation. Although there is much to be learned from these systems, one particularly relevant lesson is that the selection of silvicultural operations for managing non-timber forest resources should always be guided by Occam's razor: never opt for something complicated or expensive when something simple and cheap will produce the same result.

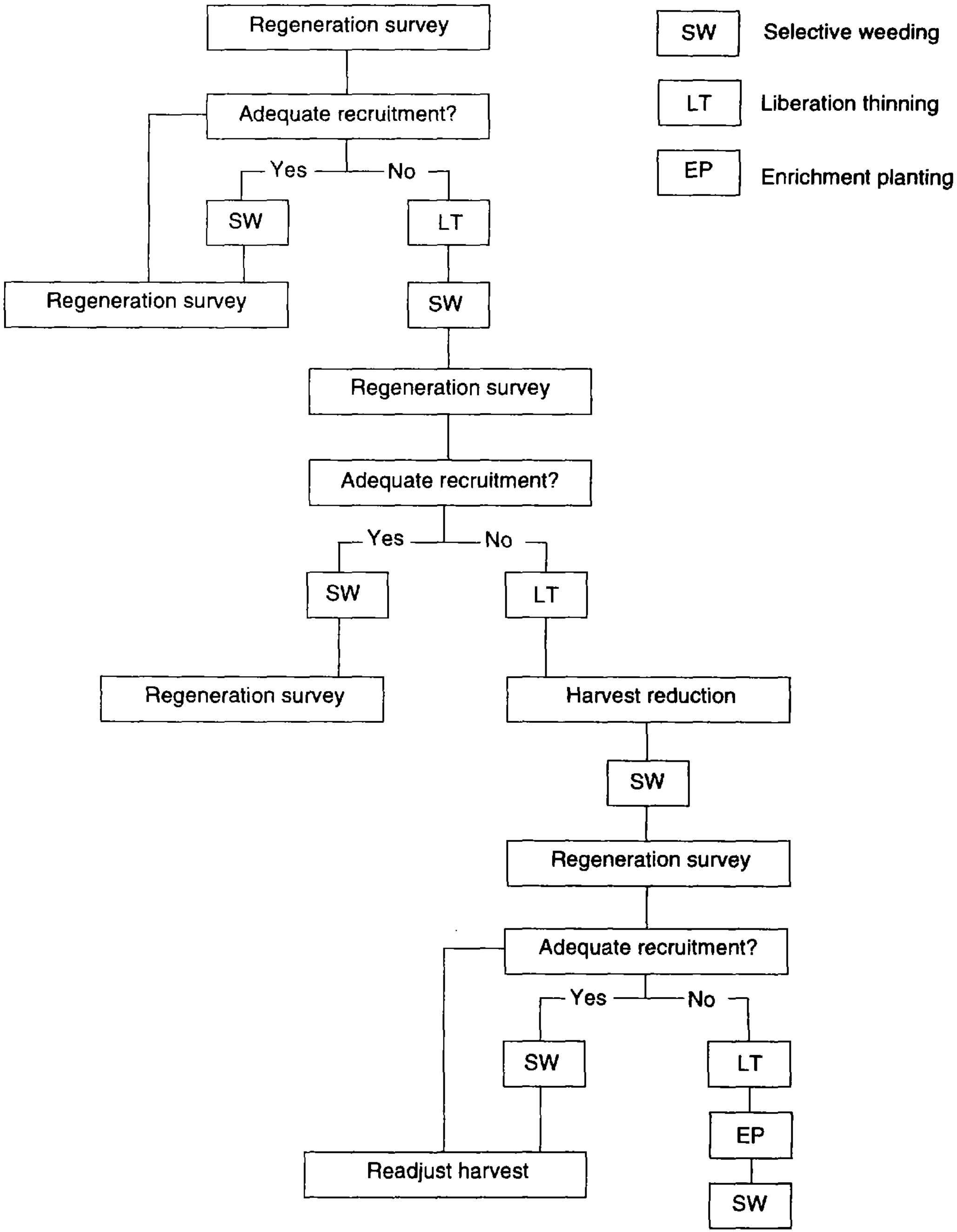
Steps Toward a Silviculture for Non-Timber Forest Resources

An unavoidable conclusion to be drawn from the preceding analyses is that both conventional and indigenous silviculture practice have something useful to offer in designing systems for the sustainable management of non-timber forest resources. Ideally, it would seem that such systems should cause minimal disturbance to the canopy, should be relatively easy and inexpensive to apply, should be subjected to regular and frequent impact monitoring, and should opt for the gradual, rather than instantaneous, manipulation of resource density and abundance. Based on these considerations, a general framework for guiding the silvicultural treatment of non-timber forest resources is shown in figure 4.1.

It is important to emphasize at the outset, that the sequence of operations shown in this figure does not represent a silvicultural system. Rather, it is a recommended series of trials, an exploration of the response of different forest types and species to treatment, that can later be used as a foundation for developing a functional and cohesive silvicultural system. Adopting the philosophy of the indigenous resource manager, the procedure attempts to identify the most basic and simplest combination of operations that can be applied to achieve the desired result. Using the experience gleaned from conventional silvicultural practice, periodic diagnostic sampling is included as an important component to provide quantitative information about the relative success of each intervention. The procedure can be applied to any species or type of resource. It is suggested, however, that the scale of initial operations be kept relatively small. Once a successful response has been obtained, the treatments can then be safely applied on a larger, more commercial scale.

The procedure outlined in figure 4.1 is comprised of three basic silvicultural operations: selective weeding, liberation thinning, and enrichment planting. An additional treatment, the implementation of harvest controls, may also be occasionally required. As can be appreciated, the focus of treatment is primarily on the seedling and sapling stages. Whenever possible, silvicultural treatment attempts to facilitate the natural regeneration

Figure 4.1 Proposed Sequence of Silvicultural Operations for Enhancing the Regeneration, Growth, and Productivity of Non-Timber Tropical Forest Resources



Note: See text for timing and application of specific operations.

of the desirable species already growing in the management area. If this is lacking, supplementary operations are initiated to enhance the reproductive success of these species. Only in extreme cases, when even these treatments prove ineffective, is the selective enrichment of a particular species considered as an alternative. These latter activities may be given higher priority depending on the actual management objective. The introduction of especially high-yielding or vigorous genotypes for stand improvement, for example, will obviously require a coordinated planting program.

In most situations, silvicultural treatment is required either to increase resource density, abundance, and productivity or to procure the regeneration of especially recalcitrant species that may be in danger of overexploitation. Given these management objectives, the first step is to consult the results from the most recent regeneration survey of the area (chapter 3) to assess the size and distribution of current seedling populations. If existing seedling crops of the desired species are sufficiently large, selective weeding operations should be begun immediately to enhance the growth and survival of this regeneration. All woody vines, shrubs, and the seedlings and saplings of undesirable species should be removed during this operation. In all probability, the most intensive cleaning will be required directly under or quite near to the crowns of adult trees. If, on the other hand, advance regeneration is severely lacking, light liberation thinnings should be conducted to open the canopy slightly and to increase light levels in the understory. The stems to be eliminated should be selected from the middle canopy, and except in the case of extremely valuable timber species, girdling or poisoning, rather than felling, should be employed. This operation will be most effective if conducted several months prior to the normal fruiting season of the species in question. Approximately six months after seedfall, selective weeding is applied to thin out and release any recruitment that may have taken place.

As suggested in chapter 3, regeneration surveys should be conducted at five-year intervals. These diagnostic samplings become especially important once silvicultural treatment has begun because they are the basis for developing and refining further prescriptions. If regeneration is found in the survey to be sufficiently abundant, an additional selective weeding should be all that is required to maintain this regeneration and to allow it to slowly mature. If, however, adequate recruitment has yet to be obtained, an additional series of operations must be initiated, including both liberation thinning and a reduction in existing harvest levels. The net result of these operations is a further reduction in canopy cover and, hopefully, an increase in the total number of seeds that are available for germination on the forest floor. Undesirable stems from both the middle and upper canopy should be removed during this "second-degree" liberation thinning, taking special care not to open the upper canopy so extensively that the growth of climbers and weedy secondary vegetation is triggered. Any new seedlings obtained through treatment should later be selectively thinned.

In many cases, these procedures will prove effective in providing an adequate quantity of seedlings and saplings. If successful, the resultant regeneration should later be selectively weeded and harvest intensities returned to their pretreatment levels. The failure of these treatments, however, will necessitate the last phase of operations shown in figure 4.1. As indicated, a final liberation thinning is conducted, and at this point, stem removal should concentrate on upper-canopy trees. Girdling, rather than felling, is still the recommended method for creating gaps in the canopy. Nursery-grown seedlings (either wildlings or seed stock) are then carefully transplanted beneath these canopy openings. Taking into account the inevitable mortality that will occur, a sufficient number of seedlings should be planted to provide a final crop of approximately one hundred established seedlings per hectare. These seedlings should be tended with selective weedings to ensure their ultimate establishment.

At first glance, the sequence of operations described may appear excessively complicated, tedious or costly. It should be realized, however, that not all of these steps will be required, or even considered, for many species. Based on the long experience of indigenous foresters, selective weedings and light canopy openings alone may be sufficient to elicit the regeneration of a large number of primary forest trees. Given our current level of understanding about the ecology and management of non-timber resources, the critical issue at this point is to figure out exactly which combinations of treatment are most appropriate for different species, forests and management objectives. This can only be accomplished through a systematic, step-by-step assessment of cause and effect, starting from the simple and then moving, as necessary, to the more complex. There is an urgent need to develop silvicultural systems for managing non-timber tropical forest products on a sustained-yield basis. The overall strategy outlined above is perhaps the quickest, least expensive, and most effective method of achieving this objective.

Chapter Summary

1. Controlled harvesting and periodic regeneration surveys alone can frequently be a simple and effective method of achieving a sustainable harvest of non-timber forest products. The hallmark of this "passive" form of management is that the intensity of human intervention is adjusted in response to the ecological dynamics of the target population, instead of the other way around.

2. In some situations, however, an "active" or intensive form of management may be warranted: for example, increasing the density and productivity of selected resources in response to changing market conditions, enhancing the regeneration of recalcitrant species in danger of overexploitation, or improving the genetic composition of the stand.

3. Professional foresters have been developing and refining silvicultural techniques of managing tropical forests for more than one hundred years. Most of these systems, however, have been specifically designed to maximize the production of timber. Silviculture systems for fruit and latex-producing trees that can be harvested nondestructively have received much less attention. This is not to say that such systems do not exist. Innumerable indigenous communities in the tropics have developed their own form of silviculture for managing non-timber tropical forest resources.

4. Every conventional silvicultural system is composed of a series of individual operations or components that contribute in different ways to fulfilling the overall management objective. The most common silvicultural operations applied in tropical forest may be divided into seven basic groups: harvesting, refinement, thinning, liberation, selective weeding, diagnostic sampling, and enrichment planting.

5. The silvicultural systems that have been developed for use in tropical forests are of two types—polycyclic and monocyclic. In polycyclic systems commercial trees are harvested repeatedly in a continual series of felling cycles. The Indonesian Selective Felling System is a common example of a polycyclic system. In monocyclic systems, on the other hand, all of the merchantable timber is harvested in a single felling operation and rely almost entirely on newly recruited seedlings to produce the next crop of trees. The Malaysian Uniform System and the Tropical Shelterwood Systems are widely employed examples of monocyclic systems.

6. Indigenous systems of forest management have been little studied largely because of the "invisibility" of these practices. The few systems that have been studied, however, exhibit several common characteristics. First, they are usually focused on the management of a large variety of different species and resource groups. Second, they rarely involve any type of drastic canopy opening, and any tree felling is usually of a low intensity and selective nature. A final feature of many traditional systems of forest management is the seemingly haphazard or casual manner in which they are applied. Detailed analyses of two such systems, the forest orchards (*tembawangs*) of West Kalimantan and the managed flooded forests in the Amazon estuary, indicate that both systems are ex-

tremely successful and well adapted to existing forest and market conditions.

7. Both conventional and indigenous silvicultural practice have something useful to offer in designing systems for the sustainable management of non-timber forest resources. Based on this consideration, a general framework for guiding the silvicultural treatment of non-timber forest resources is presented here.

8. The proposed procedure is a series of trials, an exploration of the response of different forest species to treatment, that can later be the foundation for developing a functional and cohesive silvicultural system. The procedure attempts to identify the simplest combination of operations that can be applied to achieve the desired result. It is comprised of three basic treatments: selective weeding, liberation thinning, and enrichment planting. An additional operation, the implementation of harvest controls, may also be required occasionally.

Notes

1. Large areas of dipterocarp forest in Southeast Asia were being treated silviculturally over a century ago (Dawkins 1961), and the first management plans for the teak forests of Burma were completed in 1870 (U Kyaw Zan 1953). The first manual of Indian silviculture appeared in 1988. Interestingly, the first attempts to bring logged-over tropical forest under scientific management are reported to have begun at the turn of the century, when silvicultural treatments were developed to stimulate the growth of Palaquium gutta, an important latex-producing species in Peninsular Malaysia (Wyatt-Smith 1963). Excellent reviews of the history of tropical silviculture are provided in Taylor (1962), Baur (1964) and Jonkers (1987).

2. A detailed discussion of the ecological impacts of commercial logging in tropical forests is presented in chapter 2.

3. Further information on these forest resources is contained in Chapters II and III. Tengkawang is a valuable oil seed in Southeast Asia; Brazil nut and almendro, also an edible seed, are native to Amazonia. Balata and jelutung are important latex-producing species in Amazonia and Kalimantan, respectively. All five species are large, upper-canopy trees of primary tropical forest.

4. Jessup (1984), writing about the management of forest fruits in Indonesian Borneo, provides a useful and surprisingly relevant discussion about the potentials and limitations of this silvicultural operation.

5. Additional descriptive data about this forest type are provided in chapter 1; chapter 2 contains a brief discussion about the marketing and uses of the *Euterpe* palm.

6. Readers desiring a more comprehensive discussion of silvicultural systems in the tropics are referred to the excellent textbooks of Broun (1912), Troup (1952), Haig, Huberman, and Aung Din (1958), Taylor (1962), Baur (1964) and Synnott (1979) and Matthews (1989).

Appendix 1. Key Issues

Key Issues in the Ecology and Management of Non-timber Forest Resources

The preceding four chapters have presented a large amount of information concerning the ecology of tropical trees, the impact of resource exploitation, the planning for sustainable management and the silvicultural treatment of non-timber forest resources. To make this information more accessible to project managers, policymakers and researchers, an annotated outline of the major factors effecting the sustainability of intensive fruit, latex, medicinal plant, rattan, resin or oilseed harvest is presented below. Whenever appropriate, the specific sections or chapters related to a given topic are shown in brackets for easy reference.

1. Site

1.1. Forest type

All tropical forests are not the same in structure and composition. Forests exhibiting high species diversity usually contain a low density of useful resources. Management is simpler and productivity per unit area higher in forests with low species-richness. Even forests of extremely high diversity, however, can be successful exploited if proper precautions are taken.

See Tree diversity and density, chapter 1; chapter 3.

1.2. Location or access

Forest with easy access will require less effort to manage and exploit. Costs will also be reduced. Unfortunately, it is usually these areas that are converted to other forms of land use. Transport costs will also be lower if the management area is located near a market.

See chapter 2; Initial planning operations, chapter 3; Forest inventory, chapter 3.

1.3. Slope

Steep slopes are obviously harder to work on than flat land. The potential for erosion due to tree felling or intensive harvest activities is also increased in these habitats. Forest composition usually reflects the topography.

See Regeneration and growth, chapter 1; Impact on soils and site fertility, chapter 2; Initial planning operations, chapter 3.

1.4. Soils

Fertile soils will exhibit higher productivity than degraded soils and be more resilient to nutrient losses resulting from intensive exploitation. Riparian and seasonal swamp forests receive a nutrient subsidy through periodic flooding.

See Impact on soil and site fertility; chapter 2.

1.5. Animal populations

Forest animals (mammals, birds and insects) present a dilemma for resource managers.

They are responsible for large amounts of seed destruction and seedling predation, yet they also perform essential ecological services such as pollination and dispersal. Silvicultural treatment can usually compensate for seed or seedling losses; the lack of a pollinator is irreparable. Special care should be taken to preserve the intricate plant-animal relationships that abound in tropical forests.

See Pollination, chapter 1; Breeding systems, chapter 1; Seed Dispersal, chapter 1; Impact on animal populations, chapter 2.

2. Species

2.1. *Type of resource*

Some types of non-timber resources must be harvested destructively (for example, rattan, certain resins, and palm heart). These resources will require a more concerted management effort than those that can be simply collected or tapped (fruits or latex). Ease of harvest and frequency of production are also important parameters to consider. Careful selection of the resources to be exploited can greatly enhance the potential for sustainability.

See Phenology of flowering and fruiting, chapter 1; Reproductive propagules, chapter 2; Plant exudates, chapter 2; Vegetative structures, chapter 2; Selection of species and resources, chapter 3; chapter 4.

2.2. *Life cycle characteristics*

These three simple words describe the essence of a species response to controlled exploitation. Some species are inherently better equipped to maintain a continual level of population recruitment when subjected to harvest than others. These same species are also the ones exhibiting the quickest and most positive response to silvicultural treatment. The importance of knowing as much as possible about the life cycle characteristics of different resources cannot be overemphasized. Species selection, planning activities, definition of a sustainable harvest level, management operations, and silviculture are all contingent upon this information. The collection of such data should be considered of highest priority. Reproductive biology and the site requirements for successful regeneration and growth are especially important topics.

See Flowering, fruiting and reproductive dynamics, chapter 1; Regeneration and growth, chapter 1; Population structure, chapter 1; Selection of species and resources, chapter 3; Table 3.1; Yield studies, chapter 3; figure 3.7; Defining a sustainable harvest, chapter 3; chapter 4.

2.3. *Productivity or yield*

The more productive a resource, the more frequently and intensively it can be harvested. Quantifying this basic parameter is a critical, yet frequently ignored, management activity. It is not possible to define a sustainable yield in the absence of information about how much the forest produces.

See Yield studies, chapter 3; Defining a sustainable yield, chapter 3; figure 3.1.

2.4. *Market value*

Although not strictly related to the parameters being discussed, high-value resources will produce greater revenues that, it is hoped, will permit a more effective level of management. Productivity and yield are important components of a species' total market value.

3. Management planning

3.1. *Cartography and aerial imagery*

Aerial photos or satellite images can greatly facilitate the construction of base maps, the location of sample plots for inventory work and the delineation of selected management units. Whenever possible these images should be purchased; the initial investment will be rapidly repaid by their frequent utility.

See Initial planning operations, chapter 3.

3.2. Inventory data

Detailed information about the distribution and abundance of different plant resources within the forest is fundamental to exploitation and successful management. By stratifying inventory operations by habitat or forest type, the site specificity of different species can also be clarified. Management operations cannot proceed without inventory data.

See Forest inventory, chapter 3; boxes 3.1 and 3.2; Selection of species and resources, chapter 3; Yield studies, chapter 3; Defining a sustainable harvest, chapter 3; Steps toward a silviculture for non-timber forest resources, chapter 4.

3.3. Yield studies

Yield studies are a prerequisite of economic planning and forest valuation. They are also the key to defining a sustainable level of resource extraction. The fact that this information is frequently lacking sheds some doubt on the long-term viability of many current efforts to promote the increased utilization of non-timber resources. Yield studies are an essential and unavoidable management activity that should be given the highest priority.

See Yield studies; chapter 3; figure 3.5; table 3.2; Estimating total population productivity, chapter 3; Delineation of production areas, chapter 3; Defining a sustainable harvest, chapter 3.

3.4. Definition of sustainable harvest

There is a lot of talk about sustainable harvesting, but very rarely has it actually been defined for any non-timber resource. Simple techniques for doing so exist, and these should be employed for every resource and site being considered for exploitation. Perhaps most importantly, the results from these analyses should be applied and strictly enforced.

See Defining a sustainable harvest, chapter 3; Successive approximation, chapter 3; Plant demography, matrix models and computer simulations, chapter 3.

4. Silvicultural treatment required

4.1. Increase density, abundance, or productivity

This is largely determined by management objectives and the particular species and sites selected for exploitation. Such treatment will frequently be warranted in cases of improved market conditions or the scattered and low-density distribution of particularly valuable resources.

See The components and application of tropical silviculture, chapter 4; Steps toward a silviculture of non-timber forest resources, chapter 4; figure 4.1.

4.2. Facilitate regeneration of recalcitrant species

This treatment is usually employed as a response to incipient overexploitation. It may, in some cases, be extremely difficult and costly to achieve. Whenever possible, the species to be managed should be selected carefully based on ecological criteria to avoid the need for this type of silvicultural treatment.

See Regeneration and growth, chapter 1; Population structure, chapter 1; Selection of species and resources, chapter 3; Table 3.1; chapter 4; figure 4.1.

5. Available infrastructure

5.1. Labor

It goes without saying that a sufficiently trained and efficient labor force is required for harvesting, management, and silvicultural operations. Largely dependent on the size of the management area and the complexity of the operations plan. Inventory and silvicultural treatment are particularly labor intensive.

5.2. Funding

Supplemental sources of funding will probably be required during the initial phases of management planning and exploitation. This need for support should decrease once a workable management plan has been developed and a predictable level of harvest has been established.

5.3. Institutional backing

The support, both financial and political, of established local institutions (preferably at the central level) will greatly enhance the potential for success of any program of sustainable non-timber forest resource exploitation. The failure to procure such support can result in continual problems.

5.4. Long-term commitment

It makes no sense to invest time and money in developing a management plan if there is no guaranteed long-term commitment from all parties involved. Trees grow very slowly, and the inherent sustainability of resource exploitation can, in reality, only be assessed over decades or centuries. This key consideration is frequently overlooked by project managers and policymakers alike.

Appendix 2. Annotated List of Relevant Plant Taxa

The plant taxa referred to in the text are summarized here according to family, "local" name, and notes on their relevant market or biological features. The English names are provided for as many species as possible; the vernacular names are based on personal observations by the author.

Genus and Species	*Family*	*Local Name*	*Notes*
Achras	Sapotaceae		genus includes several species of edible fruits
Aleurites moluccana	Euphorbiaceae	candle nut	seeds contain a useful oil
Annona	Annonaceae		genus includes several important market fruits (e.g., guanábana and soursop)
Aquilaria	Thymeliaceae		
A. malaccensis	Thymeliaceae	aloes wood	heartwood contains a useful resin; incense wood
Araucaria cunninghami	Araucariaceae	hoop pine	important timber species; occasionally cultivated as an ornamental
Arenga pinnata	Palmae	sugar palm	phloem sap from inflorescence used for making sugar
Artocarpus heterophyllus	Moraceae	jackfruit	common market fruit in Southeast Asia; a single fruit may weigh 20–30 kilograms
Astrocaryum	Palmae		
A. mexicanum	Palmae		understory palm in Mexico and Central America
Avicennia	Rhizophoraceae		type of mangrove

Genus and Species	*Family*	*Local Name*	*Notes*
Baccaurea	Euphorbiaceae		genus includes several important market fruits (e.g., tampui and rambai)
Bactris gasipaes	Palmae	peach palm	cultivated source of palm heart
Bambusa	Graminae		type of bamboo
Bixa orellana	Bixaceae	achiote	seeds used as a coloring agent
Bertholletia excelsa	Lecythidaceae	brazil nut	edible seeds; important export commodity from Brazil
Brosimum	Moraceae		
B. alicastrum	Moraceae	breadnut	source of edible fruits and seeds, forage, and medicinal compounds
Calamus	Palmae		important rattan genus
C. caesius	Palmae	rotan sega (Indonesia)	high quality rattan cane for use in furniture manufacturing; cultivated
C. diepenhorstii	Palmae	rotan batu (Indonesia)	cane used locally for cordage and basketry
C. exilis	Palmae	rotan lilin (Malaysia)	cane used locally for cordage and basketry
C. manan	Palmae	rotan manau (Indonesia)	premier large diameter rattan cane; of unsurpassed quality for making furniture
C. ornatus	Palmae	rotan kesup (Indonesia)	important rattan cane for making furniture
C. peregrinus	Palmae		large cane rattan; widely used in Thailand for making furniture
C. trachycoleus	Palmae	rotan irit (Indonesia)	important small cane rattan; used for making mats
Calophyllum	Guttiferae		genus contains several important timber species; latex from some species used as a fish poison
Canarium	Burseraceae		genus contains several species with edible fruits or useful resins
Carapa	Meliaceae		
C. guianensis	Meliaceae	andiroba (Brazil)	important timber species

Genus and Species	*Family*	*Local Name*	*Notes*
Caryocar	Caryocaraceae		genus contains several important timber species; seeds of some species are edible (e.g., almendro)
Cecropia	Moraceae		common pioneer species in Central and South America
Cedrela	Meliaceae		important genus of timber species; source of tropical cedar
Ceiba acuminata	Bombacaceae		
Ceiba pentandra	Bombacaceae	kapok	seed fibers used for stuffing pillows
Chamaedorea	Palmae		genus includes several important ornamental species; leaves of some species are used in flower arrangements
Citrus	Rutaceae		genus includes several common market fruits (e.g., orange, lemon, and lime)
Cocos nucifera	Palmae	coconut	widely cultivated throughout the tropics
Couma macrocarpa	Apocynaceae	sorva (Brazil)	species produces edible fruit and a useful latex
Dacryodes	Burseraceae		genus contains several species of edible fruits
Daemonorops	Palmae		important rattan genus
Derris	Leguminosae		roots contain a potent fish poison
Dialium	Leguminosae		aril surrounding the seeds of some species is edible
Dipterocarpus	Dipterocarpaceae		genus contains several important resin-producing species and timber trees
Durio	Bombacaceae		
D. zibethinus	Bombacaceae	durian	important market fruit in Southeast Asia
Dyera costulata	Apocynaceae	jelutung (Indonesia)	source of useful latex
Endospermum medullosum	Euphorbiaceae		long-lived pioneer species in Southeast Asia
Eusideroxylon zwagerii	Lauraceae	ironwood	extremely durable and valuable construction timber

Genus and Species	*Family*	*Local Name*	*Notes*
Eugenia	Myrtaceae		large genus (about 1,800 species throughout the tropics); many species produce edible fruits
Euterpe oleracea	Palmae	açai (Brazil)	edible fruits and an important source of palm heart; species forms oligarchic forests
Euterpe precatoria	Palmae	huasai (Peru)	source of palm heart and edible fruit; solitary stem
Faramea occidentalis	Rubiaceae		common subcanopy tree in Central America
Ficus	Moraceae		large genus containing several species of edible fruits; bark of some species used for cordage or making cloth
Garcinia	Guttiferae		genus contains several species of edible fruits
G. mangostana	Guttiferae	mangosteen	important market fruit in Southeast Asia
Genipa americana	Rubiaceae	huito (Peru)	edible fruit
Gilbertiodendron dewevrei	Leguminosae		species forms oligarchic forests in central Africa
Gnetum gnemon	Gnetaceae	melinjo (Indonesia)	edible seeds; ground and used to make chips
Grias peruviana	Lecythidaceae	sacha mangua (Peru)	edible fruits; an oil can also be extracted from the fruits
Hevea	Euphorbiaceae		
H. brasiliensis	Euphorbiaceae	rubber	source of commercial rubber
Hura	Euphorbiaceae		genus contains important timber species
Inga	Leguminosae	inga	aril surrounding seeds is edible in several species
Iriartea	Palmae		stems used for construction materials
Jessenia bataua	Palmae	ungurahui (Peru)	fruits are edible and contain a high-quality oil; species forms oligarchic forests
Korthalsia	Palmae		important rattan genus
Lansium	Meliaceae		

Genus and Species	*Family*	*Local Name*	*Notes*
L. domesticum	Meliaceae	langsat	important market fruit in Southeast Asia
Litsea	Lauraceae		genus contains several timber trees; the bark of some species is used as an insect repellent
Lonchocarpus	Leguminosae		the roots of some species in this genus contain rotenone, a potent natural insecticide
Macaranga	Euphorbiaceae		a large genus of common pioneer species in Southeast Asia
Mammea	Guttiferae		genus contains several species of edible fruits
Mangifera	Anacardiaceae		genus contains numerous species that produce edible fruits and timber
M. indica	Anacardiaceae	mango	mango
Manilkara	Sapotaceae		genus contains edible fruits and latex-producing species (e.g., sapodilla)
M. bidentata	Sapotaceae	balata	timber species
Mauritia flexuosa	Palmae	aguaje (Peru)	important market fruit in South America; species forms oligarchic forests
Maytenus	Celastraceae	chuchuhuasa (Peru)	bark of some species used medicinally
Mora excelsa	Leguminosae	mora	timber species
Myrciaria dubia	Myrtaceae	camu-camu (Peru)	edible fruits with high concentration of vitamin C
Myristica fragrans	Myristicaceae	nutmeg	source of commercial nutmeg
Nephelium	Sapindaceae		genus contains numerous species of edible fruits
Nypa fruticans	Palmae	nipa	leaves provide thatch and sap from inflorescence is tapped to make wine
Ochroma	Bombacaceae	balsa wood	common pioneer species in Central America; wood extremely light
Ocotea	Lauraceae		genus contains several important timber species

Genus and Species	*Family*	*Local Name*	*Notes*
Orbignya phalerata	Palmae	babaçu (Brazil)	seeds contain an oil useful for cooking, soap-making and burning; species forms oligarchihc forests
Palaquium	Sapotaceae		genus contains several timber species
P. gutta	Sapotaceae	gutta-percha	important latex-producing species; gutta percha used to make golf balls, insulate electric cables, and fill cavities in certain dental procedures
Pandanus	Pandanaceae		some species in genus produce edible fruits; leaf fibers used as weaving material
Parahancornia peruviana	Apocynaceae	naranjo podrido (Peru)	edible fruits
Parkia	Leguminosae		
P. speciosa	Leguminosae	petai (Indonesia)	species produces edible seeds
Persea	Lauraceae		genus contains several species of edible fruits (e.g., avocado)
Phytelephas macrocarpa	Palmae	tagua (Peru)	source of vegetable ivory
Pouteria	Sapotaceae		genus contains several species of edible fruits (e.g., mamey and yellow sapote)
Protium	Burseraceae		genus contains important resin-producing species
Psidium	Myrtaceae		genus contains several species of edible fruits (e.g., guava)
Quararibea	Bombacaceae		genus contains several species of edible fruits
Rheedia	Guttiferae		genus contains several species of edible fruits
Rhizophora	Rhizophoraceae		a genus of mangroves
Shorea	Dipterocarpaceae		important genus of timber trees in Southeast Asia; collective trade name of timber is meranti
S. albida	Dipterocarpaceae	alan (Malaysia)	important source of red meranti timber; species forms oligarchihc forests
S. atrinervosa	Dipterocarpaceae	balau hitam (Malaysia)	species produces useful timber and oil-rich seeds (illipe nuts)

Genus and Species	*Family*	*Local Name*	*Notes*
S. curtisii	Dipterocarpaceae	seraya (Malaysia)	important source of red meranti timber
S. macrophylla	Dipterocarpaceae	tengkawang (Indonesia)	valuable timber and important source of illipe nuts
S. multiflora	Dipterocarpaceae		
S. pauciflora	Dipterocarpaceae		source of red meranti timber
Sloanea	Elaeocarpaceae		genus contains some timber species
Socratea	Palmae		stems used for construction materials
Sonneratia alba	Sonneratiaceae	perapat (Indonesia)	mangrove species of sandy tidal flats
Spondias	Anacardiaceae		
S. mombin	Anacardiaceae	hog plum	species produces edible fruits and bark is used medicinally in some regions
Swietenia	Meliaceae		valuable timber genus; source of mahogany
Syzygium	Myrtaceae		genus contains numerous species of edible fruits
Theobroma cacao	Sterculiaceae	chocolate	widely cultivated throughout tropics; grows wild in Amazonian flooded forests
Theobroma grandiflorum	Sterculiaceae	cupuaçu (Brazil)	popular market fruit
Trema	Ulmaceae		genus contains several common pioneer species
Virola	Myristicaceae		
V. surinamensis	Myristicaceae		important timber species
Xanthophyllum	Polygalaceae		genus contains several species of edible fruits
Xerospermum	Sapindaceae	genus contains several species of edible fruits; like rambutan	

Glossary

Abiotic Non living. Abiotic ecological factors include soil, water, sunlight and nutrients.

Acaulescent Appearing to be without a stem, the stem usually more or less subterranean.

Allometry The proportional relationship of the size of different plant parts.

Anther The male reproductive structure of a flower that contains the pollen grains.

Anthesis The opening of flower buds on a plant.

Apomixis Asexual production (without fertilization) of seeds. The seeds produced by apomixis are genetically identical to the parent.

Aril A gelatinous outgrowth surrounding the seed of some species. Frequently brightly colored and sweet (for example, in *Nephelium, Lansium,* and *Durio*).

Autogamy A type of self-fertilization in which pollination occurs within a single bisexual flower. Contrast with geitonogamy.

Basal area The cross-sectional area of a tree trunk measured at diameter breast height (DBH); used to estimate tree volume.

Coevolved To evolve together, each organism exerting a major selective pressure on the other.

Community A group of populations of different species living together in the same environment; includes both plants and animals. In the ecological hierarchy, this level of resolution falls between the population and the ecosystem.

Compensation point The light level at which the rate of photosynthesis equals the rate of respiration.

Congeners Of or pertaining to individuals of the same genus.

Conspecific Of or pertaining to individuals of the same species.

Cross-fertilization The transfer of pollen from the male flower of one plant to the female flower of another plant. Same as outcrossing.

Demography The statistical study of a population with reference to its size, density, distribution, and growth.

Dendrometer Instrument used to measure small changes in the radial growth of trees.

Density-dependent The change in rate of a demographic factor (such as mortality, growth, or reproduction) as the density of the population increases.

Dichogamy Temporal separation of pollen release and stigma receptivity within a single flower. See protandry and protogyny.

Dioecy Male and female flowers produced on separate plants.

Dispersal agent The animal or abiotic (for example, wind or water) mechanism that transports viable seed away from the parent tree.

Diversity An ecological measure that incorporates both the absolute number of species and their relative abundance within a community.

Dominant latent root The largest positive root of a square matrix which is equal to the finite rate of increase of a population. This important result is also known as the eigen value or lambda (λ) of a matrix. See transition matrix.

Dormancy A resting condition with reduced metabolic rate found in the non-germinating seeds of some species. Three types of seed dormancy are usually recognized: innate, induced, and enforced.

Ecosystem The sum total of the living (plants and animals) and non-living (soil, water, sunlight, and nutrients) components that interact to produce a given ecological system.

Embryogenesis The formation of an embryo. May result from either sexual or asexual reproductive processes.

Emergent trees Trees that grow taller than the general forest canopy and hence appear to emerge from below.

Ethnobotany The study of the relationships between people and plants.

Fecundity schedule A table showing the number of fruits or seeds (progeny) produced by plants of different size.

Frugivores Animals that eat fruit. The seed may or may not be destroyed in the process.

Geitonogamy A type of self-fertilizaton in which the pollen from one flower is used to pollinate a different flower on the same plant. Contrast with autogamy.

Germination The initiation of seed growth. The process by which a seed splits open and the young root (radicle) and first seed leaves (cotyledons) emerge.

Growth rings Visible discontinuities formed in the stemwood of trees in response to alternating periods of rapid and slow diameter growth. When the periodicity of these growth phases occurs with predictable regularity (such as in the temperate zone where trees grow fast in the summer and slow n the winter), growth rings can be used to determine tree age. Given the aseasonal climate in most of the tropics, tropical trees typically do not form well-defined growth rings.

Guilds Ecological types. Species that can be grouped together based on their similar ecological characteristics or requirements (for example shade tolerant species or light demanding species).

Habitat The natural environment of an organism including both biotic and abiotic factors.

Herbivores Animals that eat plants or plant parts.

Hermaphroditic flowers Flowers containing both male and female structures. Also known as perfect flowers.

Importance value A derived ecological index incorporating relativized frequency, density, and basal area data; used to rank tree species in terms of their relative importance in the forest.

Inbreeding Reproduction involving a single individual or a limited number of closely related individuals. In general, inbred populations have lower genetic variability than populations that exhibit a large degree of outcrossing.

Incompatibility mechanisms Biochemical adaptations possessed by some species that prohibit the occurrence of self-fertilization.

Infructescence Fruit-bearing structure of a plant.

Keystone plant species Plant species that provide the food resources necessary to sustain animal populations during periods of fruit scarcity.

Life history The life history of a plant defines the interval from germination to senescence including seedling establishment, growth, and reproduction.

Life table A tabular format for organizing the demographic data collected from a population. Traditionally contains only size-specific rates of mortality, but may also include birth rates and the rates at which individuals move from one class to the next.

Light demanding Species adapted for growth and reproduction under high light levels; usually fast growing. Contrast with shade tolerant.

Meiosis A form of nuclear division in which the chromosome pairs are split. This halving of the chromosome number ($2n$ to n) compensates for its doubling during sexual reproduction. Also known as reproduction division.

Meristem The buds or growing points of a plant; cells capable of dividing and developing into various organs and tissues.

Monoecy Separate male and female flowers on the same plant.

Neotropics Floristic region that includes Central and South America and the Caribbean (thus, New World Tropics).

Nutrient cycle A biogeochemical cycle in which inorganic nutrients circulate through the soil, living organisms, air, and water.

Optimal foraging An ecological theory developed by animal ecologist to explain the different patterns observed in the way that animals search for food. In many cases, the theory has proved quite effective in explaining reality.

Outcrossing The transfer of pollen form the male flower of one plant to the female flower of another plant. Same as cross-fertilization. May be an inviolate biological requirement for fruit formation (obligate) or not essential (facultative).

Overexploitation Harvesting a greater quantity of resource from a plant population than can be maintained over time.

Oviposition The act of depositing or "laying " eggs on a given plant part as practiced by innumerable species of insects.

Peccary A pig-like mammal with long, dense bristles found in tropical America.

Pedicel The stalk of an individual flower within an inflorescence.

Pericarp The fleshy part of a fruit, frequently divisible into three distinct layers: endocarp, mesocarp, and exocarp. Botanically, this tissue is the ripened wall of the ovary.

Phenology The timing or seasonality of specific biological events (for example, leaf fall, growth, or the production of flowers and fruits).

Pistillate Bearing female reproductive structures (stigma, style, and ovary).

Pollination The transfer of pollen from a dehiscing anther to a receptive stigma.

Pollinators Insects, birds, or mammals that facilitate the transfer of pollen from one flower to another.

Polyploidy An organism or cell having three or more complete sets of chromosomes.

Population A group of organisms, all of the same species, that occupies a particular area and exhibits a high potential for interbreeding.

Population dynamics The change in the size and structure exhibited by a population over time.

Population structure The numerical distribution of individuals of differing size or age within a population at a given moment of time.

Protandry Flowers in which the male reproductive structures develop before the female reproductive structures.

Protogyny Flowers in which the female reproductive structures develop before the male reproductive structures.

Raceme An elongated inflorescence in which stalked flowers are arranged along a common stem.

Radial symmetry The arrangement of floral parts around a central axis such that the flower can be divided into mirror images by a variety of different vertical planes. Also known as actinomorphic.

Recruitment The influx of new individuals into a population through seeding establishment.

Regeneration niche The specific combination of ecological conditions, both biotic and abiotic, that allow a seedling to express its optimal rate of photosynthesis and growth. To a large extent, the area and distribution of suitable niches regulate the number of seedlings that become established on a given site.

Regression A statistical method of estimating the relationship between two variables by expressing one in terms of a linear (or curvilinear) function of the other.

Reproductive propagule A collective term used to describe a fruit and all of its component botanical structures (seeds, arils, calyx, lobes, and so on).

Seed predators Animals that attack, eat, lay eggs on, or otherwise destroy seeds. The seed may be attached while they are still on the tree (*pre-dispersal predation*) or after they have fallen or been transported to the ground (*post-dispersal seed predation*). Insects are notorious seed predators.

Self-fertilization Pollination involving the flowers from a single plant. See autogamy and geitonogamy.

Senescence The deteriorative growth phase of an organism after full maturity that ultimately results in death.

Shade tolerant Species adapted for growth and reproduction under low light conditions; usually slow growing. Contrast with light demanding.

Species-area curve A graph showing the number of species plotted against the total area sampled. The point at which the curve flattens out is frequency taken as the minimal sample area for the sample community.

Size-class distribution The number of individuals of differing size found in a population at a given moment of time.

Species richness The total number of species per unit area found within a community.

Staminate Bearing male reproductive structures (anther and filament).

Stigma The female reproductive structure of a flower that receives the pollen.

Stochastic Random or unexpected.

Suppressed A weakened physiological condition or reduced vigor. For example, a plant that maintains only a small net photosynthetic gain because of its low light environment.

Survivorship curve Graph showing the number or proportion of individuals in a population that survive over time.

Sustainable Within the present context, a sustainable system for exploiting non-timber tropical forest resources is one in which fruits, nuts, latexes, and other products can be harvested indefinitely from a limited area of forest with negligible impact on the structure and dynamics of the plant population being exploited.

Taxa A group of related organisms of any taxonomic rank (for example, family, genus, or species).

Transition matrix A square matrix, M, that contains transfer rates for each size-class in the population as well as mortality and fecundity data for each size-class. Multiplying the current structure of the population by this matrix yields the size structure of the population at one time interval in the future. Also known as a Lefkovitch matrix.

Viability The probability that a seed will successfully germinate.

Zygomorphic The arrangement of floral parts in such a manner that the flower can only be divided into two mirror images by a single vertical plane. Also known as bilateral symmetry.

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Chapter 1

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Chapter 3

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