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# RAIN FOREST

# REGENERATION AND MANAGEMENT

Edited by

MALCOLM HADLEY

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# RAIN FOREST REGENERATION AND MANAGEMENT

**REPORT OF A WORKSHOP**

Guri, Venezuela
24 - 28 November 1986

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Unesco-Man and Biosphere (MAB) Programme
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## PREFACE

In early November 1986, Venezuela opened the most recent phase of the Guri dam project at the time the world's largest hydroelectric complex, having a capacity of 10,300 megawatts with a reservoir covering an area almost twice the size of Luxembourg. Some two weeks after the formal opening of the dam, Guri was the venue for an international workshop on rain forest regeneration and management.

Plans for the Guri workshop were elaborated by a small working party organized by Arturo Gomez-Pompa at Harvard Forest in July 1985. This working party was, in turn, convened in the light of a recommendation by the International Coordinating Council for the Man and Biosphere (MAB) Programme of Unesco, at its eighth session in December 1984, that rain forest regeneration might provide a suitable focus for future comparative work on tropical ecology within the framework of MAB.

Hosted by the state hydroelectric company CVG Electrificación del Caroní, CA (EDELCA), the Guri workshop was organized from 24-28 November 1986 as a joint venture by the Man and Biosphere (MAB) Programme of Unesco, the Decade of the Tropics of the International Union of Biological Sciences (IUBS), the United Nations Environment Programme (UNEP) and the Instituto Venezolano de Investigaciones Cientificas (IVIC). Additional technical and financial inputs were provided by the Food and Agriculture Organization (FAO), the World Resources Institute and the Commonwealth Science Council. Participants included some 20 research workers and forest managers from Venezuela together with some 40 invited specialists from 20 other countries and international organizations. The list of participants is given as Annex 1.

The workshop was concerned with the interface between research and management and was aimed at exploring the implications to management of present scientific knowledge on rain forest regeneration. In addition to producing a synthesis of scientific information on rain forest regeneration, subsidiary aims were to identify gaps in information and understanding, in respect to both scientific hypotheses and the needs of management, and to explore directions for future collaborative research and action. The intention was not to prepare an encyclopedic or comprehensive literature review. Rather, the workshop was concerned with the review of selected technical issues and ecological processes within the context of management. The motivation was to help bridge the gap between the sciences associated with the wet tropics and on-the-ground management.

The workshop was based on the presentation and discussion of thematic reviews, complemented by case studies (see Annex 2). Synthesis reviews dealt with such topics as sylvigenesis and architectural diversity, regeneration dynamics at various spatial scales, physiology of fastgrowing species, reproductive biology and genetics, fruit and seedling ecology, nutrient cycling, current management programmes. Case studies dealt with research and management experience in particular locations and regions. A dual challenge to those presenting case studies was to inform a wider audience of the experience gathered in a particular project or technical field, but also to suggest what might be the wider practical applications of the case study for rain forest management. Links between science and technology between research and resource use - came within the ambit of the reviews and case studies. The broader economic and societal context of rain forest regeneration and management was not within the direct terms of reference of the workshop. Not that issues like land tenure, economic evaluation of forestry schemes, international trade, etc., are not important. The inverse is true - their importance is overriding. But such an objective and focus would have called for a completely different type of workshop agenda and participants' list. Though the focus was on ecological and biological concerns, social and economic issues were inevitably raised during discussions, and this is reflected in particular case studies and in the penultimate section of this report.

Revised versions of the synthesis reviews and case studies are being published in book form, as one of the initial volumes in the new Man and the Biosphere Book Series. The present report is intended to complement the substance of that book, by distilling in readily available form, some of the recent advances and management implications of present scientific knowledge concerning rain forest regeneration highlighted during the workshop. It is designed primarily for technical personnel involved in land use planning and resource management issues in the forested lands of the humid and subhumid tropics. The concern is with mixed rain forest ecosystems (both "intact" and secondary) but not with plantations.

The report results from the combined efforts of all the workshop participants. Some sections are largely based on synthesis reviews prepared for the workshop, as modified by the author(s) following group discussions. For these sections, authors are given, thus allowing readers a direct contact for clarification and further information. In some other sections, the source of materials (e.g. edited extracts from particular case studies) are indicated in the text. In order to keep this summary report and its bibliography section within reasonable bounds, many of the source references cited in papers presented to the Guri workshop are not included. They are referenced in the book based on the workshop.

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## 1. SETTING THE SCENE: TRENDS IN TROPICAL LAND USE

A number of recent initiatives have served to focus world attention on tropical forest ecosystems and their resources. They include the Tropical Forestry Action Plan coordinated by FAO (FAO 1986, 1987), the World Resources Institute's Call for Action on Tropical Forests (WRI 1985), the Dutch Tropenbos programme (Tropenbos 1986, van Beusekom et al. 1987a, 1987b), etc. These reports provide a rich source of information on status and trends in tropical forest land use, updating and complementing earlier state-of-knowledge reports such as that prepared a decade ago by Unesco, UNEP and FAO (Unesco 1978). Among the items of background information that can be drawn from these several reports, together with the introductory overview of the Guri workshop (Gomez-Pompa and Burley, in press), are the following:

> Forests cover more that 4000 million hectares, or one-third of the earth's land surface. Of the total forest area, about 42% is found in the developed countries (almost all temperate) and 58% in the developing countries (mostly tropical).


**The humid tropics - a region unknown to many, with many unknowns to science, during a period of rapid, far-reaching change. One of 36 coloured posters (120 x 80 cm) from the Ecology in Action exhibit, produced by Unesco in 1981.**

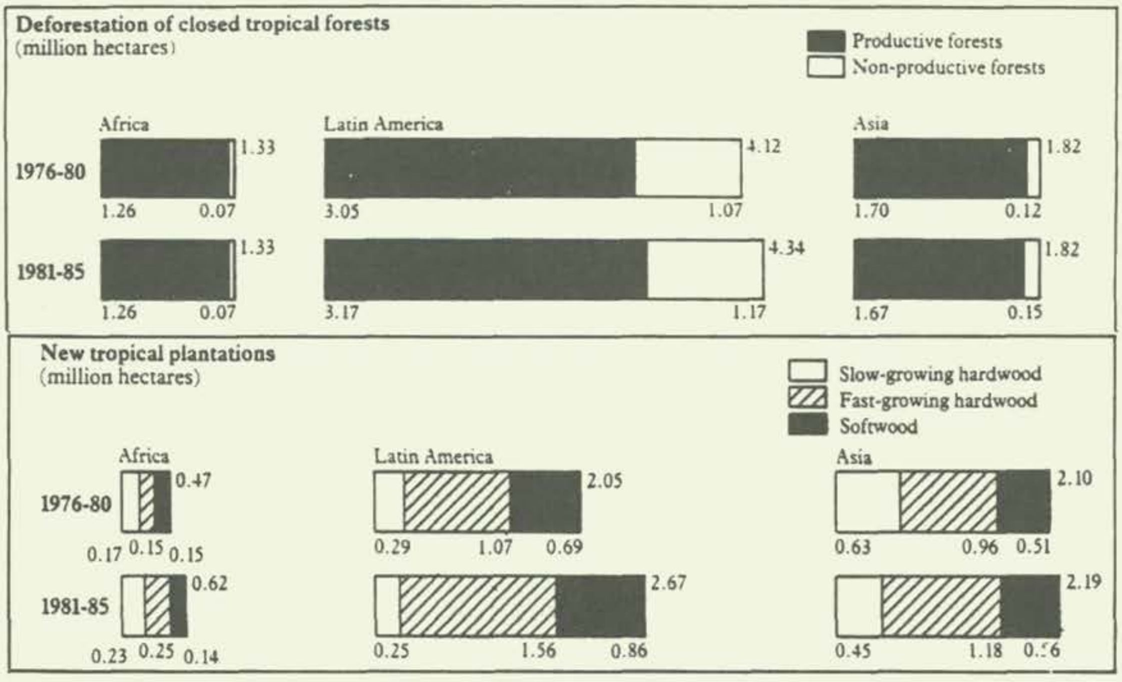
Tropical forests can be divided into two main types: closed forest, where the trees and undergrowth combine to cover the ground, as in the closed humid forests found in high-rainfall regions of the Amazon Basin and the islands of South East Asia; and open formations with continuous grass cover, such as the open savanna woodland found mainly in Africa. In addition, there are other types of forests, including bamboo which, although not strictly a tree, is an important forest resource in many tropical zones, and mangroves, a key element in marine food chains, which can be important sources of wood for fuel and building materials.

Forests provide energy (half the world's population depends on fuelwood), industrial wood products (20% of which come from developing countries), food, fodder, pharmaceutical products, and other non-wood products such as fibres, rubber, gums and resins. Forests are also a priceless ecological resource, protecting land and water resources, controlling floods, warding off wind erosion, storing and cycling nutrients, and providing habitats for wildlife. They constitute a rich stock of valuable genetic resources, and may have an important role in mediating changes in global climate.

Estimates of rates of forest conversion have been the basis of continuing controversy, caused in part by different definitions. Thus, Myer's (1980) study, prepared under the auspices of the US Academy of Sciences, was concerned mainly with the transformation of tropical moist forests from a "primary" stage to various human-impacted categories, and with the resulting likely impact on biological diversity and species survival. The FAO/UNEP assessment, on the other hand, was based on the conversion of forest to non-forested land (FAO/UNEP 1981, Lanly 1982). Comparisons of the results of the two types of survey have been made by Molofsky et al. (1986), among others.

According to the FAO/UNEP criteria, 7.5 million hectares of closed forest and 3.8 million hectares of open forest are cleared each year in the tropics (Figure 1), in total an area almost equivalent to that of Java. The underlying causes of

**Figure 1. Deforestation of closed tropical forests and new tropical plantations. From FAO (1987), after FAO/UNEP (1981)**



deforestation and forest degradation are poverty, inequitable land distribution, low agricultural productivity, poor land-use policies, inappropriate development (including projects outside the forestry sector), weak institutions and rapid population growth.

In spite of these high rates of deforestation, there are 36 countries with at least one million hectares of tropical forest, suitable for productive management, representing more than 90% of the world total (Table 1).

**Table 1. Largest national areas of productive closed broad-leaved forest[1]. Estimated for 1985 (x 106 ha). From Schmidt (in press)**

| Country | Total[2] | Logged over | Country | Total[2] | Logged over |
|---|---|---|---|---|---|
| Brazil | 295.5 | 13.5 | French Guyana | 7.6 | 0.2 |
| Zaire | 79.2 | 0.4 | Philippines | 6.3 | 3.7 |
| Indonesia | 67.5 | 34.5 | Madagascar | 6.0 | 4.6 |
| Peru | 42.8 | 6.4 | Kampuchea | 5.0 | 0.5 |
| India | 37.8 | 3.9 | Vietnam | 3.5 | 2.3 |
| Colombia | 36.0 | 0.8 | Central African Rep. | 3.4 | 0.4 |
| Burma | 21.8 | 5.5 | Nicaragua | 3.2 | 0.1 |
| Gabon | 19.8 | 9.9 | Thailand | 2.9 | 2.9 |
| Venezuela | 18.8 | 11.4 | Panama | 2.8 | 0.8 |
| Bolivia | 17.0 | 2.0 | Laos | 2.4 | 2.4 |
| Cameroon | 16.6 | 10.6 | Angola | 2.2 | 2.2 |
| Malaysia | 14.4 | 5.7 | Paraguay | 2.2 | 1.9 |
| Papua New Guinea | 13.9 | 0.4 | Guatemala | 2.8 | 1.2 |
| Congo | 13.6 | 3.4 | Côte d'Ivoire | 1.8 | 1.8 |
| Guyana | 13.5 | 1.4 | Nigeria | 1.6 | 1.5 |
| Suriname | 12.5 | 0.5 | Honduras[3] | 1.1 | 0.1 |
| Mexico | 11.4 | 0.3 | Ghana | 1.2 | 0.1 |
| Ecuador | 9.7 | 0.1 | Sri Lanka | 1.0 | 1.0 |

1) *Definitions: "Productive closed broadleaved forests ... cover ... a high proportion of the ground and do not have a continuous dense grass layer ... their characteristics ... allow (or might allow) for the production of wood for industry". "Logged over one or more times during the last 60 to 80 years"., From: FAO/UNEP (1981).*

2) *The forest is not all lowland tropical in all cases. For example, in the Brazilian Amazon the estimate for tropical forest is (x $10^6$ ha): 185.9 dense forest; 10.0 dryland forest; 76.6 open forest; 42.3 transitional and seasonal formations (total 314.8).*

3) *Revised from FAO/UNEP 1981 based on personal communication (1987) from T.W.W. Wood to R. Schmidt.*

There are three main possibilities for using rain forests. First, is conversion of species-rich forests into simplified, species-poor systems of various kinds, such as plantations, croplands, etc. Second, is the retention of mixed forests, with the extraction of some of their products but with the main functional characteristics maintained. Third, is the total preservation of samples of "natural" ecosystems. These three uses can be seen as complementary, choice depending on the intrinsic characteristics of a particular system. Unfortunately, these three principal possibilities are too often viewed as competitive and opposing. Proponents of one possibility are often not interested in the other two, and institutions and professionals concerned with tropical forests divide all too frequently along well demarcated lines of opinion, interest and ideology. In Mexico, for example, the first group is dominated by economists and agronomists, the second by foresters, the third by biologists. The result of these differing perceptions is that the group with the greatest economic influence on decision-makers holds the greatest sway, and this has been the first mentioned group.

The main obstacles to the sustained management of the resources of tropical forests seem to lie in the lack of policital commitment and of financial and institutional support. At the same time, scientific research has a contribution to make in helping the policy-maker and manager in their task.

**Tropical Forest Resources Assessment (1990)**

From 1978 to 1981, a global survey of the world's tropical forests and woodlands was carried out by FAO and UNEP. The assessment covered 76 tropical countries and provided a set of quantitative estimates in a standard format on the situation and trends at that time. The results of the study did much to raise the awareness of decision-makers and alerting public opinion to the seriousness of the problem of deforestation and of its harmful consequences for the environment and socio-economic development of tropical countries. It also served as a basis for the formulation by FAO of the Tropical Forestry Action Plan, subsequently adopted by the international community as a framework for harmonizing and strengthening cooperation in support of national efforts to fight deforestation.

Ten years have elapsed since the first survey was initiated, and FAO is now planning a new Tropical Forest Resources Assessment. The project aims to assess the forest resources of the tropical countries by end 1990, to estimate changes that have taken place since 1980, and to build alternative scenarios about forest changes by the year 2000. The assessment for 1990 will largely follow the methodology developed in the previous survey, with some new features including: assessment of total wood volume; integration of assessment of tropical and non-tropical zones; updating of vegetation maps, their computerization and integration with other useful data and maps; study of environmental implication of deforestation and forest degradation in the tropics; and dissemination of the methodology to developing countries.

A two-step approach will be followed. In the first step, all existing information (reports, maps, etc.) for the countries concerned will be collected. Where existing data are not reliable, interpretation will be made of satellite imageries for obtaining an up-to-date area of the various vegetation classes. In a second stage, all area and growing stock figures will be adjusted to a common reference date, namely 1990. This will make the data comparable at regional and global levels. Estimates will then be made of the past rate of changes during the period 1980-90 and of the projected changes during 1990-2000.

## 2. WHAT THE MANAGER NEEDS TO KNOW

J. Palmer

The objectives of a management agency, at a given time and phase, will determine its needs for information. It may be difficult for managers to articulate their information needs, sometimes because they may find it embarrassing to explain or defend the current practices of their governments in respect to forest management, in other cases because there is a lack of clear policy in respect to management or time might just not be available for putting existing tools and approaches into use.

One such approach is through decision charts and checklists, which are useful for training forest managers and have been produced by Colyear Dawkins for Ghana and Uganda, by Frank Wadsworth for Puerto Rico and extended to the rest of the neotropics, and by John Palmer for the Unesco/UNEP/FAO State-of-knowledge Report on tropical forest ecosystems (Unesco 1978). The charts are useful also to managers for explaining their needs and time scales to politicians and to Ministries of Finance. One highly simplified chart on what a manager of tropical rain forest needs to know, in approximately chronological sequence, is shown as Figure 2. For simplicity the chart is confined to a primary management objective, the production of valuable timber on a large scale (tens of thousands of hectares) to feed a capital-intensive forest industry. The sheer size of areas under the control of a tropical silviculturist or a forest manager forces acceptance of a high level of heterogeneity in their forests, augmented by the effects of logging operations. This difference in scale surely accounts for much of the difference in approach to problems between the tropical rain forest manager and the ecologist. The chart is limited further to the permanent forest estate, that is, the forest which is reserved legally for the supply of forest products to fulfill the national domestic (and perhaps export) requirements, in accordance with the national forest policy.

The concern here is not with forestry for the recovery of water catchments damaged through improper land use, nor with the management of forests scheduled for conversion to other forms of land use on the basis of land capability surveys and subsequent zonification. Nor is the concern with the management of small communal or privately owned woodlots, which are legitimate areas of interest in considering the issue of tropical rain forest management, but would require separate and somewhat different treatment.

Ten principal steps are identified in the decision-chart presented here, which deals with an objective common to large areas of tropical rain forest - that of producing valuable timber on a large scale within a capital-intensive forest industry.

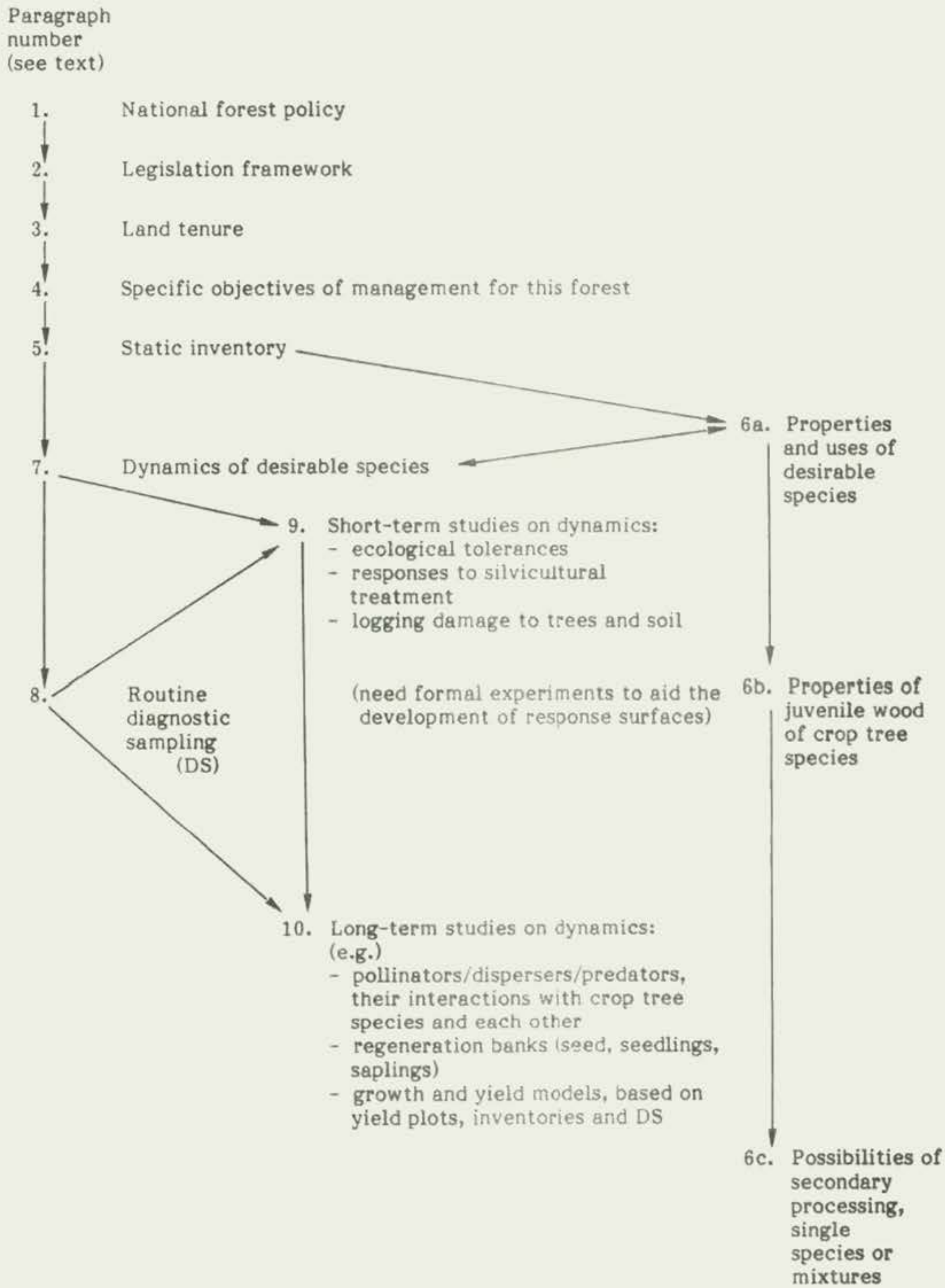
1. **National forest policy:** dictates the broad outlines of work for the national forest service.

2. **Legislative framework:** places the forest service and forest operations in their legal context. Unfortunately the forest law is too often set aside by short term considerations of political and personal pecuniary advantage (= bribery and corruption).

3. **Land tenure:** the forest service may find it hard to determine the true traditional rightholders or land owners (especially in the southwest Pacific), or there may be no simple answer, or there may be political interference with the operatiion of the statute law on land tenure. Note that difficulties caused to the forest manager on this and the two previous points are often due to the deliberate setting aside of the law by politicians.

4. **Specific objectives of management:** these should take into account the historical demands on the forest, and the commitments to supply local consumers as well as large industries. The objectives are not set on a once-for-always basis but should be kept under review. Formal

**Figure 2. What a manager of tropical rain forest needs to know**




(Note that paragraphs 5 to 10 should feed back to 4) forestry Working Plans usually require a quinquennial or decennial revision. There should be feedback from the succeeding steps in the decision chart to ensure that objectives are adjusted to cope with long-term market changes and with improvements to the knowledge base for silviculture and management. The objectives may imply large-scale and year-round operations, or small-scale and perhaps seasonal operations; or a combination. For example, a large forest industry might remove the big logs with heavy machinery and a second stage licence might permit local people to remove residues for firewood and to collect minor forest products.

5. **Static inventory:** this is possibly the field in which scientific knowledge has had the greatest impact, since electronic computers took the drudgery out of sample calculations and data sorting and tabulating. Inventories are now multipurpose, to suit multiple objectives, but just as there has to be a primary objective so there must be a primary suite of variables to be estimated, which determines the sampling scheme. Sub-sampling examines regeneration. Nowadays that would include the seed bank in the soil, and here it is perhaps salutory to record that silviculturists were studying the soil seed banks before university ecologists became enthused by the subject.

6. **Assess properties and uses:** the properties and uses of mature trees of species found by the inventory to be available in commercial quantities should be reviewed or researched. Note that in all, or almost all, tropical countries the number of species tested and found to be industrially suitable by forest products laboratories exceeds the number of species actually marketed from tropical rain forest. The difference is partly a reflection of the strongly conservative marketing of the timber trade and partly an indication of the pressure which the forest industries business can bring to bear on the relevant minister. Subsequent studies (6b) examine the properties of juvenile wood of the second crop species, to see if an early harvest would provide technically adequate timber; more advanced studies (6c) look into the possibilities of mixing species in a single processed product, such as chipboard or paper, as well as methods of adding value by secondary processing (such as overlaying printed films and plastics onto plywood, or selling furniture made from mixed species instead of only fine timbers).

7. **Dynamic inventory:** study should concentrate on the population dynamics of the desirable species. These are defined primarily on the basis of timber properties and secondarily on observed ecology (growth habit, position in relation to the canopy in appropriate seral phases after logging, growth rate).

8. **Diagnostic sampling:** DS is a generalized and improved form of the various linear sampling methods developed in Malaya, Nigeria, Sabah, Sarawak and Uganda. As the name implies, it is used to determine the appropriate type of silvicultural treatment (if any). There is now more emphasis on early identification of potential final crop trees ("Leading Desirables") and a concentration on their liberation from competition. In many tropical countries there is a more or less explicit land policy of "Use it or lose it", so there is strong pressure for a forest service to re-establish its claim to manage the forest after a logging operation. An early silvicultural treatment, not necessarily poison-girdling of undesirable species, is thus often politically desirable. However the forest service needs to establish the scientific worth of the treatments applied after best-guess interpretations of the DS.

9. **Short-term studies on dynamics:** as in DS the emphasis is on those desirable species (defined at step 7) and considered together as a crop, rather than on the individual species. Three classes of studies are especially indicated by forest managers:

- ecological tolerances, determined by sample surveys in space and time as well as by formal experiments;

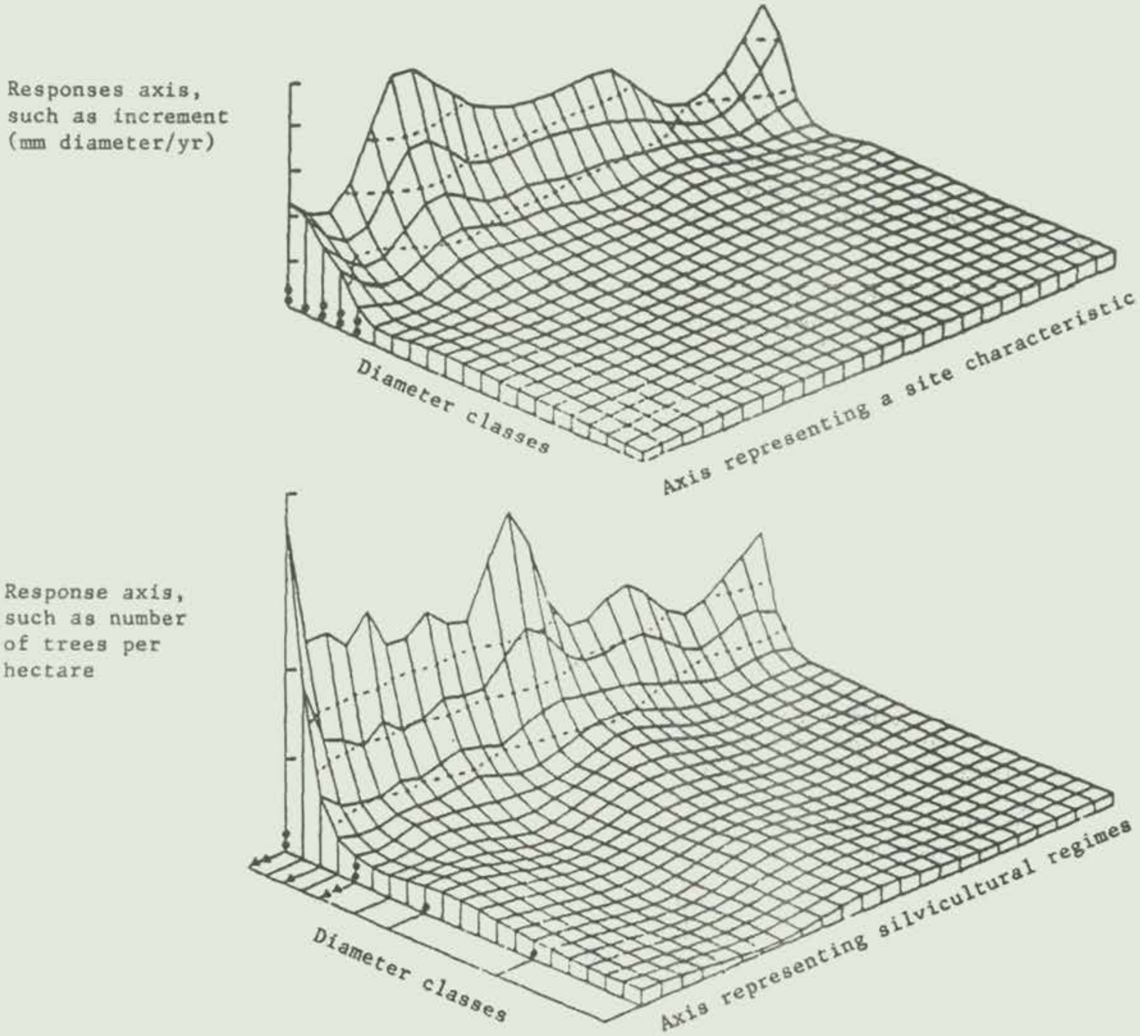
- response to silvicultural treatments (see step 8 above), including response to the major intervention which is usually the logging operation itself. Failure to quantify the pre- and post-logging states of the forest before the application of experimental silvicultural treatments has resulted in a regrettably large number of uninterpretable experiments. The difficulty experienced by many forest services in establishing and maintaining silvicultural trials in tropical rain forests is perhaps reflected in there being relatively few published case studies reporting such experiments (see however boxes on the work in Côte d'Ivoire and Suriname later in this report);

- effect of actual and simulated logging damage to standing trees and to the soil;

The emphasis should be firmly on experiments rather than on observation. Hypothesis testing is rarely necessary, it is the quantification of the response which is needed. Results of the trials should be incorporated into growth models (based mainly on yield plots, see step 10) whose sensitivity is often determined by the quality/quantity of data at the extremeties of the site/silviculture/growth response surface (Figure 3). Such conventional trials provide just that framework suggested in Carl Jordan's review of nutrient cycling processes (see also Section 3.6 of the present report).

10. **Long-term studies on dynamics:** these are intended to provide the bulk of the data needed for growth modelling and yield control systems. The main data source should be a well-stratified and regularly remeasured system of yield plots, supplemented by occasional

**Figure 3. Two illustrations of response surfaces shown as three-dimensional graphs**



inventories to improve spatial coverage, and making provision for incorporation of routine DS results. The high rate of turnover which is now known to apply to natural forest previously thought to be very stable applies also to Leading Desirables (LDs). This makes modelling difficult if not impossible from data collected only from LDs. It would seem that there is no satisfactory alternative to recording data from yield plots for all stems of desirable species, over a defined minimum size. Much more effort needs to be invested in growth studies and modelling, since the failure to make secure predictions of future yield makes forest services vulnerable to arbitrary political decisions concerning logging operations. Three classes of studies from those summarized in the workshop review papers and in Section 3 of this report, would be particularly helpful to forest managers:

- critical conditions for pollinators/dispersers/predators of the crop tree species, their interactions with the trees, as well as with each other.

- dynamics of the regeneration banks (seed, seedlings, saplings/poles).

- the ecology of climbers (lianes, trepaderos), particularly those of silvicultural importance such as *Merremia* in Southeast Asia and the southwest Pacific and *Acacia ataxacantha* in west Africa.

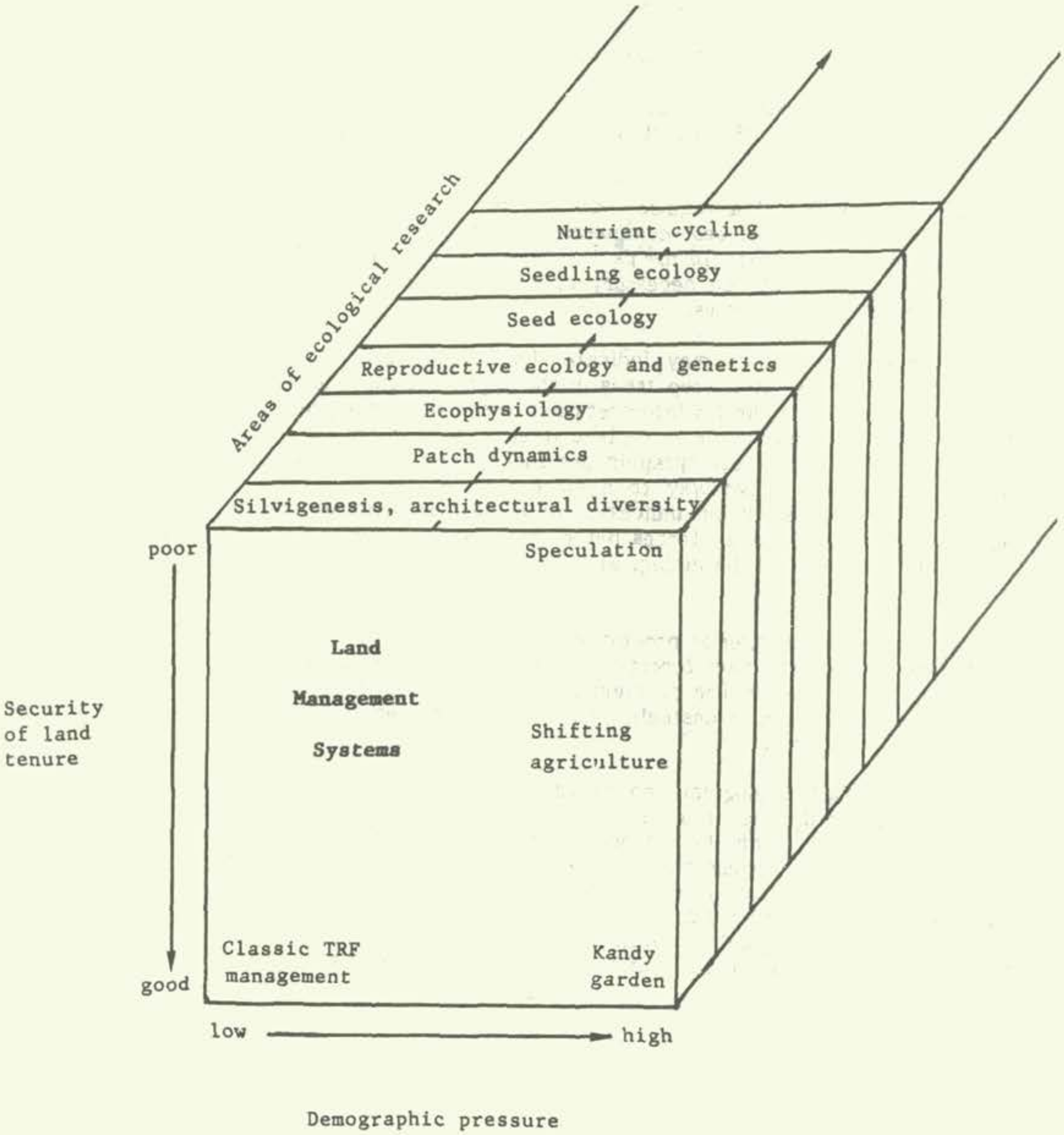
Some managers would add a requirement for studies on nutrient cycling. However, since 4 $m^3$ $ha^{-1}$ $yr^{-1}$ is about the best commercial growth rate that could be obtained in lowland tropical rain forest, and since 10 $m^3$ $ha^{-1}$ $yr^{-1}$ seems to be about the rate above which some artifical fertilization would be necessary to sustain yields, nutrient studies are not high in this particular listing of priorities.

Routine diagnostic samplings may indicate that some areas of forest have less than the minimum number of potential crop trees in the regeneration. Depending on how the critical stocking levels are set in the DS interpretation instructions, the prescription may be to enrich the forest with line plantings or to replace it entirely with artificial plantations. The latter may also be prescribed if demographic pressure or market demand increase so much that the natural forest must give way to a more directly productive form of land use. Such conversion is not necessarily an indication of managerial failure: the forest may have been damaged by natural or human forces before it passed to the control of the forest service, or the demand may exceed the biological capacity of the natural forest to produce the desired materials.

Departures from the managerial process outlined above are caused by social, economic and political pressures. Plantation forestry has suffered as much as tropical rain forest from budget failures and land tenure problems: maybe more, because plantation forestry is the management of intentionally unstable systems and requires timely interventions to prevent the collapse of the system.

In summary, although ecological knowledge implicitly underpins forest management, in an explicit form it is only one of a number of factors influencing the management of tropical rain forest. Ecologists might have more influence if they interpreted their research in terms of potential impact on management, while managers should articulate their research needs more clearly and phase them into grant-sized projects as understood by ecologists. The land manager should be able to indicate his research needs for any one land management system in any one area of ecological research, as suggested by the matrix shown in Figure 4. Such approaches would facilitate collaboration between forester and scientist in tackling particular management problems.

**Figure 4. Relating ecological research and different management needs in the humid tropics**



# 3. ECOLOGICAL PROCESSES AND RAIN FOREST REGENERATION

## 3.1 THE TROPICAL FOREST ENVIRONMENT

F.A. Bazzaz

Light, temperature, moisture, nutrients and herbivory are among the factors affecting plant germination, photosynthesis and growth, that need to be considered as part of the environmental setting within which rain forest regeneration takes place.

### The light and temperature environment

The upper canopy of the forest in wet tropical regions receives less radiant energy than the canopy of other tropical forests because water molecules in the humid air absorb this energy. Much attenuation occurs as the light passes through the vegetation; the amount of radiant energy available near the forest floor can be extremely low. The slope of the light attenuation curve varies greatly and is determined by leaf area density and leaf absorbance characteristics. The strata that affect vertical light distribution are more recognizable in forests dominated by one or a few species. Another aspect of the forest's light environment is the shift in spectral quality as the light passes through the canopy. The foliage absorbs red over far red light, so the light near the forest floor has little red wavelength light.

The substantial three-dimensional variation in the light environment is largely due to the distribution of the vegetation. Because of sunflecks, a shoot or a single leaf may experience rapid shifts from very low to very high light levels. This affects carbon-gain capabilities, and the growth and resource allocation of seedlings. Sunflecks are an important part of the light environment and carbon gain of understory plants, and rapid response of photosynthesis to sunflecks may be important for them.

The light environment dictates the temperature of air, plants, and soil in tropical forests. Although the temperature of emergents and outer parts of the forest canopy may rise during midday, there are no detailed or accurate measurements of this rise. In the understory, daily variation in leaf temperatures may be small and leaf and air temperatures remain close except during sunflecks.

Soil temperature may differ little from air temperature in the understory but may be much higher than air temperature in gaps and clearings. The differences are most pronounced near the soil surface, where the germination and early seedling growth usually occurs. It is important to recognize that plants as individuals may experience much variation in the levels of resources as they grow from small seedlings to mature, reproducing individuals, and that parts of the same individual may simultaneously experience different environments.

At the level of the leaf, vertical microclimatic gradients govern, to a large extent, the energy balance of individual leaves and their carbon-gain capacities. Though leaf energy balance measurements for tropical trees are very limited, studies suggest that there may be no fundamental differences in energy balance between tropical and temperate forest trees.

In the forest, both sun and shade leaves may be found on the same individual. Their carbon-gain capacities and contribution to the total carbon budget of that individual are probably different. Furthermore, within a species, shade-grown seedlings generally have lower light saturated photosynthetic rates than do sun-grown seedlings, though there are exceptions. This is also true for leaves on the same individual. Recent data also confirm previous conclusions that understory species have lower photosynthetic rates than do primary canopy species and those in turn have lower rates than pioneers. These trends in photosynthesis are similar to those in temperate forests and the rates are not very different between these two systems.

**Water economy**

Landsberg's (1984) theoretical analysis of the water economy of tropical rain forests showed that when the canopy is thoroughly wet, significant stemflow can be expected and the soil at the base of large emergent and canopy trees may become considerably wetter than the rest of the forest. This might contribute to spatial heterogeneity of resources in the forest. Evapotranspiration from the canopy may be large and is driven by the energy balance of the canopy, resistances to water flow, and soil moisture levels. Incoming radiation and the albedo are the most important controllers of evaporation; the latter is high in clearings with exposed soil surfaces or dry vegetation, lower in gaps, and lowest in intact forest.

Energy in the forest canopy is dissipated by evapotranspiration, latent heat transfer, and sensible heat transfer, which includes advection and convection. Low evaporation from soil and low air mixing in dense tropical forests lead to high relative humidity, which in turn reduces evapotranspiration. Of course, the amount and distribution of rainfall may vary considerably among locations. This affects forest dynamics by changing the morphology, physiology, and behaviour of forest organisms. In gaps and large clearings, relative air humidity may be low and may limit the establishment and growth of some forest species. However, soil moisture content may be high in these locations. Patterns of rainfall are likely to interact with forest structure and dynamics to generate complex patterns of water economy for different individuals, and there is evidence that in some places tropical trees may experience severe water stress, which may not be comparable to water stress observed in temperate forests.

**Nutrients**

Reviewing literature on nutrient dynamics in 62 tropical forests, Vitousek (1984) concluded that, in general, lowland tropical forests have more nitrogen and a lower dry mass to nitrogen ratio in litterfall than do most temperate forests. Phosphorus return, however, is very low. Vitousek concluded that usually phosphorus, but not nitrogen, is limiting in these systems. Plants growing in different soils in Amazonia have different concentrations of nitrogen, phosphorus, calcium, and magnesium concentrations and different nutrient-use efficiencies (Cuevas and Medina 1986). Different vegetation types in a given area may be limited by different elements. In Amazonia, Tierra Firme is phosphorus limited, Caatinga is nitrogen limited, while Bana appears to be limited by both nitrogen and phosphorus. Cuevas and Medina related differences in the degree of sclerophylly and leaf duration among these three vegetation types to nutrient availability. The issue of nutrient cycling is further discussed in Section 3.6 of the present report (pages 33-35).

**Growth**

Because of the length of the growing season, most tropical trees grow faster (especially above ground) than do temperate deciduous trees. It is also well established that pioneer species grow faster than do climax forest species. Reports of extremely fast growth of pioneer species are common. Growth has been measured most commonly as height extension because of the ease and non-destructive nature of the measurements. Height growth rates of over 2 m $yr^{-1}$ have been recorded for some tropical trees. Girth growth has also been recorded for a large number of species.

The range of possibilities for timing growth is best viewed as a spectrum from continuous growth to annual rhythmic growth. Annual growth rings are uncommon in most tropical trees. On the other hand, some species do have clear zonations of wood that resemble annual rings but are not necessarily the result of annual growth.

In a comprehensive long-term study of growth of 46 common species in a Costa Rican tropical forest, Lieberman et al. (1985) have reported that: (a) shade-intolerant canopy and sub-canopy species have maximum growth rates and are short-lived; (b) shade-tolerant sub-canopy trees live about twice as long as understory trees and grow at approximately the same maximum rate; (c) canopy and sub-canopy trees that are shade tolerant but respond opportunistically to increased light levels have long life spans and high maximum growth rates; and (d) understory species have slow maximum growth rates and short life spans.

**Herbivory**

Herbivores may sometimes play an important role in forest regeneration through the removal of photosynthetic and support tissue. This may result in changes in architecture and, in extreme cases, the death of individuals. Herbivory may indirectly increase mortality by providing entry for pathogens. Insects seem to be the most important herbivores in tropical forests. Massive defoliation does occur, but more commonly parts of leaves or of individual plants are consumed. The average value of leaf area consumed by herbivores in many tropical forests seems to be between 10 and 20%. The removal of tissue at the seedling stage is especially crucial.

The contribution a damaged leaf makes to the carbon economy of the plant depends on when in its life-span the leaf was damaged. There is good evidence that young leaves are more susceptible to herbivory than old leaves and in some forests leaves of pioneers are more susceptible than climax species. Removal of seed tissue by herbivores may be even more critical for the fate of the resulting seedlings.

## 3.2 FOREST DYNAMICS AND QUESTIONS OF SCALE — T.C. Whitmore

Primeval tropical rain forest, undisturbed and stable since the dawn of time, is a myth. Rather, tropical forests are in a continual state of flux, changing all the time. Instability occurs on several time-scales.

In secular terms, the climate of the humid trcpics has fluctuated throughout the Quaternary and probably the Tertiary too, and various lines of evidence show that tropical rain forests have expanded and contracted as climate has fluctuated. Today, their natural extent is at or near the maximum ever achieved.

At the other end of the temporal scale lies dynamic change due to the growth and death of the trees of the forest. The forest canopy is a mosaic of gaps, patches of juvenile trees growing up in former gaps, and mature forest. We may recognize a forest growth cycle of gap, building and mature phases. What grows up in a canopy gap determines the composition of the forest for a long time, usually at least decades and sometimes centuries. Hence, the establishment of building-phase forest is in some respects the most important part of the growth cycle. A crude distinction may be drawn between forest regeneration on small and large surfaces, in small and large gaps respectively, with recruitment from various sources of propagules varying in respect to gap size and severity of disturbance (Bazzaz in press; Figure 5). The seedling bank is most important in small gaps, while seed banks become more important in larger gaps.

In a canopy gap created by the death of one or a few trees, seedlings already present in the undergrowth are 'released' and grow up into building-phase forest. In a big gap by contrast (a gap created by multiple windthrow, landslide, vulcanism, cyclone, etc.), pre-existing seedlings die, there is a major shift in microclimate near and below the ground and this may sometimes cause death (though we lack hard evidence), otherwise physical disruption does. Whatever the cause of death, the gap is filled by new seedlings which were not present below the previous canopy.

Thus we have two sorts of tree species, those with shade-bearing (or shade-tolerant) seedlings and those with light-demanding (or shade-intolerant) seedlings. The latter cannot regenerate under any shade, including their own. These two species classes are often known also as climax or primary and pioneer or secondary species respectively, referring to their abilities to perpetuate *in situ* or not. Many other prcperties are linked to these seedling characteristics, to form two contrasting syndromes (Table 2).

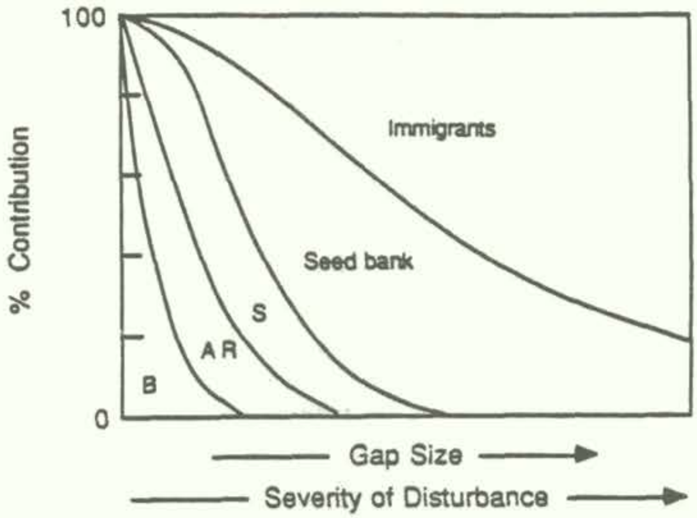
If the return-time of large-gap creation is longer than the life-span of the pioneer trees then as these die, small gaps will form in the forest canopy and climax species will invade in a second growth cycle. This is secondary succession, which is defined as a directional shift

Table 2. Character syndromes of the two contrasting ecological classes of tree species - pioneer and primary. From Whitmore (in press)

| | Pioneer species | Primary species |
|---|---|---|
| Synonyms | shade intolerants, light-demanders, nomads, pioneers, secondary spp. | shade tolerants, shade-bearers, dryads, climaz spp., primary spp. |
| Seed | copious, small, produced continually or continuously | less copious, large, produced annually or less than annually |
| Dispersal | wind or animals, for considerable distances | diverse, including gravity, sometimes only local |
| Dormancy | often (?always) present; never (?) recalcitrant | often absent; often recalcitrant |
| Soil seed bank[1] | present | absent (? always) |
| Height growth | fast | slower |
| Wood | usually pale, low density, not siliceous | often dark, high density, sometimes siliceous |
| Growth[2] | indeterminate, no resting buds (viz sylleptic) | determinate, with resting buds (viz proleptic) |
| Forking[3] | high | low |
| Leaves[2] | short-lived, one generation present, viz high turn over | long-lived, several generations present, viz slow turn over |
| Roots[4] | superficial | some deep |
| Root/shoot ratio[2,4] | low | high |
| Photosynthesis rate[5] | high | low |
| Toxic chemicals[6] | low | high |
| Leaf susceptibility to predation[7] | high | low |
| Geographical range | wide | often narrow |
| Phenotype plasticity[8] | high | low |

1. Whitmore (1983)
2. Boojh & Ramakrishnan (1982)
3. Whitney (1976)
4. Shukla & Ramakrishnan (1984)
5. Koyama (1978), Oberbauer & Strain (1984)
6. speculative, evidence slight and equivocal
7. Coley (1983)
8. Baker (1965)

Figure 5. Relationship between gap size and the relative contribution of various guilds to gap filling. Increased severity of disturbance during gap creation moves the time axis to the right. B = branches, AR = advance regeneration, S = sprouts. From Bazzaz (1984)




with time in floristic composition. The pioneer species may be short-or long-lived, and these grow to be small and large trees respectively.

The forest which first colonizes big gaps is known as secondary, and throughout the tropics it consists of stands of only one or a few species per hectare, in contrast to most climax forests which have numerous species. Moreover, the total pioneer tree flora is everywhere small with some of its species very widespread. There are fewer pioneers in America and Africa than in Asia, where in *Macaranga* alone there are over 100 pioneer species.

Eventually, probably usually after several centuries, there will no longer be a directional change in floristics; composition at a given spot will change from one tree generation to the next but overall a steady-state will have been achieved. This is the climax forest in which cyclic replacement occurs of climax species of similar ecology. In some forests this condition may never be reached because the return-time of cataclysms is too short.

In recent years, there has been growing awareness of the importance of cataclysmic events and other large scale processes in shaping the regeneration of rain forests. At least four groups of phenomena can be recognized:

- Cyclones are a powerful factor in affecting forest growth, especially in the neotropics.
- Fire has been shown to be a widespread and long-dated phenomenon in several parts of the tropics; examples include the extensive fires in East Kalimantan that followed drought in 1982-83, and the repeated fires that have occurred in southern Venezuelan rain forest during the past six millenia (Sanford et. al. 1985).
- River dynamics are an important factor affecting forest regeneration in areas such as Western Amazonia (see box "River dynamics, rain forest regeneration and species diversity").
- Plate tectonics is another mechanism which has been shown to have important implications to rain forest dynamics in the western Amazonia, through the effect of Sub-Andean tectonics on fluvial perturbance (Räsänen et al. 1987). The suggestion is that the western Amazonia is a fluviodynamic mosaic and that the river dynamics have affected the biota since the early Tertiary.

**River dynamics, rain forest regeneration and species diversity**

Recent research has suggested that lateral erosion and channel changes of meandering rivers may be an important cause of large-scale natural forest disturbance and primary succession in lowland rain forests. Work in the upper Amazon region (Salo 1987, Salo et al. 1986, Salo and Kalliola in press) has indicated that primary succession on newly deposited riverine soils is a major mode of forest regeneration. The river dynamics modify large areas because of the flat general topography, their high load of suspended solids and the easily erodable alluvial substrate.

Landsat imagery analyses show that 26.6% of the modern lowland forest has characteristics of recent erosional and depositional activity; 12.0% of the Peruvian lowland forest is in successional stages along rivers, is under the influence of the modern erosion-deposition cycle. These findings contrast with some traditional views of Amazonian rain forest, which have tended to emphasize stability, with the dominant mode of forest regeneration occurring in light gaps created by fallen trees.

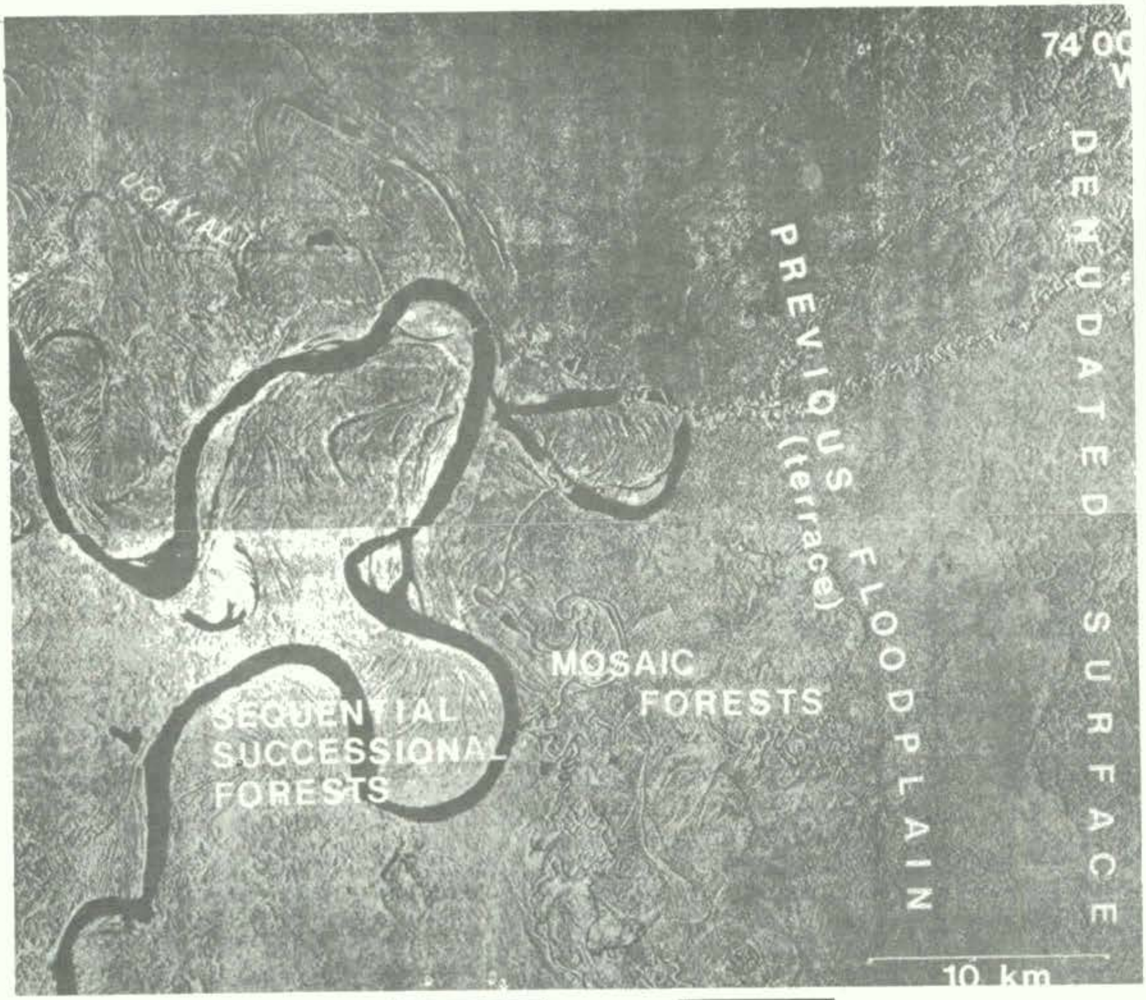
The research of Jukka Salo and his colleagues indicates that though much of the area of western Amazonia is covered with structurally more or less monotypic forest, the forest is a mosaic of forest patches different in their age, history and present day environmental conditions. Modern rivers repeatedly disturb the areas formerly considered to be stable Pleistocene refuges. The disturbance creates habitat mosaics, and favours the maintenance of the high between-habitat ( $\beta$ -type) species diversity characterizing the upper Amazon. This process may be viewed as complementary to or even replacing the Pleistocene refugia hypothesis for high species richness in this area.

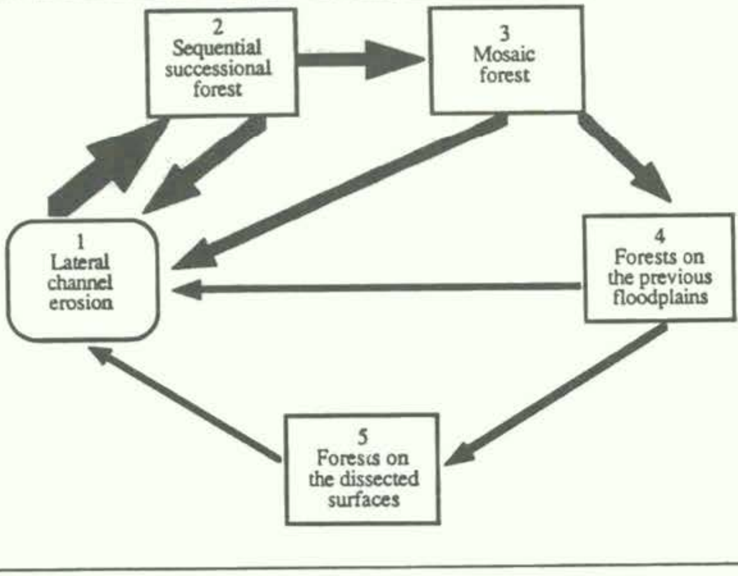
Understanding of questions related to river dynamics is considered important for the planning of conservation policies in the region. Firstly, there is need for protecting large areas including whole catchment areas (like the Manu national park). Secondly, protecting a stretch of all rivers is the best guarantee for protecting local floras and mechanisms for forest regeneration.

Reproduced here is a sideways-looking airborne radar (SLAR) image of western Amazonian forests (from Salo and Kallio, in press, image courtesy of ONERN, Lima). It shows the fluvial regeneration cycle on present and former floodplain generations in central Ucayali floodplain at Pucallpa, Peru. The forest regeneration cycle is initiated by lateral channel erosion and subsequent sedimentation of point-bars and migrating channel islands. The primary succession on these deposits follows a sequential pattern due to (i) further migration of the channel, (ii) formation of age stuctured sets of cohorts of the early successional trees according to the seasonal sediment accumulation and (iii) competition between species.

The mosaic forest is formed on the present floodplain generation composed of cut-off meanders (sequential successional forests) and oxbow lakes. Transitional forests with increasing autogenic light-gap regeneration dominate the older floodplain generations outside the presently active meander plain. Finally the colluvial processes cause dissection of the floodplain reliefs, resulting in the dominance of denuded forest beds.

In the accompanying figure, the relative width of the arrows indicates the areas most recently disturbed by the channel erosion. These are the areas most likely to be re-disturbed.


74 00
W
UCAYALI
PREVIOUS FLOODPLAIN
(terrace)
DENUDATED SURFACE
MOSAIC FORESTS
SEQUENTIAL SUCCESSIONAL FORESTS
10 km


2
Sequential successional forest
3
Mosaic forest
1
Lateral channel erosion
4
Forests on the previous floodplains
5
Forests on the dissected surfaces

## 3.3 TREE CHARACTERISTICS, SYLVIGENESIS AND ARCHITECTURAL DIVERSITY

R.A.A. Oldeman–J. van Dijk

Determination of the architectural diversity of tropical rain forest areas requires large-scale as well as small-scale analytical methods (Figure 6). Large-scale analysis may entail the use of satellite imagery and aerial photographs, which may show a given region with its mountains, valleys, rivers and forest (A) and at a more detailed scale, different forest types and forms of land use (B). More detailed surveys are needed to reveal the specific mosaic character of a particular forest type (C), while a still more detailed level of investigation (D) is required for examining the structure, processes and species composition of each kind

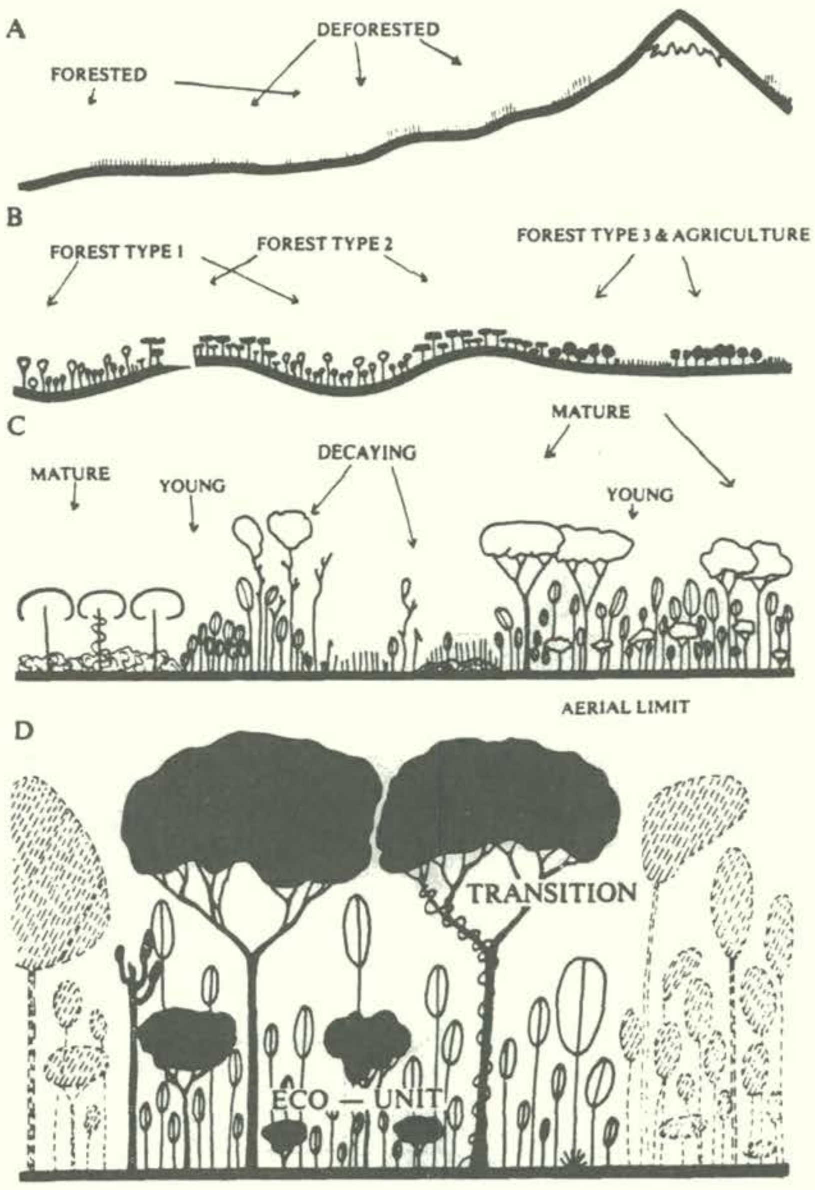



**Figure 6. Integration levels in forest architecture research, from simplified satellite image (A) to ground elevation of eco-unit (D). From Oldeman (1986).**

of forest patch or "eco-unit", an area on which forest started to grow at the self-same moment (Oldeman 1983). At a still smaller scale, individual trees or parts of trees can be analysed. All of these methods may together be used in helping to diagnose the "status" and "value" of a given area.

Tree characteristics may provide complementary diagnostic characters, particularly when considered in relation to crown characteristics, life history types and regeneration strategies. Two contrasting regeneration strategies can be distinguished, which may be called a "gambler" or "struggler" strategy (Bazzaz and Pickett 1980; Pickett 1983). Species with a gambler strategy produce large numbers of seedlings (Figure 7, Aa), which cannot survive in the shaded understory. Only those individuals survive that receive enough light from a canopy gap above them (Ab). The few individuals that find a gap may grow very rapidly towards the canopy (Ac, Ad). The reproductive efforts are high, in order to increase the likelihood that at least one individual juvenile will find a gap into which it may grow.

Species with a struggler strategy produce small numbers of very persistent juveniles (Ba) which may struggle but survive. They grow a little and some even complete their life history within the densely shaded understory (Bb). When a gap is formed above a juvenile, growth is preponderantly horizontal rather than vertical, and the increased light levels may be accompanied by maturation and reproduction (Bc, Bd). Eventually the canopy gap closes again and the tree resumes its struggler metabolism. The reproductive efforts of strugglers may be much lower than for gamblers, because the life expectancy of each individual juvenile is comparatively high.

Combining regeneration strategies with Whitmore's (1975) life history types provides a more comprehensive typology of the strategies that species may adopt to maintain themselves in the forest. The following species strategies may be recognized using as examples information obtained by Oldeman during work in the late 1960s in French Guyana.

. **Species requiring no gaps:** strugglers *in extremo*; adapted to continuously low light levels throughout their lives; crowns monolayered, more broad than deep; leaves borne on plagiotropic branches or branch-complexes or (in monocaul trees) in a whorl at the top of the stem. Growth may be preponderantly horizontal, even when a light gap is formed. In French Guyana, two groups can be distinguished; a first group of small monolayered trees, mostly much smaller than 10 m with large leaves, arranged in a single layer near or at the top of the tree, with minimal mutual shading of crowns; a second group of larger trees which may reach 10-15 m, morphologically more heterogeneous with a more complex architecture.

. **Small gap specialists:** germination in the shade. Many large economically important trees (e.g. Malaysian dipterocarps) belong to this group. Includes both strugglers (e.g. slow-growing, shade-tolerant "heavy hardwoods" such as Balau *Shorea, Vatica, Hopea*, often with plagiotropic branches or branch-complexes and monolayered leaf arrangement) and gamblers (shade intolerant, light hardwoods such as the Red Meranti *Shorea*, capable of very fast growth in a high radiation environment, often with orthotropic branches and multilayered leaf arrangements). In French Guyana, twelve examples of this group range from a pronounced gambler to a pronounced struggler strategy.

. **Large gap specialists:** germination in large gaps; gamblers *in extremo*, adapted to continuously high radiation levels; can only survive by outgrowing competitors. The well known architecture of the pioneer tree comprises a single leader, not (or sparsely) branched, with large leaves in a single layer at the top. In French Guyana, two different growth strategies can be recognized among the seven examples studied; first, that of outgrowing competitors by fast height growth achieved at the cost of building up a horizontally spreading crown (e.g. in *Didymonpanax moroteni)*; second, that of building up a densely foliated, spreading, phyllomorphic crown that occupies space horizontally and that may outshade competitors (e.g. *Annona paludosa, Apeiba burchelli*).

It would seem that architectural features combined with crown characteristics may reflect a tree's environmental requirements and its capability to adjust to a changing environment. Common architectural features and crown characteristics of juvenile trees

Figure 7. Diagrammatic representation of two contrasting regeneration strategies. Undulating arrows represent incident radiation: length of the arrows indicates intensity. See text for further explanation. After Oldeman and van Dijk (in press)

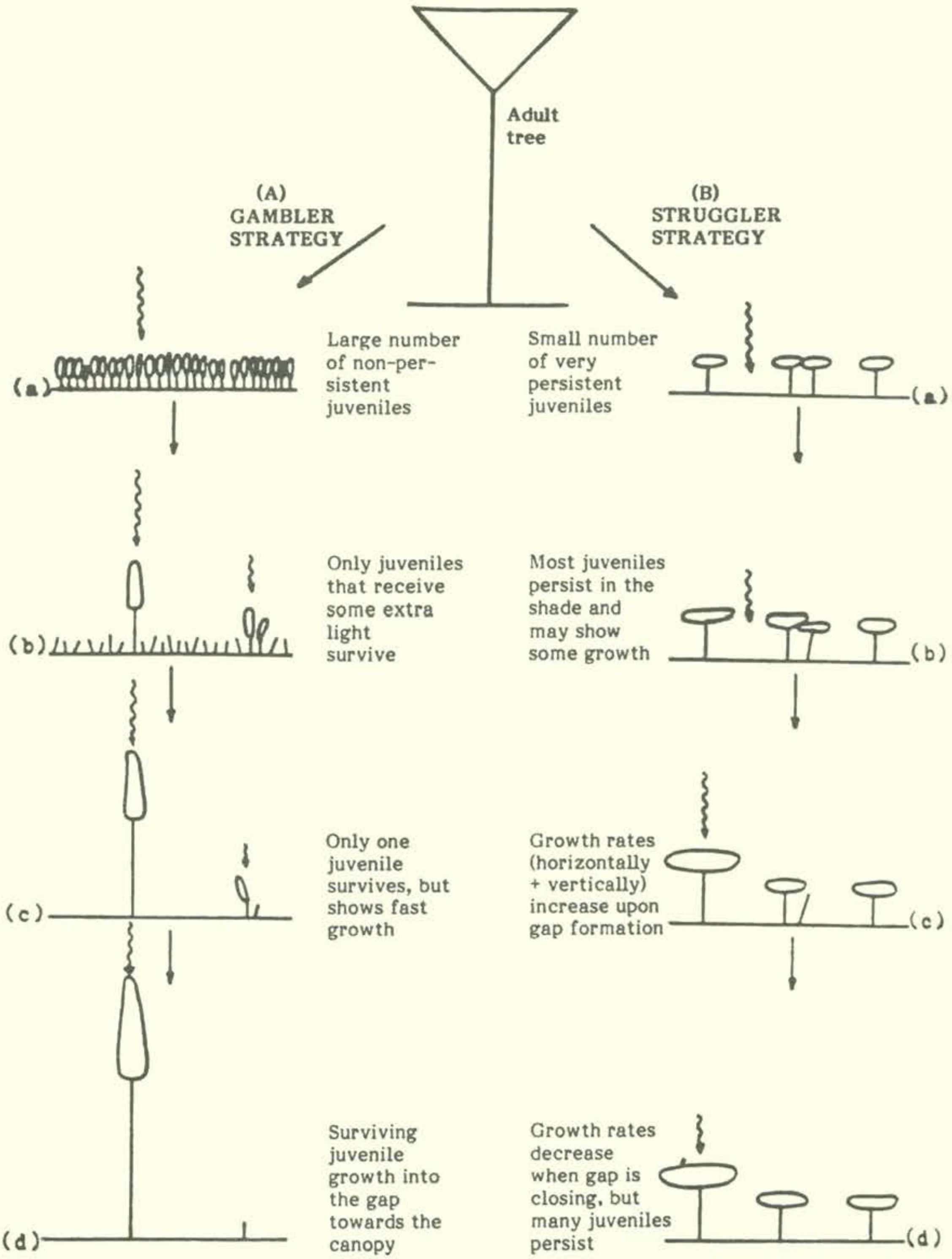


Table 3. Diagnostic characters and characteristics of trees with different species strategies. After Oldeman and van Dijk (in press)

| Species strategy / Diagnostic characteristics | Species requiring no gaps | Small gap specialists | | Large gap specialists |
|---|---|---|---|---|
| | Strugglers *in extremo* | Strugglers | Gamblers | Gamblers *in extremo* |
| **Architecture** | | | | |
| Overall architecture | Poor and simple | Poor, simple to more complex | More complex | Poor, simple to more complex |
| Orientation | Horizontal | Horizontal to vertical | Vertical | Vertical, sometimes horizontal |
| Distribution of branches | Unbranched or branches near the top | Diffusely branched or branches near the top | Branches in distinct tiers | Several possibilities |
| Common architectural models | Chamberlain, Corner, Roux | Troll, Roux | Aubréville, Massart | Several possibilities |
| Height growth | Mono- or sympodial | Mono- or sympodial | Mostly monopedial | Mostly monopedial |
| Branch orientation | Plagiotropic | Plagiotropic | Plagiotropic/Orthotropic | Plagiotropic/Orthotropic |
| Branching sequence | Diffuse | Diffuse | Mostly intermittent | Diffuse/intermittent |
| Ramification branches | Sparsely ramified | Sparsely ramified | Strongly ramified | Sparsely to strongly ramified |
| **Crown characteristics** | | | | |
| Leaf arrangement | Very little leaf surface, in a single layer at the top | Leaves sparsely distributed throughout the crown | Leaves more or less densely packed in several distinct layers | Several possibilities |
| Leaf size | Large when unbranched, small when branched | Small | Small | Often large |

may be used as diagnostic characters in helping to determine the status of a forest area (Table 3). When there is a prevalence of trees with a struggler strategy (species strategies 1 and 2), the forest may be considered to be stable or mature, whereas a prevalence of gamblers (species strategies 3 and 4) points to a recently or frequently disturbed site. Evidence for such a correlation has been obtained in forested sites in Venezuela (van Dijk 1987), but more field testing is required to confirm or refute its value.

## 3.4 REPRODUCTIVE BIOLOGY AND GENETICS OF TROPICAL FOREST TREES

**K. Bawa-S.Krugman**

Knowledge of reproductive biology and genetic structure for tropical forests may be very limited, but there is still information and experiences that can be shared and can be helpful in deciding strategies for responsible forest management. Below is reviewed the existing knowledge about such basic features as flowering and fruiting phenology, models of pollination, sexual systems, gene flow and genetic structure of populations, emphasizing the gaps in our knowledge that are of critical importance in the management and conservation of tropical rain forest trees. Summary recommendations on future research directions and on tree improvement programmes are also presented (Table 4).

### Flowering and fruiting phenology

Flowering. Tree species in a tropical rain forest display much variation in the timing, duration and frequency of flowering. Flowering may occur annually, supra-annually, or several times a year. In those species that flower more than once a year, quantitative variation in the intensity of flowering among episodes has been documented. Species that bloom annually may also show variation in flowering and fruiting intensity between years.

At the community level, flowering of related species is often sequential if the taxa are pollinated by the same guild of pollinators. Pollinators probably switch from one species to another as the floral resources of one species decline and that of the other increase.

The temporal variation in flowering should be of considerable interest to managers. The number of seeds (and fruits) produced are often positively correlated with the number of flowers, but we do not know how the quantity influences the genetic quality of the seeds.

The relationship between seed quantity and quality is of particular interest in species that bloom supra-annually. Many species do produce a small number of seeds in off years. Whether the quality of the seed is comparable to that produced in mast years is not known.

The staggered blooming periods of related species also have management implications. Some of the sequentially blooming species may provide resources to the pollinators at critical times when other food items are in short supply. If so, their removal from the community could influence the pollinator guilds, and consequently, the plant guilds that depend upon these pollinators.

Fruiting. As in the case of flowering, there is considerable variation among species with respect to timing, duration and frequency of fruiting. At the community level, fruiting in Neotropical rain forests is strongly seasonal. For example, in both Panama and Peru, peaks in fruit production straddle the start and the later part of the rainy season; in between the fruit is scarce. When fruit is scarce, frugivores are believed to sustain themselves on a handful of "keystone" plant species that provide nectar and fruits.

At first glance, such community level patterns may not be of much interest to a resource manager interested in a particular species, but the particular woody species may be dependent upon certain frugivores for seed dispersal. These frugivores in turn may rely on other species during lean periods of fruit abundance. The example also emphasizes the wide variety of ways in which the life cycle of a tropical forest tree is linked with the ecology of other plant

**Table 4. Reproductive biology and genetics of tropical forest trees: five recommendations for future research, and five recommendations concerning tree improvement programmes. After Bawa and Krugman (in press)**

<u>Recommendations for future research</u>

- Information about flowering and fruiting phenology, plant pollination interactions, sexual systems and mating systems at the level of communities and individual species is critical for success in management practices that impinge on variation in species composition. Such information is also vital for forest tree breeding programmes.

- For conservation and long-term management purposes, it is imperative we begin to gather data on the spatial organization of genetic variability at different scales.

- Given that genetic research is expensive and that tropical forests are diverse, it is suggested that a management approach incorporating genetic principles be focused on particular ecosystems or groups of species in a given geographical area.

- Genetics work must be an integral part of the overall management effort. Apart from forest tree breeding programmes, geneticists can contribute in many ways to the sustained management of natural forests and reforestation of degraded lands.

- Geneticists working with tropical forest trees must shed the bias accrued through experience with temperate zone conifers. The richness of biotic interactions encountered by tropical forest trees is greater by several orders of magnitudes; consequently, the genetic outcomes are more complex and diverse.

<u>Recommendations concerning forest tree improvement programmes</u>

- The justification, technical direction, and resources committed to a tree improvement effort must be closely related to the national or regional forest policy.

- It should be clearly understood at the outset that a successful tree improvement programme is only one element of forest management and not isolated from more traditional forestry activities.

- Another criterion essential for a successful tree improvement activity is the careful evaluation of technical skills available to implement an appropriate level of activity.

- Tree improvement programmes are of little value if the seeds and/or pollen cannot be collected, stored, and grown in a nursery. A nursery operation needs to be a major element of the tree improvement programme. Without a successful nursery programme, there is no way a tree improvement activity can succeed.

- A tree improvement programme is only as good as the field tree planting programme. Good professional plantation establishment and management are essential to the success and continued acceptance of improved material.

and animal species in the community. This makes it difficult to design a sound management strategy on the basis of biological knowledge of the subject species alone.

**Pollination modes**

There is a tremendous diversity of pollination modes among tropical rain forest trees. The pollinators range from tiny wasps in the case of figs to large bats in the case of *Cieba pentandra* and other Bombacaceae.

From the management perspective, pollination biology of individual species is of the greatest interest. Yet, even for most prominent species, such information is largely anecdotal, scant and incomplete. At the level of individual species it is particularly important to know the extent to which the various species are dependent upon particular pollinators. In cases of extreme specialization, the management of the pollinator population becomes as important as the management of the tree species serviced by these pollinators. The degree of specialization may differ for particular guilds of pollinators.

An adequate management strategy must also take into account the way the populations of pollinators might be influenced by changes in the frequency and composition of forest species. Tropical rain forests pose a tremendous challenge in this regard because, as mentioned earlier, groups of species often share the same pollen vectors. Because we know virtually nothing about the phenology and population dynamics of the pollinators, we cannot assess the impact of changes in frequency of various plant species on the population of their pollinators.

**Sexual systems**

The diversity of pollination mechanisms in tropical rain forest trees is matched by the diversity in sexual systems. Most species bear bisexual flowers, but are self-incompatible. Many are dioecious.

In terms of management, the degree of inbreeding displayed by the individual is a critical issue in assessing the genetic quality of the seed crop. The amount of inbreeding is not only dependent upon the genetic propensity towards selfing of an individual, but also on the spatial configuration of the relatives. To the extent that the management involves alteration of dispersion patterns, the effect of changing spatial patterns on the amount of inbreeding becomes an important issue. In dioecious species, optimal spacing of male and female trees is an even more complex issue and cannot be ignored, especially in those cases where the product of economic interest is seed or fruit.

**Mating systems, pollen flow and effective population size**

A convenient way to estimate the amount of outcrossing (or inbreeding) is to analyze the mating system by means of genetic markers. The mating system is determined by the degree of self-fertilization, dispersion pattern of related individuals (family structure) and the characteristics of pollen flow. The parameters that determine mating system also define the effective population size, which in essence describes the boundaries of genetic neighbourhoods within which the individuals mate freely with each other.

Mating system has been so far quantitatively analyzed in two species of tropical rain forest trees: *Bertholletia excelsa* (Brazil-nut) and *Pithecellobium pedicellare*, a mimosoid legume. The data indicate that the outcrossing rate in both species is very high, and that there is considerable variation among individuals in outcrossing rates. There are absolutely no data on gene flow in tropical forest tree populations.

From the management perspective, it is important to know the amount of inbreeding within a population and whether or not individual trees significantly differ in outcrossing rates. Selective removal of trees can alter the mating patterns with unknown consequences on the (genetic) quality and quantity of the seed crop. If populations are structured on a local scale, and if neighbours are more related to each other than to individuals farther away, the thinning of the stand may reduce inbreeding by consanguineous matings and may actually result in greater outcrossing. But if the selective removal were to increase the distance among conspecifics to an extent that it could not be bridged by means of pollen flow, the removal may result in lower fecundity.

In the case of tree-breeding programmes, information about the extent of pollen flow is vital. On the one hand, one might wish to locate seed orchards near the native forest to draw pollinators, but on the other hand such pollinators may "contaminate" the pollen reaching stigmas of flowers within the orchards.

**Genetic variation within and between populations**

Little is known about the spatial organization of genetic variability. In particular, we do not know the spatial scale over which allele and genotype frequencies change. Nor do we have any knowledge about the extent to which populations are genetically differentiated.

In terms of management, high levels of heterozygosity suggest that populations of each species may carry considerable genetic load. A reduction in population size in those species could result in increased homozygosity and lowered reproductive output. The data from mating systems in widely outcrossed species also indicate that the conservation of such species may require preservation of individuals scattered over a wide area. Information on spatial organization of genetic variation and the degree of genetic differentiation among populations is critical to the design of conservation strategies, but, as mentioned above, we know virtually nothing about these parameters.

**Forest genetics and tree improvement**

In many tropical zones, dry and moist, reforestation of degraded lands is the most important management objective. If there is going to be a reforestation programme, why not plant the best trees possible? A proven method for increasing forest productivity is the careful application of basic genetic knowledge.

There are probably as many tree improvement strategies as there are forest geneticists. Once the key criteria of a programme are understood, tree improvement activities can be tailored to the needs of forest management. A first step is the selection of species to be improved. Most often, species priorities are initially based on their commercial importance or high value in meeting other management needs, i.e., species selection for shelterbelts and windbreaks can be a priority need in addition to fibre and fuel production.

Next,priority selection is based on the amount of genetic variability within the species. The greater the genetic variability, the greater is the opportunity to make useful improvements in desirable characteristics. Finally, the degree of heritability of the desired characteristics to be improved must be considered. There is little value in attempting to improve those desired features of a tree that have a low heritability.

The next step is the identification of a base population to provide the source for seeds. Adequate documentation of seed origins is a critical requirement at this stage. No matter if a native or exotic species is to be planted, seed of all species must come from an identified source. Many a failure has been repeated because the same wrong seed source has been employed.

Frequently there is a need to have a more intensive genetics programme. If there is sufficient biological and reproductive information and the species are of high priority, a superior tree selection testing and screening programme can be initiated. In a typical programme, phenotypically superior trees are selected from natural stands and the selected trees are established in seedling or grafted orchards. In this manner, phenotypically superior trees are permitted to mate and produce seeds. A tree may be superior phenotypically but not genetically. While seeds from such orchards are on the average superior to wild seed collections, it is normal practice to begin testing the offsprings from the orchards to ensure the genetic superiority of the parents. In other words, individual trees are selected that have characteristics more desirable than the original base population. The initial selection will

## Towards a functional classification of forest systems at Sierra del Rosario Biosphere Reserve in Cuba

Since 1974, researchers at the Institute of Ecology and Systematics of the Cuban Academy of Sciences have carried out studies at the Sierra del Rosario Biosphere Reserve in the province of Pinar del Rio of western Cuba. The predominant vegetation type is tropical submontane evergreen forest, with areas cf thorny xeromorphic and herbaceous communities. The topography is dissected, with an altitude range of 50-600 m. Based on 20 years' data, annual rainfall and temperature average 2014 mm and 24,4°C, respectively.

Over a period of about ten years, data have been collected from different stands which could be classified as Restoring Primary Forest or Mixed Primary Forest - the former subsclerophyllous at a site called locally Yagrumal-Majagual, the latter mesosclerophyllous at Vallecito.

Two different groupings of functional characteristics and performance can be recognized in the accompanying table, the mesosclerophyllous forest being less productive than the subsclerophyllous one. Caution is expressed in presenting such a comparison. From the forest management standpoint, there is no intention to suggest that the subsclerophyllous type should be imitated everywhere, since it is a forest type that is environmentally restricted. Also, the results obtained from plant formations functionally associated with the tropical evergreen submontane forest system cannot be extrapolated to the semi-deciduous forest systems occurring in the Cuban plains.

These caveats notwithstanding, a functional classification of tropical forest ecosystems is being refined by the Cuban research group. It is based upon five major characters: distribution of litterfall over the entire year; average degree of sclerophylly; decomposition and nutrient cycling rates; distribution of rains and total precipitation; edaphic characteristics. In addition, in considering forest regeneration and management, account also has to be taken of the original plant formations that were able to grow under the environmental conditions of eight different localities studied at Sierra del Rosario.

Further information is given in several summaries and syntheses of the results of ten years' research at Sierra del Rosario (Herrera et al. 1986, *in press* a, in press b).

**Functional characteristics of mesosclerophyllous forest (Vallecito) and subsclerophyllous forest (Yagrumal-Majagual) at the Sierra del Rosario Biosphere Reserve[a]**

| Functional Character | Vallecito | Yagrumal-Majagual |
|---|---|---|
| Root mat | Seasonal to permanent | Absent |
| Layer of dead leaves | Constant | Seasonal (only during "dry" season) |
| Hardness of rootlets | Higher | Lower |
| Biomass of rootlets | Higher | Lower |
| Living rootlets (%) | Lower | Higher |
| Vertical distribution of rootlets | Concentrated in the top layers | More uniformly distributed |
| Decomposition rate of leaves | Lower | Higher |
| Decomposition rate of rootlets | Lower | Higher |
| Vertical distribution of VA mycorrhizal extramatrical mycelia (MEVA) | Approximately the same | Approximately the same |
| Vertical variation of MEVA: rootlet ratio (ug mg-1) | Increasing with depth | Uniformly distributed |
| Production of MEVA | Lower | Higher |
| Production of rootlets | Lower | Higher |
| Growth rates of trees | Slow growth | Fast growth |
| Nutrient content of leaves | Lower | Higher |
| Organic detritus in soil | Higher | Lower |
| Decomposer (faunal) populations | Lower | Higher |
| Productivity[b] | Lower | Higher |
| Turnover rates | Lower | Higher (about double) |

[a] Actual figures corresponding to each character can be obtained from the authors.

[b] Considering stands of the same age.

form the production plantations; but, following additional testing and further selection, they are used to develop the next generation of improvement, sometimes called the expanded breeding population.

There are many different ways to make selections, establish seed orchards, to test the progeny and continue to increase the genetic base of the programme. Such details need to be carefully developed for the species involved and the conditions of the selection. Many reports, plans and some books have now been written to provide these details.

## 3.5 TROPICAL FOREST SEED ECOLOGY

D. Janzen–C. Vazquez-Yanes

There is already an enormous data base on tropical seed biology in the literature and in human memory. This data base is growing rapidly while its source is shrinking even more rapidly. The relevance of any particular part of this data base to the management of mixed tropical forests is extremely dependent on situation, just as is the case with the management of other ecosystem components. The components of the management process are the site (what particular forest), the management goal(s), the raw materials (plant and animal forest occupants), and the competence of the managers. The guiding principles are 'know thy organisms' and 'know thy habitat'. The habitat determines the relevance of any particular aspect of seed ecology. A thorough knowledge of the literature on tropical seed biology is unlikely to provide specific answers to any particular management problem, but on the other hand, the seed biology literature often suggests relevant possibilities. While some generalizations about tropical seeds themselves are a necessary part of the management framework, they are only distant or indirectly useful to a person actually attempting to grow or manage a particular forest on a particular site. Of far greater use is understanding of the natural history and of system interactions in particular circumstances.

Four processes interact to generate the seed "shadow" that finally produces a seedling "shadow": seed production, predation, dispersal and dormancy. The processes that determine subsequent adult tree recruitment from that seedling "shadow" are the same, except for the deletion of dispersal and the addition of growth. With this in mind, it is evident that seeds and seedlings are not the only juveniles potentially available for manipulation by the managers; for example, releasing 'teen-age' trees from competition may be much more effective than planting seeds or seedlings of a desired species, as foresters well know.

### Seed production

Individual- and species-specific seed production patterns vary within the individual, population, year, season and habitat. In general, species of the primary forest canopy wait longer (up to many years) between seed crops, and tend to be more synchronous at the level of the population and habitat than are the species that form early successional forests. Within a species, an individual's pattern of seed production among years is nearly always very situation-dependent rather than locked into a genetically-fixed cuing system. Individuals in arboreta and other isolated circumstances are notorious for fruiting in years when the population at large does not fruit.

There is enormous inter- and intra-specific variation in the size of the seed crops of individual trees. A large crop may range from only a few dozen huge seeds to several million small seeds. Likewise, it is commonplace for a given individual to vary as much as 100-fold in the size of its seed crop among years. Within an individual tree's crop, the lightest viable seeds frequently weigh less than half of the heaviest viable seeds.

While seed production is often a critical part of the process that leads to restoration of a particular forest, its study in the abstract is of little assistance in management. In general, habitat disturbance increases seed yields for the surviving individuals, if the pollinator services have not been depressed (or altered to an extent where pollinators produce detrimentally inbred genotypes through their patterns of pollen movement) and if the new environment is not detrimental to the tree's reproductive physiology. The increase in seed production comes about directly through increased resources for the tree and indirectly through decreased seed predation by specialist insects and certain forest-loving vertebrates. The increased seed yields may be 'pleasant' for the surviving frugivores and seed-predators (as well as for those persons that are collecting seed), but they will also severely alter the proportional demography of the seed rain onto the site. Whether this is prejudicial or beneficial to management depends on the management goals.

Flowering is often conspicuous but is not a good indicator of where and when mature seeds will be available, either for collection or dispersal by natural agents. Likewise, some tropical trees are functionally male, and therefore their density and location as flowering individuals is a poor indicator of the density and location of seed-bearing individuals.

Since seed production varies strongly among and between years, the time of year and the year in which a reforestation project or a forest alteration scheme begins will strongly affect the subsequent outcome. Likewise, as long appreciated by Malaysian foresters, the number of years since the last mast seeding will influence the number of seedlings that are available to generate new trees at the time that the forest is perturbed. As mentioned earlier, trees that are on strong individual, population-wide or habitat-wide seed production cycles are likely to lose their synchronization when the habitat is removed around them. With seed production coming at intervals, the seed (and hence seedling) dynamics of a given year should not be taken as necessarily representative of the subsequent years. These statements apply most strongly to primary forest, but even young secondary forest can have years of high and low seed production.

When trees are left standing or encouraged as seed trees in manipulated forest, they must be accompanied by appropriate habitat for pollinators and seed dispersers; however, substitutions of one agent by another are quite possible - even though, in any specific case, the surrogates are likely to generate a different pollination or seed dispersal pattern.

In sum, about the only kind of positive manipulation that can occur with seed crop production is species-specific reduction in environmental constraints to resources for the adult tree, undertaken in the hope that such manipulation is not followed by a concomitant increase in seed predators. While trees may be bred for high seed yield, the desirability of releasing such trees into a managed habitat will depend on goals. If seed crops are harvested, the harvester is just another kind of seed predator; harvest impact will depend on what would have been the fate of the seeds that are harvested.

**Seed predation**

Just as different species have different dispersal and germination properties, different species have different susceptibilities to different seed predators. The degree of pre-dispersal predation is extraordinarily variable and very dependent on the circumstances of the tree, year and habitat. Species range from suffering essentially no pre-dispersal seed predation anywhere, to species in which pre-dispersal seed predation intensity changes as the habitat changes, to species that suffer very high levels of pre-dispersal predation almost everywhere (except when the seed predators have been eliminated by habitat destruction). The same gradient occurs in post-dispersal predation on seeds and young seedlings, but with poor (if any) correlation.

The degree of seed predation of any given tree species does not correlate well with the abundance of individual adults of that species. However, if a given tree species suffers a given regime of pre-dispersal seed predation, then a change in that regime is likely to lead to a subsequent change in other demographic and micro-geographic traits of recruitment.

While it has not been the subject of much explicit study, it would appear that the intensity of seed predation declines as the scale and intensity of habitat destruction increases. There are multiple causes. First, some pioneer species seem to have seeds sufficiently small that they are often not fed upon by either generalist or specialist seed predators. The dynamics of seed predation are quite size dependent. Furthermore, once a seed has been dispersed, the smaller it is the greater the chance that it will be totally free of animate seed predators in any habitat. Fungi, on the other hand, appear to be more successful at killing small than large seeds. Second, isolated trees in open fields often bear crops that have no contact with the seed predators that kill large portions of conspecific seed crops within the forest. Much seed predation in forest is by animals that are quite unwilling to move into the open, with the outcome that the initial stages of secondary succession are often characterized by substantially reduced rates of seed predation. On the other hand, certain species of seed predators occur at higher density in disturbed forest than in primary forest.

It is tempting to believe that if forest restoration schemes could be set up such that the seed predators (peccaries, parrots, mice, beetles, etc.) were missing, then reforestation would occur more rapidly and desired trees might be more abundant in the new forest. Such could happen, but in general the novel habitat structure so generated would have much more the appearance of island vegetation (fewer tree species in relatively monospecific stands, each to its own habitat) than of mainland vegetation. In other words, the seed predators are in fact removing large numbers of offspring before they have a chance to express their competitive superiority, and many of these species may well be species that are not desired by the manager. Finally, many seed predators are also dispersers, notably primates, ungulates, and large rodents. These move seeds and kill them. Furthermore, the elimination of a rodent that is, for example, killing a large fraction of a seed crop may simply mean that some other mortality agent takes over. Likewise, even if the plant becomes more common or more locally widespread, it may well not occur in the pattern desired by the forest manager.

**Seed dispersal**

Seed dispersal agents and processes are essential (though not sufficient) for forest to move onto land that has been cleared and for return of partly perturbed forest to its original state. This places a premium on questions of the distance (in time as well as space) of seed sources from the manipulated forest. The soil seed bank (see below) contains representatives of only a tiny fraction of the species of trees in a tropical forest (just as in the case in extra-tropical forest), and these seeds are in haphazard proportions having little to do with any particular desired forest structure. They are, however, almost all pioneer species. The dispersal agents are an essential link in the establishment of the seed shadows that will generate the seedling-environment interaction that will eventually maintain the multi-species pattern of tree species in the forest. Seedling establishment and growth to maturity is highly dependent on the number of 'tries' at a given site, which is in turn dependent on seed dispersal systems. The seeds have to get to a gap or other safe site before they can survive and grow there. Since there is both attrition in the soil through death and germination, and since old seedlings may have different chances of surviving than do new seedlings, if a gap or other favourable growth circumstance is opened up, the pattern of seed input will have a strong impact on the pattern of both appearance and success of recruitment attempts.

Most tropical forests are mixes of wind and animal-dispersed seeds. As perturbation increases, or as the forest invades an open area, these two processes are differentially affected. In a forest from which the vertebrates have been largely removed, the animal-dispersed species begin to decline in numbers and change their relative abundances, and the wind-dispersed species do the opposite. The first seeds of large trees to arrive in a large clearing or pasture adjacent to forest are often wind-dispersed; furthermore, wind-dispersed seeds almost always mature in the driest part (windiest part) of the year, with the outcome that their seeds are more resistant to the desiccating conditions of an open site than are those of many other forest trees.

While a given species of tree often has many dispersers, each disperser tends to make a different contribution to its seed shadow. The outcome is that the selective removal of one species of disperser may not result in a significantly diminished rate of seed removal from the parent tree yet result in the plant generating quite a different seed and hence seedling shadow. Different dispersers display different timings of fruit removal (which in turn alters the percent of the seeds that are killed by seed predators) and different dispersal agents generate seed shadows with different susceptibilities to seed predators.

In contrast to seed predators, certain seed dispersers may be sufficiently controllable that they become management tools. Cattle and horses in the neotropics are in this category if used with care at moderate density; they consume large quantities of certain fruits and disperse the seeds among seasons as well as over large areas. Simultaneously they may trample and graze herbaceous plants in a manner so as to reduce their competition with tree seedlings and saplings, and reduce the amount of fuel during wildfires. Certain wild animals may also have these effects, and therefore have importance in forest management quite aside from the question of whether the forest is maintaining them in their own right or whether they are being harvested. Management of animals in forest regeneration may also legitimize concern for management of areas that are far removed from the site in question. Many frugivorous birds are highly migratory, as are some of the moths that are important pollinators.

**Dormancy**

The seeds of tropical perennial plants are extremely variable in their dormancy traits. Interspecific dormancy ranges from dry forest tree seeds that can remain dormant for tens of years in a bottle or soil (even wet soil) to those that are already growing when they hit the ground. Germination tends to occur within a few weeks after dispersal in rain forests, but there are many exceptions. These are based both on traits intrinsic to the seed and on the weather at the time of dispersal.

The soil seed pool is very different between forests and disturbance regimes. It would appear that the wetter the forest throughout the year, the poorer is its soil in seeds of forest plants. This is usually because the wetter the forest, the less likely are the seeds to be dormant and waiting for germination cues at the time of dispersal. Second, the soil seed bank is almost entirely made up of pioneer species with a high turnover rate; these ruderals are usually professional colonizers of new light gaps or long-term disturbances such as riverbanks and steep slopes. Measurement of their presence in so-called rain forest soils is severely confounded by the fact that most sample sites in the forest have been within a few kilometers of extensive tracts of secondary forest that generate extremely dense and far-flung seed shadows (produced by animals and by wind) that overlay apparently pristine forest. When tree-falls occur in large expanses of truly pristine neotropical flatland forest, many of the so-called gap colonizers (e.g. *Cecropia, Trema, Ochroma*, large *Piper*) are absent from the regeneration.

In dry habitats, there has been selection for the ability of seeds to remain dormant during the dry season if the fruits mature in the dry season (just as is the case in extra-tropical trees with respect to the winter). In more humid forests, a large proportion of species may wait for the beginning of the rainy season to germinate; in dry forest with a six-month rain-free period there is virtually no germination of seeds until the rainy season begins. Once into a dormant mode, even large tree seeds may simply wait (a long time in captivity) until a cue comes along; from this standpoint, seeds that mature and disperse in the rainy season are likely to display a very different dormancy pattern than are seeds that mature in the dry season. Once dormancy has evolved, there is then the obvious opportunity for further selection towards spreading the germination pattern of a seed crop in time as well as space.

Since large tree seeds are not maintained in the soil seed bank, more attention must be paid to the relationship of the locations of seed trees, seedling/sapling pools, seed predators and dispersal agents, to recruitment. Equally difficult, even where there are barriers between seed trees and seed predators and seed dispersers, large stores of seeds do not accumulate in the soil beneath maternal parent trees (but management of seedling pools may be in order). Finally, there is the annoying fact that while the large seeds of many species of large trees do not remain dormant in the soil, a relatively rich flora of ruderal herbs, vines and treelets may be dormant there at the time of forest perturbation.

It is particularly important not to use the potential dormancy of seeds in laboratory storage as a measure of their likelihood of dormancy in wildland soils. Many tropical trees disperse their seeds during the dry season, and if these dry season conditions are maintained during seed storage, at least several years of dormancy may be achieved. In nature, however, germination at the beginning of the rainy season, coupled with continuous post-dispersal seed predation, soon eliminates the seed reservoir. This caveat applies even to legumes with extremely hard and dry seeds that can last for tens of years in the herbarium.

If management involves the accumulation, storage and dispersal of seeds, it is critical to realize that there is an obvious decline from dry forest to very wet forest in the proportion of the tree species whose seeds will remain dormant for several years or more. However, even in the driest sites, a substantial fraction of the trees will have seeds that cannot tolerate more than one dry season (if that). Furthermore, if management involves introducing seed stocks from elsewhere so as to replace an extinguished local population, it is likely that the incoming seed genotypes will have dormancy traits that match their home habitat better than the destination habitat (this is, however, not necessarily detrimental to a management programme). On the other hand it is also possible that there is considerable within-population variation in genetic traits for dormancy, opening up the possibility of rapid ecological or evolutionary selection for stocks that have exceptionally dormant seeds.

**Seed ecology and forest management**

In tropical seed biology, as in other domains, much remains to be done to apply science to land management. But at least the following management guidelines and implications would seem unambiguous.

1. No matter how compelling the logic, a supposition about a process in seed biology requires field trial in a particular situation before it is certain that it will apply to that situation; a rough and dirty field experiment is worth a thousand logics, at least at this primordial stage. Site specific experiments are critical.

2. A given effect (e.g. increase in density of mahogany seedlings appearing in an abandoned pasture) can be produced by altering many different parts of the overall system, rather than just by changing the relevant seed parameters.

3. Interactants with seeds, be they animals, fungi, bacteria or other plants, are only partly interchangeable: 'animals do not prey on and disperse seeds, but rather species and individuals do.

4. Participants should be viewed as ecologically rather than evolutionarily fitting together, and certainly should not be viewed as 'coevolved' unless demonstrated to be; it is certain that many if not most of the organisms that initially selected for the seed traits now observed are no longer interacting with those seeds, and that most mainland habitats are populated largely by animals and plants that arrived by immigration from the other sites where they did evolve.

5. Only the elimination (extinction) of species is irreversible; all habitat structure can be regained if the participants are still present and sufficient time and/or resources can be allocated to the project.

6. Proximity in time and space to seed, disperser and predator source matters, but not necessarily linearly.

7. Location of the beginning of a seed experiment matters as much in time and season as in space.

8. The more detailed experience that a project manager has with the details of other tropical restoration and management projects, the more likely he or she is to be able to identify those processes that will dramatically alter other processes in the focal project.

9. Seeds (and their products, plants) are only partly interchangeable; seeds are much less monomorphic than their appearance would lead one to suspect.

10. Small plants ('juveniles') may come from sources other than seeds; likewise, a seed bank in the soil or a remnant seed-bearing plant does not guarantee either persistence or influence of a plant species.

Some other statements about seed germination and seedling establishment in relation to gap creation and filling have been proposed by Bazzaz (1984, in press), drawing upon a variety of sources (Table 5).

**Table 5. A summary of present knowledge on seed germination in tropical forests. After Bazzaz (1984, in press)**

. Early successional and pioneer species flower early in life and usually produce seeds annually. In areas with mild dry seasons, plants tend to fruit at the end of the wet season. Where dry seasons are severe, plants concentrate their fruiting at the beginning of the wet season.

. Seed longevity is low in most tropical countries. Suppressed seedlings may be more important than seed bank as a source of regeneration of some tropical trees. However, seed longevity is usually higher for pioneer than for climax species and in pioneers the seed bank may be a major source of regeneration. In contrast to pioneers, seeds of most climax species have no dormancy and a short life span.

. Resprouting is common in tropical trees, but severe fire reduces it substantially. Severe fire and erosion destroy seed banks as well and regeneration will depend on immigrants.

. Seed germination of the many pioneer species is enhanced by increased irradiance.

. Germination is generally rapid in tropical trees. But there is also within-species variation in the speed of germination. Seeds with harder coats generally have a lower moisture content, are longer-lived, and take longer to germinate.

. The germination of many pioneer species is triggered by disturbance. Shifts in red/far red ratios and the temperature fluctuations that result from the removal of vegetation enhances germination. In contrast, seeds of many climax species, except for emergents, are able to germinate in the shade. It must be remembered, however, that tropical tree species vary widely in their germination responses to different light environments. Climax and pioneer species are probably not the only groups that are sensitive to changes in the light environment.

## 3.6 NUTRIENT CYCLING PROCESSES

C. Jordan

### Soil fertility, the native forest and conversion

Climatic conditions in the humid tropics are favourable for biological activity throughout the year. Continuous biological activity in the soils leads to high annual rates of decomposition and soil respiration, and these processes result in high production of carbonic acid. The high production of acid causes a high potential for nutrient loss. Where soils have been subjected to these processes for millions of years, soil fertility is usually low. Low soil fertility in tropical humid ecosystems occurs primarily in lowland areas having latosols (oxisols and ultisols, or ferralsols). However, even in younger volcanic soils, the continual biological activity can result in a rapid decrease in nutrient availability, when native forests are cleared for agriculture, pasture, or plantation forestry.

The high potential for nutrient loss does not affect forest growth, as long as the native forest remains intact, because naturally occurring adaptations of the trees conserve the nutrients. The community of below-gound organisms is an important mechanism which conserves nutrients in natural forests. As long as the below-ground food chains remain intact and functioning, few cations are leached, little nitrogen is volatilized, and phosphorus remains mobile and thus available to plants.

More and more rain forests are being cut, and converted into agriculture, pasture, or plantations of exotic trees. When the forest is cut, the nutrient conserving mechanisms are destroyed, and the below-ground community largely disappears. Within a few years, agriculture, pasture, or intensive forestry become problematic or impossible without heavy fertilizer inputs.

**Nutrient conservation**

The below-ground community plays a principal role in conserving nutrients and in sustaining plant productivity. This community depends for its existence upon both the energy and the nutrients derived from decomposing organic forest litter. Continuous input of organic litter into the soils depends on a management scheme which provides for at least part of the site having a continuous cover of trees or other long-lived plants. Such a system also improves soil micro-climate and soil physical properties, important for sustained productivity.

**Alternatives to even-aged monocultures**

Substitutes should be sought for even-aged monocultures of agricultural crops or forest trees, especially if the monocultures are of exotic species. In addition to the problem of disease spread in genetically uniform monocultures, such plantations may be inappropriate from the soil fertility aspects, because:

. Simultaneous harvesting deprives the soil ecosystem of energy sources, and disrupts life cycles of symbionts and other soil organisms which prevent nutrient loss.

. Simultaneous harvesting exposes the soil to high temperatures, and to rainfall which clogs the soil pores. This inhibits the functioning of the below-ground ecosystem, as well as the growth of new seedlings.

. Simultaneous harvesting removes nutrients en-masse, and sometimes results in nutrient limitation for future crops.

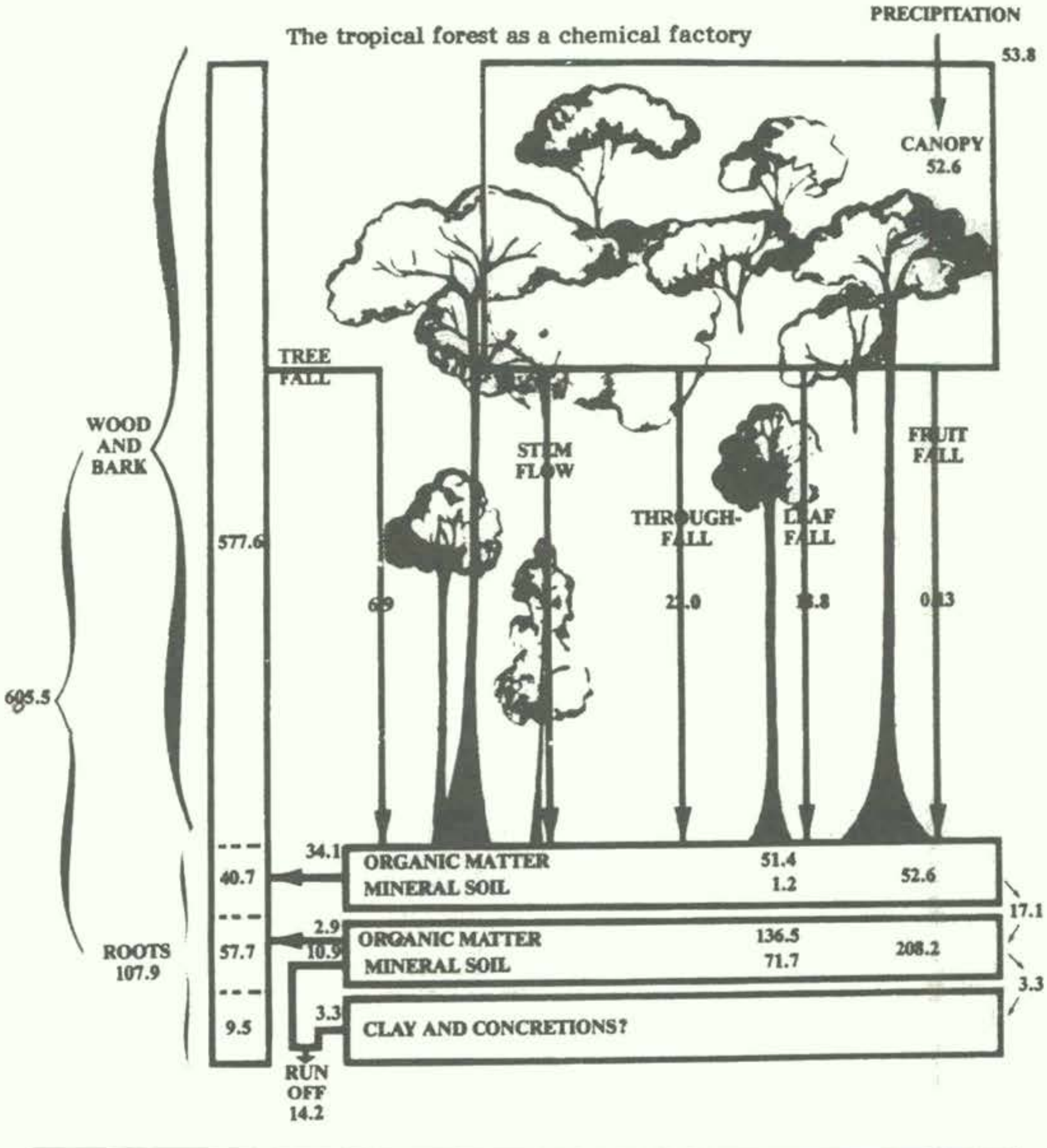
. A monoculture uses excessively a certain suite of nutrients and a certain soil niche, while leaving underutilized other quantitative combinations of nutrients and other soil niches.

**Mixed-species polycultures**

Uneven aged, mixed combinations of native species are much better able to maintain the recycling mechanisms of the forest, and ensure sustained productivity. Because only part of the forest is harvested at one time, the soil communities are never totally deprived of energy or protection. Because native species are used, the nutrient conserving mechanisms are better adapted to local conditions. Because a variety of species are used, a greater proportion of the soil resources can be utilized.

A tree cover which is continuous in time, and partially continuous in space, can be achieved by various means. Where annual food crops are part of the production goal, agroforestry is a good approach. In this system, economically valuable annual crops are mixed with tree species. Where forest products are desired, mixed species polycultures are most desirable.

Agroforestry has often proved to be practical for development of agricultural products. More difficult has been achieving practical sustained yield management of forests for wood products.




Graphic from the Ecology in Action poster exhibit, produced by Unesco in 1981. Shown are stocks (kg $ha^{-1}$) and flows (kg $ha^{-1}$ $yr^{-1}$) of Ca, K and Mg in evergreen forest at San Carlos, Venezuela: compartments in kg $ha^{-1}$, fluxes in kg $ha^{-1}$ $yr^{1}$. Tropical forest systems on nutrient poor soils such as at San Carlos depend on efficient recycling of nutrients. Internal cycling is high compared with output by drainage. Less than 8% of total nutrients are found in mineral soil; most are contained in living forest, litter and humus. This contrasts with tropical forests on volcanic soils and on recent sediments, and with most temperate forests. In the non-disturbed "factory" shown here, loss of nutrients through drainage is low. But, as most nutrients are contained in the living forest, when the forest is cut, most nutrients are lost and the factory can no longer work. This has important implications for the development of tropical forests.

Selective harvesting of uneven aged, mixed forests has generally not been successful in the humid tropics where excessive damage has been done to young trees and seedlings. Management where patches or strips of even-aged forests are intermingled with plots or strips of other ages holds promise as a workable compromise. Clearings less than 50 meters in width or diameter can quickly be filled with litter falling from the adjacent undisturbed trees. Thus the nutrient cycles in the clearing will be kept at least partially intact, enough for the establishment of another crop of trees. From the loggers' viewpoint, clearings this size are large enough to allow felling, and permit movement of skidders with minimum damage to the forest bordering the clearing.

In some areas where harvested trees are relatively small, and where elephants or human labour are used to haul logs from the forest, the harvest of very small patches or even single trees has been used without seriously damaging the remaining forest.

**Nutrient cycling research and improved forest management**

Long-term experiments are required, designed to achieve a forest management system which will ensure a minimum of disturbance to soil or soil cover, and leave undisturbed a significant portion of each management unit during each harvest sequence. Experiments are also recommended on regeneration of degraded areas, such as overgrazed and abandoned pastures now common in many tropical areas.

Such projects should include:

. Studies on the quality of different types of litter, and how quality influences decomposition and subsequent nutrient release, and the energy supply for the below ground ecosystem. Especially to be encouraged is the work proposed within the international programme on Tropical Soil Biology and Fertility (TSBF), a joint venture of IUBS-Decade of the Tropics and Unesco-MAB which aims to relate rates of biological release of nutrients from soil organic matter with plant requirements that depend on these nutrients (Swift 1985, 1987).

. An examination of how the below-ground ecosystem helps sustain productivity of the above-ground crops and trees, by influencing the cycling, retention, and availability of nutrients in the soil. Certain aspects of this are already known, such as the role of mycorrhizae in increasing nutrient uptake by trees. Other aspects, such as the role of the below-ground community in mobilizing phosphorus bound by iron and aluminium, is relatively unexplored.

. Microsite variability, and how it can be manipulated to enhance success of rain forest regeneration. For example, seedlings planted in close proximity to decomposing logs, or in small depressions might grow better than those planted strictly according to a pre-ordained grid pattern.

. An examination of the relative success of various combinations of trees, such as successional legume species with shade-demanding climax species. Other combinations should include economically valuable species with others which maintain ecosystem structure and function. Still others should include trees which are economically valuable in the short term, such as fruit trees, with those valuable in the long run for their saw timber. Combinations could include some species valuable for supporting native wildlife.

. A quantification and refinement of the effects of symbionts such as mycorrhizae and nitrogen fixing bacteria in improving the nutritional status and growth of forest species.

. Experiments on alternatives to heavy machinery for site preparation prior to forest planting. Such alternatives could include new safe herbicides.

. A continual monitoring for effects of increasing industrialization, such as the effects of acid rain on structure and function of ecosystems.

### 3.7 RESEARCH SITES AND CASE STUDIES

Ecological aspects of rain forest regeneration, such as those touched upon in Sections 3.1-3.6 above, have been studied in the last few years at a score and more research sites in the humid tropics, and results from some of these sites were included in case studies presented at the Guri workshop. Some brief indications of work undertaken and results obtained - in these and a handful of some other intensively studied sites in the humid tropics - are given in Table 6. This is by no means comprehensive, but gives an indication of the sort of research which has been undertaken over the past decade and more.

**Table 6. Ecological research on rain forest regeneration at a sampling of sites in the humid tropics: insights and examples. For each site, up to four indicative references are given, as an entry to the literature.**

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**Barro Colorado, Panama:** Island of 1500 ha, isolated from surrounding mainland in 1914, after Chagres River dammed to form Gatan Lake (central portion of Panama Canal). Island declared a reserve in 1926, placed under jurisdiction of Smithsonian Institution in 1946, and became Smithsonian Tropical Research Institute. Much research on influence of seasonal rhythms. Regeneration-linked research includes work on tree mortality rates, treefall frequency and timing, forest production, flowering, fruiting, seed germination, dispersion, etc. Long-term tree demographic study based on 50 ha plot. Leigh et al. (1982).

**Danum Valley, Sabah, Malaysia:** Study on effects of disturbance on rain forest dynamics started in 1985-86.

**East Kalimantan, Indonesia:** Regeneration after clear-cutting and burning on two contiguous plots at Lempake. In early stages of succession, seedlings play more important role than resprouts. Number of species, percentage of cover and frequency of seedlings and resprouts, as well as number of primary forest species, greater in the unburnt plots than those in burnt ones. Dominant species in unburnt and burnt plots differed although they were lying side by side. Suspected that recovery in unburnt plot attributable mainly to undisturbed soil seedbank. Ongoing studies in East Kalimantan include nutrient absorbtion by roots, and role of mycorrhizae in dipterocarp regeneration. Riswan et al. (1985), Riswan and Kartawinata (in press).

**Gogol, Papua New Guinea:** Regeneration following clearfelling for pulpwood in 66,000 ha. Regeneration rapid. Ten year regrowth 20 m tall. Many of early secondary species originate from seed in topsoil; sprouting common, especially among climax forest species. Early patterns of regeneration after logging suggest that forests recovering both structurally and floristically. Saulei (1984), Saulei and Lamb (in press), Webb (1977).

**Hainan and other sites, China:** Long-term studies on dynamics of tropical rain forests on Hainan island and southern Yunnan province - as well as man-made forest ecosystems in Xiaoliang - launched in 1987 within the framework of Cooperative Ecological Research Project (CERP), a joint venture of China, Federal Republic of Germany and Unesco-MAB. Brünig et al. (1986).

**La Selva, Costa Rica:** Intensively studied site which has included work on forest tree growth and dynamics, pollination, seedling biology, and many other aspects of rain forest regeneration. Permanent plots established in 1969, censused in 1982, indicating mortality of 2% of trees per year, with a stand half-life of around 34 years. Lieberman and Lieberman (1987).

**Luquillo, Puerto Rico:** Site in northeastern Puerto Rico, with active tradition of forestry research since the late 1800s. Vegetation studies have included work on physiognomy, microclimatic profiles, biomass and primary productivity, effects of disturbances (damage and recovery from irradiation, herbicides and experimental cutting, hurricanes). Brown et al. (1983).

**Makokou, Gabon:** Regeneration-linked studies have included research on floristic and structural analysis of vegetation,

**Table 6 continued**

gap-phase dynamics, reproduction and growth of lianes, germination and seedling ecology, reconstitution of forest after shifting cultivation, impact of fruit morphology and biochemical composition on frugivore consumption, role of animals as seed dispersers, interrelations between several species of figs and pollinating wasps, agroforestry trials in experimental forest plots and village gardens. Gautier-Hion (1984), Hladik and Blanc (1987), IRET/ECOTROP(CNRS)/Unesco (1987).

**Omo, Nigeria:** Regeneration and successional patterns studied by comparison of enumeration data taken before (1952) and after (1981) treatment of the forest by selective canopy opening and climber-cutting or clear-felling and burning. Twenty-eight years after treatment, number of species and families similar to those in 1952, though treated plots dominated by early succession species. Data available on basal area, mean annual increment, seedling regeneration, standing crops, ground flora dynamics. One conclusion is that structural organization and species composition of top canopy synusia of mature secondary rain forest may be determined quite early in stand development. Okali (1979), Okali and Ola-Adams (1987), Okali and Onyeachusim (in press).

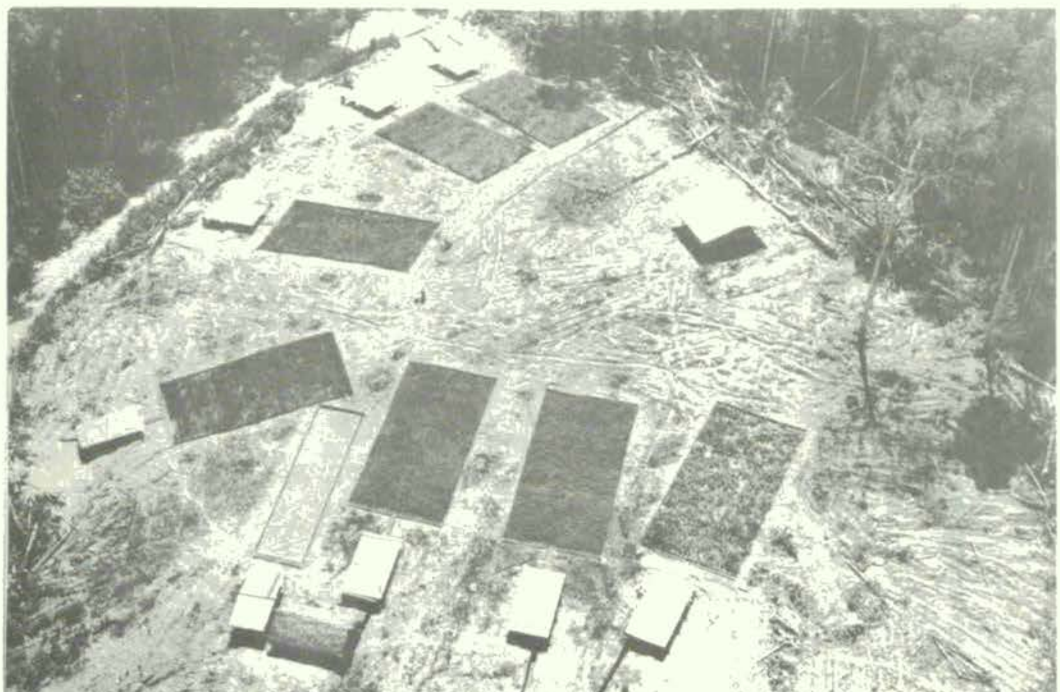
**Saint Elie and other sites, French Guyana:** Multidisciplinary studies on effects of different management practices within ECEREX project (acronym derived from EC-Ecology, ER-Erosion, EX-Experiment) have included clearfelling of 25 ha area, and management of 10 watersheds under different treatments. Regrowth dynamics driven by six major sets of factors: fire; drainage (itself linked to topography and erosion); proportion of soil surface covered by abandoned logs; soil seed bank present after experimental exploitation and fire; seed transport into and within the clear-cut area after exploitation and fire; proximity of forest borders. Other research related to forest regeneration has touched on reproductive ecology, effects of hunting on seed dispersal, structure and species composition of regrowth, organic matter inputs to soil, changes in hydrological and erosion regimes under different management treatments. Suggested implications include the crucial role of litter in revegetation of compacted and charred soils (including the differential effect of *Cecropia* litter), and the manipulation of dispersers to favour establishment of desirable plants. CTFT-ORSTOM (1983), Maury-Lechon (1982. in press), Sarrailh (1980).

**San Carlos de Rio Negro, Venezuela:** Site of intensive studies involving Venezuelan, German and US scientists. Emphasis on nutrient cycling within tropical forest on poor soils. Comparison of San Carlos and other sites along Upper Rio Negro shows that species composition of mature forests depends on a small fraction of climax species that survive from early stages of succession, and on the introduction of many climax species at later stages of succession. Small areas disturbed by slash-and-burn agriculture recover original species composition, but time required varies, depending on the intensity and frequency of disturbance. On larger scale, forest is a mosaic of different-aged patches and structural characteristics, with high variabiity among stands, depending on soils, microrelief, species composition, and disturbance dynamics. Approximately 140-200 years required for an abandoned farm to attain the biomass values comparable to those of mature forest. Recovery is thus five to seven times longer in the Upper Rio Negro than in other tropical areas in South America. Herrera et al. (1978); Medina and Cuevas (1987); Saldarriaga and Uhl (in press).

**Sinharaja, Sri Lanka:** Comparison of structure, floristic richness, dominance and performance of endemic and pioneer species in three sites with varying gap sizes (i.e. selectively logged site, logging trail and shifting cultivation site) and adjacent relatively undisturbed forest. Proportion of pioneer species ranged between 9-11% in the undisturbed and selectively logged sites, and between 29-32% in the logging trail and shifting cultivation site. Performance of *Swietenia* planted as exotic enrichment species in logging trail, indicates its potential for silviculture in disturbed lowland rain forests. Ongoing work includes studies on reproductive biology of nine plant species of economic importance to local communities, soil biology and nutrient cycling in natural and modified forest, performance of seedlings and saplings of *Shorea* spp. in natural gaps and under controlled light and moisture regimes in greenhouses, and development of buffer zone around core area of Sinharaja biosphere reserve. Gunatilleke and Gunatilleke (1985); de Zoysa et al. (in press).

**Sungei Menyala and other sites, Malaysia:** Sungei Menyala, one of a number of reserves in Peninsular Malaysia where studies on lowland dipterocarp forest structure and composition have been undertaken. Studies (also at Bukit Lagong) during the 44-year period 1947-1981 showed little net change in density of most species. Species richness remained almost steady. Mortality greater than average for understory species and lower for emergents. At another lowland dipterocarp forest site (Pasoh), long-term study on demography of tree populations started in 1986 in a 50 ha plot, taking advantage of methodology and experience gained in Barro Colorado. Manokaran and Kochummen (1987); Wyatt Smith (1966).

**Taï, Côte d'Ivoire:** Morpho-structural and floristic analysis of forest succession in largest remaining block of humid tropical forest in West Africa. Four main successional phases, with three groups of species important in forest reconstitution. Root grafts may play important role in rapid superficial cover of soil surface. More recent work by scientists from Wageningen Agricultural University focussed on vegetation dynamics and detailed study of frequency, distribution and causes of tree fall, and definition of maximum number and frequency of chablis that can be tolerated without compromising processes of forest growth and succession. Alexandre et al. (1978), Dosso et al. (1984), Kahn (1982), Vooren (1987).



**Experimental plots for studying run-off and erosion under different treatments. CTFT-ORSTOM research area, Oyapok drainage basin, French Guyana. Photo: J.M. Sarrailh (CTFT).**

**Demographic studies at Pasoh, Malaysia**

Recently, several large-scale, long-term forest plots have been established or planned in the New and Old World tropics to provide demographic data on juvenile tropical trees. Understanding the natural regeneration of tropical forest trees through their complete life cycle, and in their natural community setting, is one of the principal objectives of these studies. One such study at Pasoh (Malaysia) has entailed the establishment of a 50-ha plot (divided into 1250,20 metre square sub-plots), with all saplings and trees of 1 cm diameter and above being tagged and identified. Recensusing of all individuals will be undertaken every five years.

*Shorea maxwelliana*, one of the heavy dipterocarp timbers in lowland rain forest at Pasoh. The tree spotter is Mr. Tahir from the Forest Research Institute of Malaysia, which is carrying out the demographic study in cooperation with scientists from the Smithsonian Institution and Harvard University. Photo: B. Rollet.

# 4. ISSUES IN MOIST FOREST MANAGEMENT, LAND USE AND SILVICULTURE

## 4.1 CURRENT PROGRAMMES IN TROPICAL LAND USE AND FOREST MANAGEMENT

Schmidt (1987, in press) has provided a status report on the management of humid tropical forests, while several case studies at the Guri workshop reported on experimental management experience in particular locations. A conclusion is that only a very small proportion of existing tropical rain forests are currently managed in any real sense of the term. Even when management is attempted, any shortcoming - whether silvicultural, socio-economic, political or institutional - rather effectively prevents success. So intractable might seem these factors that there is a tendancy among many involved in resource management and land use planning to discuss mixed tropical forest management as unrealistic, unworkable or unpractical.

Examples are, however, becoming available to help counter such scepticism. Though few in number, they do suggest that management of mixed tropical forests can be made to work, given the right circumstances and mix of ingredients. Examples of such case studies include the Malayan Uniform System and its modifications and the Selective Management System (Appanah and Salleh in press; Salleh and Baharudin 1985), and two examples described on following pages - experimental management plots in three forest areas in the Côte d'Ivoire and the Celos Silvicultural System in Suriname.

Management for the sustained production of timber should not be isolated from the search for workable multiple-use management systems, which seek to take advantage of the inappropriately named "minor forest products" such as rattans, resins, latex, drugs, fruits, etc. Though timber production leads to loss of diversity of the forest in many ways, forest management under various regeneration systems can also be excellent habitat for many species of wildlife. Research in northern Queensland for example (Crome 1985, in press) has led to guidelines whereby managers can incorporate the needs of wildlife (particularly birds and bats) simultaneously with wood production, under selective logging both with and without silvicultural treatment. Prescriptions include further protection of stream-sides, retention of intact canopy areas, maintenance of certain levels of plant species diversity, and measures to ensure the continued existence of sufficient individuals of those plant species that maintain frugivores through lean periods, over wide areas.

Prospects for the conservation of wildlife and biological diversity in the tropics are in turn linked to measures for reafforesting degraded areas. In the decades ahead, an increasing proportion of tropical lands will support human-impacted ecosystems, while degraded areas cover an important and growing land area in the tropics. Such human-impacted and degraded systems have received comparatively little attention compared to "natural" ones, even though the former may well hold the key for long-term solutions to human-environment problems in these zones. Whence an increasing interest in restoration ecology and the search for improved scientific understanding on which the effective management of impacted systems (including rehabilitation of degraded areas) could be based (Lugo 1986).

An example of a case study in restoration ecology is provided by Guanacaste National Park in Costa Rica, where a plan has been developed to grow 500 $km^2$ of dry tropical forest in Guanacaste Province, of sufficient area and complexity to maintain both species and habitats into perpetuity (Janzen 1986). The plan uses extant technology and concepts, and native species and habitat fragments. It is compatible with current land use concepts at the site and with the socio-political environment in which it will be embedded. Components of the plan include

*continued on page 50*

**Large-scale experimental plots and silvicultural treatments in the Côte d'Ivoire**

The reaction of the tropical rain forest to different silvicultural operations - logging and thinning - has been investigated in three reserved forests in the Côte d'Ivoire - one evergreen, one semi-deciduous, one transitional between the two (Maitre 1986, in press; Maitre and Hermeline 1985). A similar 400 ha experimental area has been laid out in each forest type, each area being divided into 25 plots of 16 ha (see adjacent figure). Three sets of measurements, made on more than 48,000 individual trees over a span of four years, have provided data on diameter growth and annual increment of more than 50 merchantable species, thus yielding information formerly unavailable about the requirements and behaviour of these species. Taking into account growth, mortality, and regeneration of the entire stand, silvicultural operations frequently result in a doubling of annual production, and also favour the recruitment of the most desirable species. Relatively simple, low-cost treatments of thinning and harvesting provide for maintenance and even increase in woody production of valuable species, with a financial return proportionally higher than that obtained in plantations.

Thus, the annual production of principal species ranges between 0.5-2% of standing volume in the untouched plots, 1.5% in exploited plots and 2-3.5% in thinned areas. Just for commercial species, annual increases in volume for individuals > 10 cm. dbh are 0.7-1.8 $m^3$ $ha^{-1}$ $yr^{-1}$ for untouched areas, about 2.5 $m^3$ $ha^{-1}$ $yr^{-1}$ for exploited areas and 2.2-3.6 $m^3$ $ha^{-1}$ $yr^{-1}$ for thinned plots. There is thus a doubling in production, corresponding approximately to about 270 $m^3$ $ha^{-1}$ of standing volume, of which the principal species make up something in the order of 100-150 $m^3$ $ha^{-1}$. The production of natural forest areas improved through silvicultural intervention bears comparison with that in man-made commercial plantations such as 4-5 $m^3$ $ha^{-1}$ $yr^{-1}$ obtained for teak (*Tectona grandis*) and 7-8 $m^3$ $ha^{-1}$ $yr^{-1}$ for *Terminalia ivorensis*. Paradoxically, the very heterogeneity of the forest can provide an additional advantage, since the multiplicity of hardwood species is capable of providing a large range of commercial products.

A management system based on this practice would seem justified since the ratio of commercial volume to cost is greater than that of forest plantations set up in the same area. Over 30 years, the ratios for both systems may be estimated as follows:

- management of the natural forest: 25 $m^3$ $ha^{-1}$/140 US$

  thus about 1 $m^3$ produced for every US$ 5.6 invested. (This assumes untreated natural forest would produce 60 $m^3$ and treated forest 85 $m^3$ of commercial volume).

- plantations: 250 $m^3$ $ha^{-1}$/1,860 US$

  thus about 1 $m^3$ produced for every US$ 7.4 invested.

It must be remembered that natural forest investments are usually compounded for a longer period, but the figures indicate the costs involved. If a wider range of species from the natural forest can be introduced in local markets, the economics of the operation improves.

As a result of these findings, a larger-scale pilot programme in forest management is being carried out in a 10,000 ha block of evergreen tropical forest at Yapo by the national body responsible for forestry development (SODEFOR), with technical back-up provided by the

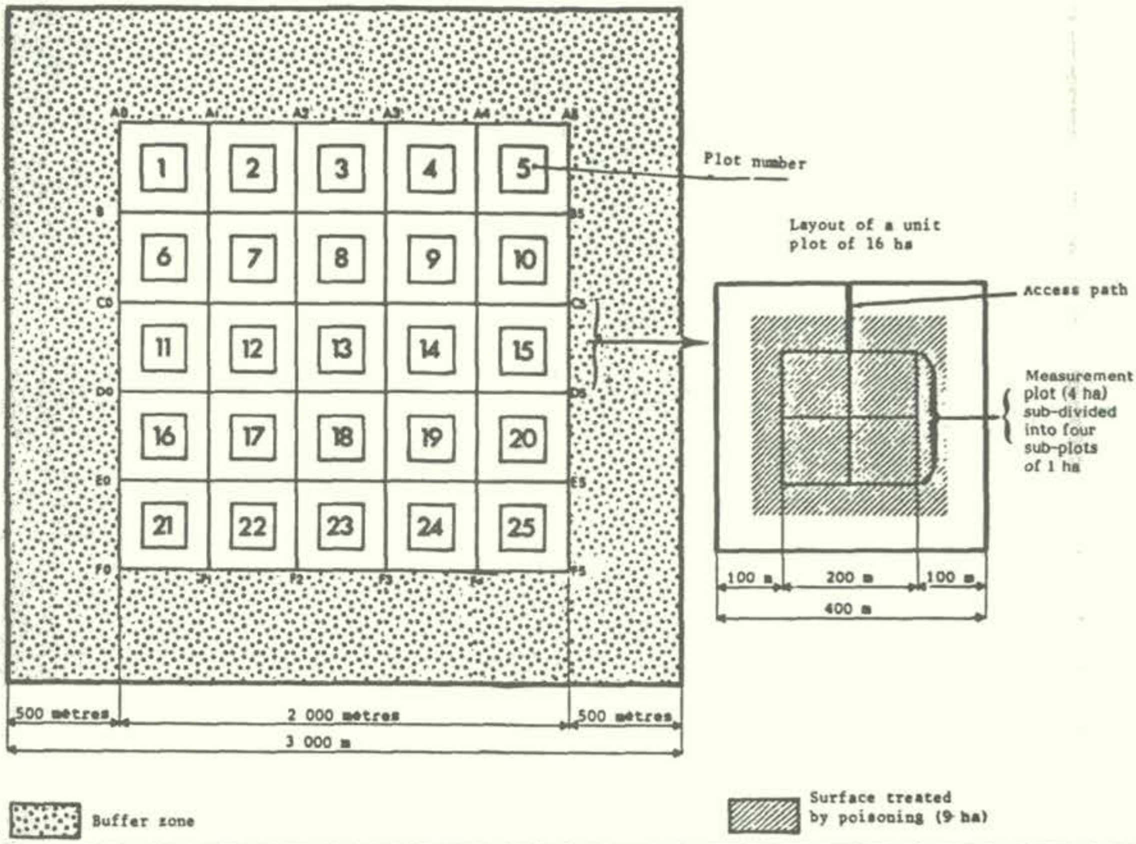
Technical Centre for Tropical Forestry (CTFT). Other operations are envisaged over larger surface areas.

The extensive silvicultural trials have been planned and financed by the government of the Côte d'Ivoire. The determination of the national authorities to seek out ways of economically managing the mixed forest on a long-term basis, combined with the promising results obtained in the experimental silvicultural trials, has encouraged international bodies to contribute already to the financing of these operations.

In more general terms, the Côte d'Ivoire experience would indicate that successful management of the mixed tropical forest depends, in the first place, on the necessary political will and commitment being present at the national level. Such will and commitment need to be put into effect through an official, stable institution, armed with the necessary means and the trained manpower motivated to work in the forest. Finally come the technical problems to be resolved, and here it would seem important to develop a continuum of actions - practical, goal-oriented research leading to pilot demonstrations and then to actions at a larger regional scale.

**Experimental plot layout at three forest sites in the Côte d'Ivoire**

Identical numbering system at each site. Surface area 900 ha : 400 ha central area, surrouded by 500 ha buffer zone



**Celos Silvicultural System**

Profile diagrams are one way of recording the structure of a forest, in both horizontal and vertical terms. They can be used to compare different forest stands, as well as to follow changes in a particular piece of forest over a period of time. The six profile diagrams shown here are from a study published in 1986 by Dutch scientist N.R. de Graaf. They illustrate some of the steps in a silvicultural system for managing certain types of tropical forests, whereby a restricted amount of about 20 $m^3$ of quality timber is taken out of each hectare once about every 20 years, in a well controlled selection felling operation.

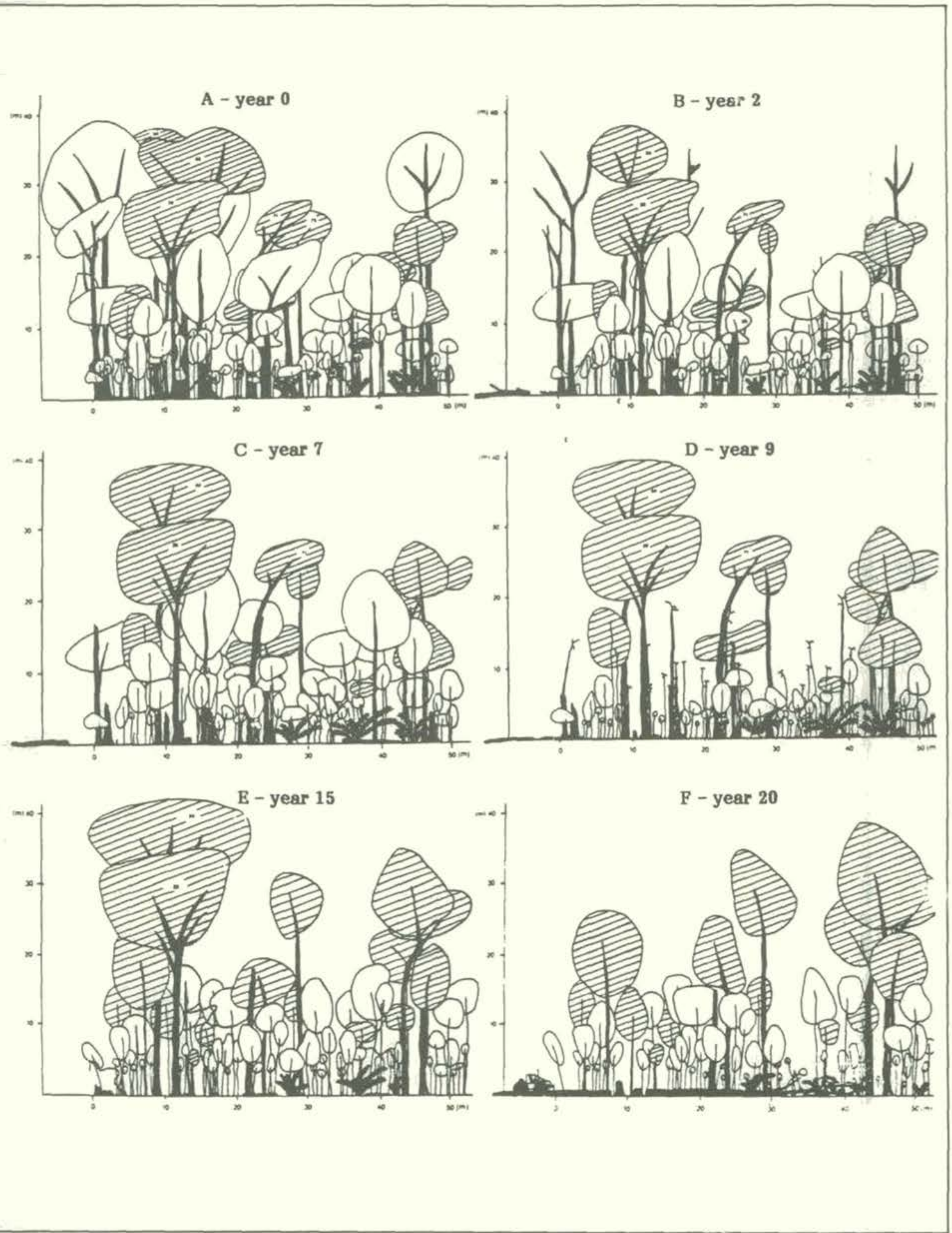
The system was developed within a MAB project undertaken as a joint venture by scientists from the Universities of Wageningen and Suriname. The so-called Celos Silvicultural System - named after the agricultural station in Suriname where the research was undertaken - holds promise as an economically and ecologically viable approach to managing highly mixed forest growing on very infertile soils, in areas of low population density.

It was found that selection felling had to be followed by refinement using arboricides, three times during the cycle (in year 0, year 8 and year 16), to release commercial species, and provide economically sufficient increment. The system was tested experimentally over more than a decade. The main principles were maintenance of a high level of biomass to prevent leaching of nutrients from the ecosystem and minimum interference.

Simplified profile diagrams show changes in forest structure during a 20-year period of harvesting and refinement.

- **A - year 0.** The hatched crowns are the commercial species.
- **B - year 2.** After a light harvesting of two trees and a refinement in which all non-commercial species above 30 cm dbh have been killed to provide growing space for remaining trees.
- **C - year 7.** Immediately prior to second refinement. Most dead trees have fallen. Commercial species have grown considerably. Non-commercial species have increased, and these need to be reduced in number to improve increment and recruitment of commercial species.
- **D - year 9.** After second refinement in which all non-commercial species above 10 cm dbh have been killed.
- **E - year 15.** Immediately before a third, light refinement. Trees have increased in size and numbers, and much recruitment has passed the diameter limit for being represented in this type of diagram.
- **F - year 20.** After the third light refinement (in year 17, which eliminated mainly lianas and a few small trees of undesirable species) and after a second light exploitation in year 20, during which two trees were removed. Height is comparable with that of the original forest, but more open structure indicates less competition. Commercial species dominate the stand, but in the lower strata, non-commercial species are still represented.

The silvicultural treatments are complemented by a strict control of harvesting operations. The aim is to curtail logging damage and logging cost, and results in a reduction of the total area affected by felling and skidtracks from about 25% in conventional logging to about 15% or less (Hendrison, in press).


A - year 0
B - year 2
C - year 7
D - year 9
E - year 15
F - year 20

### Large-scale forest transformation - the Jari project

One of the most ambitious schemes in recent decades for transforming mixed tropical forest has been the Jari project, which has entailed the establishment of 100,000 hectares of plantations in Brazilian Amazonia, with a planting rate that at one time reached 13,000 hectares per year. As such, there have been many newspaper and magazine articles on the scheme but relatively few technical papers on its research results, apart from the accounts of Rollet (1980) and Fernside and Rankin (1985), and several attempts to cover the estate as an enterprise. Whence the special interest of a case study presented at the Guri workshop by John Palmer, now of the Oxford Forestry Institute, who worked as a forest manager and researcher at Jari from 1977-79.

The conception of the Jari scheme dates to the 1950s. A shipping magnate with financial interests in many fields commissioned a review of potential multi-purpose tropical trees to form the basis for an integrated land development scheme. He was advised of projections forecasting a world shortage of paper pulp from the 1980s onwards. Since he wished to run his scheme as a wholly-owned operation, it was planned on a sufficiently large-scale to sustain the cost of establishing from scratch the infrastructural support which in most countries is the responsibility of the national government. A staff member of the New York Botanical Garden proposed *Gmelina arborea* as the preferred species, emphasizing its rapid growth and its ability to grow on a wide range of tropical sites. Trial plantings were made in various of the owner's estates in Neotropical countries. These were all abandoned sooner or later because the national governments would not or could not give the guarantees required by the owner against invasion by squatters or expropriation.

In 1967, 1.3 million hectares were purchased on both banks of the Rio Jari in Brazilian Amazonia. The Rio Jari is the last major north bank tributary of the Amazon before its estuary and is deep enough to admit oceangoing freighters to the 'port' of Munguba, below the first rapids which mark the southern edge of the Guayana Shield. Clear title was obtained to 400,000 hectares and the then military government of Brazil agreed that the land reform and colonization agency INCRA would clarify the property titles on the remainder and transfer them to what later became Cia. Jari Florestal e Agropecuaria Ltda. The shipping magnate's companies were highly experienced in large-scale construction projects and Jari was approached essentially in civil engineering terms, with engineers rather than foresters in command for the first seven years. The engineers were charged with blanketing the forest area with *Gmelina* and the existing forest was simply an obstacle to be removed. For people accustomed to moving mountains to build dams, the solution was obviously to use the largest tractors and bush-crushers on the market.

John Palmer's account of the Jari project's forestry successes and failures, takes up such topics as the choice of plantation species, the effect of machines on the loss of surface soil and compaction of sub-soil, site sensitivity, stump removal, crooked versus straight trees, site-specific matching, exploitation of native species, long-term productivity of the estate, pests and diseases (leaf-cutting ants and fungal pathogens, in particular), fire control, and conservation. In Palmer's view, successes at Jari were due to the application of conventional management techniques and conventional tropical plantation silviculture, sustained by demand-driven continuity of policy and assured finance for essential silviculture. Failures were due to ignorance of the tropical literature, employment of unsuitable personnel and a reluctance to call on people with expertise of tropical forest management gained elsewhere.

Palmer's conclusions on the broadly-applicable lessons which can be learned from Jari will be of no surprise to anyone who has followed an undergraduate forestry course. They bear repeating, however, for their relevance to land management in many parts of the tropics (and indeed other regions). Thus, Palmer concluded:

- that you can learn expensively through making mistakes, or you can learn cheaply by using a good library where the elements of tropical land development and plantation forestry are in dozens of texts and thousands of articles;
- that any development is to some extent site-specific and requires its own unique combination of techniques to be successful;
- that fast-growing trees require timely silvicultural operations to attain their commercial potential, and that in turn means agile and sustained financing, delegated authority and an efficient short-linked command structure;
- that the skill of a forest manager is in deciding what combination of operations is required for any particular situation, a skill which can be partly taught or book-learned but is mostly built up by sheer experience;
- that a forestry scheme is long-term and spatially extensive, so the land tenure of the estate and accessibility to its resources must be clearly defined and on a secure legal basis.

**Logging by machines**

A number of contributions and discussions during the Guri workshop indicated how knowledge of rain forest ecology assists management, and what important gaps there are whose filling would be helpful to management. An example is the question of logging by machines, taken up by Whitmore (in press). Tree felling and log removal creates canopy gaps, so mimics Nature and the forest responds by its natural processes. Modern logging uses heavy machines and creates conditions never found in Nature. Most important is soil compaction, which the flora is not equipped to combat. It seems to be a particularly serious problem in South America. At Jari in eastern Amazonian Brazil, forest clearance for plantations by machine was abandoned because plantation trees grew so poorly on the compacted soils. Machines also disrupt the soil surface destroying seedlings, the humus layer and superficial feeding roots. The soil seed-bank may be removed. Thus the natural sources of replacement forest are destroyed. It is common also for log extraction tracks to dam streams and thereby create swamps. The key to successful forest recovery after logging lies in minimising damage to seedlings, adolescent trees, soil surface and drainage pattern. At Bajo Calima in Colombia excellent forest regrowth occurs, despite total biomass removal, because extraction is aerially by cable and the forest floor is left intact (Ladrach 1985). In Gogol, Papua New Guinea, Saulei and Lamb (in press) have suggested that early seedling density would be improved by logging methods that reduced the level of soil disturbance. Smaller sized logging areas and more scattered residual trees would improve the rate of seed dispersal and increase structural diversity.

**Revamping shifting agriculture in northeastern India**

The importance of the constraints posed by changing social context is nowhere better illustrated than in shifting or swidden agriculture. This long established, widespread form of land use in the humid tropics has many variations, but basically involves clearing small areas of forest, burning the dried slash and raising crops for a few years on the temporarily nutrient-enriched soil. The shifting cultivators then abandon the plot to natural regrowth during the fallow phase, before they return to the same plot after a number of years have elapsed.

In India, this cycle is known as "jhum". In the past, the cycle used to be 30 years or more, which gave a reasonable time for recovery of the forest and soil, as well as yielding reasonable returns to the farmer. But increased population pressure (in northeastern India, the population has more than quadrupled in the first three-quarters of this century) and reduced land area (due to site degradation) has resulted in very short jhum cycles of 4-5 years. This in turn has accelerated the land degradation spiral, further dampened the recovery of soil fertility and diminished economic returns.

Thus, even though shifting agriculture is based on sound scientific principles, the distortions that have crept in due to the shortened jhum cycle have made this system untenable in its present form. At the same time, alternatives based on modern terracing techniques have not proven successful, in part because they have been associated with attempts by planners, administrators and scientists to impose from outside a value system that was considered to be good for the people of the region, without trying to understand the processes that operate in the traditional ecological system.

This, then, provided the context for a long - term ecological study of shifting cultivation in northeastern India, carried out by a team of scientists headed by P.S. Ramakrishnan, presently professor at the School of Environmental Sciences at Jawaharlal Nehru University in New Delhi. The study has covered aspects of nutrient cycling, hydrology, plant succession, soil microbiology, socio-economics, etc. A flavour of the detailed ecological research carried out can be given in three examples. First, analysis of the demographic characteristics, resource allocation and reproduction of annual and perennial plants has highlighted the role of weeds in conserving nutrients, checking erosion and controlling diseases and pests. Second, changing patterns of $C_3/C_4$ species in herbaceous communities have revealed that $C_4$ species generally are characteristic of early successional stages, have a high nutrient use efficiency and occupy nutrient poor microsites. Third, work on nutrient dynamics has clarified the role of different plants in the build-up of nitrogen, phosphorus, potassium, calcium, magnesium, etc., throughout various successional sequences.

The overall conclusion of these and other component studies is that low production costs, and high energy efficiency make the jhum system more viable than terrace cropping. Mixed cropping with 8 to more than 30 species grown together is efficient in light capture for photosynthesis, meets the varied needs of the community, ensures self-sufficiency of the village, provides continued plant cover during the rainy period when the rapid nutrient loss would otherwise occur, and enables weeds to be kept under control. The entire jhum operation involves efficient recycling of resources for optimizing yield through the use of crop and weed residues as organic manure and as feed in swine husbandry. On the other hand, the distortions that have occurred in the jhum system leave less scope for forest regeneration and there is little or no prospect of the forest coming back under the prevailing conditions in northeastern India.

The field research of Ramakrishnan and colleagues has led to a number of practical guidelines for improving the system of land use and resource management in northeastern India.

. Condense the time span of vegetation succession and reconstitution, through manipulation of species mixtures in time and space.

. Accelerate fallow regeneration through introduction of fast-growing native shrubs and trees.

. Redesign agro-forestry systems incorporating ecological insights on tree architecture (e.g. the canopy form of tree species should be compatible with crop species at the ground level, by permitting sufficient light penetration and through fast recycling of nutrients).

. Vary species composition in the crop mixture at different altitudes (e.g. emphasis on potato at higher elevations compared to rice at lower elevations has resulted in a many-fold increase in economic yield, in spite of low fertility of the more acid soils at higher elevations).

. Improve nitrogen economy through introducing nitrogen-fixing legumes and non legumes such as Nepalese alder.

. Use bamboo and other fast growing trees as windbreaks, to check wind-blown losses of ash and nutrient losses in water.

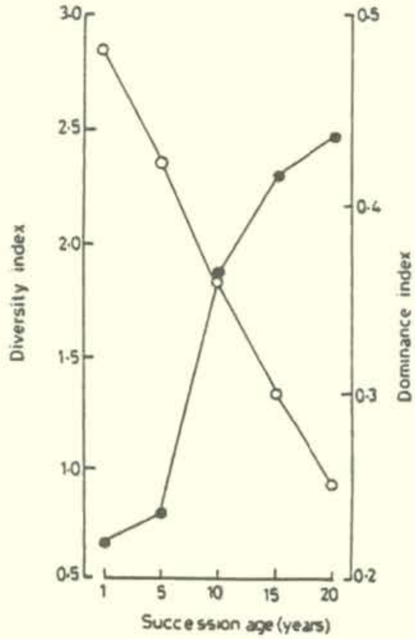
. Incorporate cash crops such as black pepper and cardamum into the agroforestry system.

. Introduce improved breeds of swine and poultry.

. Introduce improved low-level technology into the village units to relieve drudgery and increase energy efficiency (agricultural implements, cooking stoves, micro-hydroelectric projects, biogas systems).

. Encourage artisanal skills and products, based on leather, bamboo and other woods, blacksmithy-work.

Several of these recommendations have already been put into practice and are bearing fruit. Crucial to what has been achieved so far is the focus on understanding and building-upon the unique relationships between tribal people and their environment. Experience gained in the work in northeastern India provides one of the building-blocks for an evolving collaborative programme within MAB on ecosystem redevelopment in the humid tropics of Asia.




**Species diversity (•) and species dominance (o) in some successional communities in Meghalaya, northeastern India. After Toky and Ramakrishnan (1983).**

acquisition of all land as soon as possible, development of educational activities, continuation of intensive research on processes of natural forest spread into deforested habitats and on experimentally induced forest spread, extension of fire control programme, establishment of a management endowment fund, resurrection of forest laws (concerning slope management, etc.), elaboration and carrying out of detailed management plans (included six conspicuous areas of interface with the commercial world) and development of links with other dry forest reserves. The size of the Guanacaste National Park, the role of fire, the issue of species richness, the problems of poaching, and the processes involved in forest restoration (seed movement, seedling establishment, etc.) are among other topics treated in this case study that are important in the rehabilitation of degraded land.

Useful insights for designing rehabilitation schemes within multiple-use systems may come from those "tolerant" forms of management in which native vegetation is largely conserved and/or reconstituted through successional processes. Such forms of forest management may entail weeding or thinning out of less desirable competitors, and promoting the establishment and/or increasing the productivity of desirable species. An example is in flood plain forests of the Amazon Estuary (Anderson, in press) where the relatively low biological diversity and high concentration of economic species makes these forests particularly amenable to "tolerant" forms of management by the rural inhabitants (*caboclos*). In this area, many of the desirable species are rarely planted due to their natural abundance (e.g. *Euterpe oleracea, Hevea spruceana, Carapa guianensis, Spondias mombin*). As a result, forest stands in which virtually all species are useful can be generated and/or maintained with minimal effort. This form of land use indicates that extractivism and forest management can be reconciled in ways that minimize risk and maximize sustainability.

Mexico is another country where researchers have been working on ways of developing multiple use systems that take advantage of the characteristics of the local environment and that can be sustained without the need for large-scale inputs of fertilizers, capital and equipment. Scientists from the Institute of Biological Resources (INIREB), in Jalapa, recognized the special nature and success of a traditional local agricultural system, the *chinampa*, and decided to experiment with it to create a new method for meeting food needs. Satisfactory results have been obtained on a pilot scale from mixed agro-piscicultural systems. Tree crops such as papaya and banana have been successfully combined with vegetable, poultry, pig and fish production. Systems of re-cycling plant residues and animal wastes have been refined and high sustained yields of tree and vegetable crops have been recorded.

Follow-up work by Mexican researchers has included ecological analysis of Maya agriculture (Gomez Pompa 1987) and the combination of traditional tree and crop species in managing the secondary vegetation in the Uxpanapa area of Veracruz State (del Amo in press). The Veracruz studies, for example, have entailed comparison of corn field, 2-year old orchards and 9 and 12-year old secondary forest. Elucidation of recovery processes has aimed at identifying ways and means of managing and accelerating the succession towards more useful and productive stages. Clearance of some plants and enrichment with others are among the experimental treatments, which have sought to take advantage of knowledge about traditional syustems of horticulture (Mayas), multiple use of land (Lacandones), use of different ecological habitats (Chontales, Nahuas) in Mexico. Data include rates of biomass and nutrient accumulation during the fallow, and chemical interactions between and among the naturally occurring and introduced plant species. Management insights generated by the study include the use of the *acahual* like substratum for introducing valued species with different ecological strategies into the successional sequence, and the imitation to the extent possible of the "natural" structure of the various successional stages.

The results of people-environment studies such as these highlight one way forward in the search for an improved basis for ecologically sound development in the tropics - that of integrating the resource-based knowledge of local people (in such fields as multiple-cropping, manipulation of swidden fallows, etc.) with modern technological know-how in flexible ways that are capable of adapting and being adapted to changing social and economic circumstances.

Another study in Mexico has explored multi-purpose species, which are another dimension of multiple use. Peters (in press) has worked with *Brosimum alicastrum* (Moraceae), a multi-purpose forest tree whose seeds are extremely rich in protein. The species occurs naturally in almost pure stands in many regions of Mexico. To provide guidelines for the utilization and management of this important forest resource, a three-year study of the growth, reproduction and population dynamics was carried out in Veracruz. Detailed demographic data were collected, and a matrix model was used to simulate forest dynamics over time. A sensitivity analysis was then performed to determine the maximum number of seeds which could be harvested from the forest on a sustainable basis.

Demonstration of the potential utility in the management of tropical forest resources of a particular area of scientific enquiry (in this case, plant demography) was a conclusion of this case study, which could perhaps be put in a more general context. Many groups of researchers, from a wide variety of disciplines, have a contribution to make to the search for sustained production systems in the tropics, especially if such studies are placed within the broader context of economic and social realities. These contexts were not within the purview of the Guri workshop, but are nevertheless critical in considering why there is a current lack of large-scale sustained yield management schemes in vast areas of closed broadleaved forests. There would certainly not appear to be a shortage of experiments, recommendations and attempts at pilot demonstration programmes. Reasons for the lack lie elsewhere.

## 4.2 ON COSTS, BENEFITS AND ECONOMICS

Forest management is an economic activity. Investments must be justified in terms of their effectiveness to enhance future benefits to be derived from the resources they help develop (i.e. they must pay off). But the economic benefits of natural tropical forest management have proved difficult to quantify.

One aspect of the problem concerns the changing values of resources. Costs and values of the inputs and outputs figure in all aspects of a forest or land use management plan. Many of the monetary figures are relatively stable and change in traditional and expected ways. However, there is one clear maverick and that is the actual market value of the log at the stump or sawmill. The future value of wood (and indeed other forest) products is unpredictable and historically has usually been substantially different at the beginning than at the end of a rotation. An area of a tropical country tends to move from frontier to final agro-ecosystem, a process that may take as little as ten years at present to centuries over the last thousands of years. During this time, a given species of hardwood log often changes from negative stumpage (burned to clear the site) to being worth hundreds of dollars. Since the value of that log is central to a forest management plan, it means that the core basis for that plan is changing much more rapidly than are the values associated with the support structure.

Another large part of the problem is that the productive potential of resources found in abundance is undervalued. Economic analysis has not been able to evaluate adequately the larger social context, and the benefits of water quality, genetic conservation, and natural beauty that successful programmes of tropical forest management could generate. Consequences of alternative land uses further complicate the validity of a strictly economic analysis.

There are indications, however, that forest economists are beginning to realize that the apparent low economic rates of return of tropical forestry projects are illusiory. Once social and ecological values are considered, these projects become economically attractive and indeed competitive. One example of evolving perceptions is provided by Leslie's (1987) review of the economics of the management of mixed tropical forest, which reflects a change in view of an earlier (1977), somewhat pessimistic assessment by the same author. Points of significance to emerge from Leslie's review include an assessment of the weaknesses of neoclassical economics.

Leslie argues that the economic prospects of tropical forest management are greatly, and perhaps primarily, governed by the rate of interest over time. The choice of the rate of interest to use is almost entirely subjective, and there is little in economic theory or practice to guide or constrain that choice. The indications are however, that the appropriate rate is more likely to be at the lower end of any range of real rates than at the upper end. Leslie comes down firmly to say that the classical economic case against the management of mixed tropical forest is wrong and not simply because of its inherent theoretical and practical weaknesses.

It is wrong because, at the rates which theoretical considerations and empirical studies suggest should be used in forest economics, natural management of tropical mixed forest is likely to be a better economic and financial proposition than alternative land uses or management systems. Leslie's change in heart thus corresponds to what many foresters and ecologists have long claimed - that the weakness of the economic case against management is that it omits many benefits because they do not earn revenue or are external to the forest administration. Evaluation in terms of commercial timber production only may be a legitimate procedure from the point of view of an individual forest-owner whose sole interest or responsibility is the financial profitability of timber. But very little tropical forest fits into this category; most of it is under some form of public or communal ownership. Leslie concludes that management of tropical forest, wherever it is ecologically feasible, will also, on its own merits, tend to be economically preferable.

This heartening statement needs to be tempered by the deep entrenchent of neoclassical economics, whose perceived weaknesses have not dislodged it from its implicit self-professed standing as the only true economics. In Leslie's opinion, it retains this image by a powerful combination of: (a) developing a body of theory whose cumulative intellectual brilliance and logical elegance divert attention from its irrelevance; (b) ignoring criticisms or disarming them through subterfuges that twist contradictory evidence into confirmation or dismissing disserting views as belonging to special cases; (c) monopolizing the teaching of economics and the staffing of economic policy institutions with people schooled in that tradition.

Borrowing from George Bernard Shaw, each profession can admittedly be considered a conspiracy against the laity. But if Leslie's perception is anything near correct, it means that the advocates of mixed tropical forest management still have much to do to press home their case. Examples of effective management remain illusive, at least taking the triple criteria (FAO, 1985) of management being ecologically and technically possible, economically feasible and attractive, and socially and politically practicable. But as indicated elsewhere in this report, examples are emerging.

### 4.3 SOCIAL CONTEXT

Intricately linked with the issue of economic costs and benefits is that of social and policy context, and several recent studies have highlighted how government policies - both within and outside the forest sector - may serve to accelerate the conversion of tropical forest lands in ways that are inimical to sustained use of resources and to socio-economic advancement. Thus, Repetto (1987) has explored some of the impacts on tropical forest development of investment incentives, tax and credit subsidies, farm pricing policies and terms of logging concessions. Such incentives and subsidies may lead to considerable economic losses, wastage of resources, excessive costs, reductions in potential profits and net foreign exchange earnings, loss of badly needed government revenues, and unearned windfalls for a favoured few businesses and individuals (Table 7). A conclusion is that improvements in policies and policy instruments hold scope for putting tropical forest development on a more sustainable basis.

Policy formulation is, in turn, shaped by such factors as the stage of national development and the weight of human population pressure on tropical lands. The social context of densely populated countries is clearly different to that in low density areas. An example of the former is India, where Nair (in press) has provided a comparative account of silvicultural practices in three widely separated regions (Western Ghats, Andaman and Nicobar Islands, and the north-eastern region), which have a long history of management. Over time, wood production - with both polycyclic and monocyclic systems - has tended to receive priority over multiple use management. Though considerable research has been undertaken, one conclusion of Indian experience in rain forest management is that considerations such as rotation and regeneration periods, felling cycle, harvestable girth limits, etc. are not based on the growth rates and regeneration requirements of the tree species, but on exigences to increase wood supply in the short term.

**Table 7. Tropical forest development within an incentive perspective: some dimensions and examples of the impact of government policies. After Repetto (1987)**

| Policy instruments | Some effects and consequences |
|---|---|
| **A. Forest sector policies** | |
| Rent-seeking in timber concessions | Only a small proportion of economic rents are captured by tropical governments through royalties, land rents, license fees, various taxes. |
| | Contracts with concessionnaires usually reached not through competitive biding, but rather on basis of standard terms or individually negotiated agreements. |
| | Governments increase contractors' profits on timber from public lands by assuming some timber marketing costs (e.g. construction of roads, port facilities) plus environmental costs. |
| Structure of forest revenue systems | Charges generally based on timber removed, not on volume of merchantable timber in forest tract. Licensees are thus encouraged to take only most valuable trees. |
| | Concession agreements and stipulations (e.g. concerning harvesting regulations) are not enforced. |
| Incentives for domestic wood processing industries (e.g. enaction of log export bans, exemption of plywood from export taxes) | Inefficient processing may drastically reduce the rents from forests by absorbing potential profits in higher costs. |
| | Injudicious investment in wood-processing capacity, and overly generous logging agreements, may combine to increase the log harvest much beyond what it would be without these policies. Forest clearance reduces the output of many valuable non-timber forest products, and induces losses in ecological services. |
| **B. Policies outside the forest sector** | |
| Direct sponsorship and subsidy of agricultural settlements | Failure of a number of settlement and transmigration schemes, in part because of overestimation of agricultural capabilities of forest soils (often nutrient poor, easily leached and erodable). |
| Land tenure based on clearance and cultivation of forest lands | Serves to expand the area of shifting cultivation, (e.g. to encourage landless people to enter timber concessions and clear and claim logged-over areas). |
| Generous subsidies and incentives for forest conversion (e.g. for cattle ranching in Latin America) | Projects are undertaken that probably would not have been started without subsidies (e.g. income tax holidays, tax credits) and speculative hope of rising land prices. |
| | Incentives shift the margin of relative profitability, between forestry and competing land uses, and encourage more rapid land conversion. |
| | Large contrast between economic value (e.g. of livestock project) and value to the private investor. |

Management has been dictated by the rapidly changing socio-economic environment. Growing industrial demand has accelerated the rate of exploitation and very little effort has been made to restock felled areas. Management prescriptions have been changed frequently to enhance immediate wood production. Further, the pressure for conversion to other forms of use, in particular cash crop plantations, has increased. Technological developments based on ecological understanding of the forests have lagged behind. There are several political, institutional and technical constraints and one cannot be too optimistic about the future of the tropical evergreen forests in areas with heavy population pressures (e.g. India, Nigeria), given the multifarious pressures to which they are subjected.

Even in countries with low population densities, social context may be determinant in shaping management policy. An example is Papua New Guinea, where virtually all forest land is owned by village clans and there is little state-owned forest in a National Forest Estate. Forestry operations, including logging, can only be carried out with the agreement of these traditional owners. The usual practice is for the Forestry Department to purchase the rights to harvest the timber from this land for a prescribed period. This concession is then awarded to a timber company. Ownership of the land remains vested with the clans.

When the Gogol Timber Project in Madang Province was conceived, it was necessary to reach agreement with 261 clans who jointly owned the 66,000 ha of the two main blocks of land involved (Lamb, pers. comm.). This took some considerable time. Other negotiations involving the amount and manner of paying royalties on the timber were also complex. Although the project included the development of a plantation on part of the logged land, the landowners were unwilling to commit themselves to leasing land for this to the government until they could see how the earlier arrangements involving logging and royalty payments had worked.

Subsequent developments have involved continuous negotiations with the landowners. In many cases, especially in the case of royalty payments, these negotiations have been heated and acrimonious. Invariably the landowners have had definite views on what should or should not happen on their land and have been willing to express their views. The government's response has been to establish a working group made up of all the government departments involved in the project to act as a liaison body with the landowners and the timber company.

It is not yet clear whether the Gogol Timber Project will be a long term success. What is clear, however, is that all management decisions have had to be made in the context of the landowners remaining present on their land and needing to make their livelihood from it. This has made the task of land use planning more difficult but it is the only acceptable approach in Papua New Guinea today. Quite apart from being a political necessity it has the quite considerable social benefit of ensuring village people retain control of their land and independence.

## 5. CONCLUSIONS AND RECOMMENDATIONS

1. It would be foolish to maintain that the current management picture in tropical moist forests is an encouraging one. In the three main regions of the humid tropics, substantial areas of forest are being converted to other uses, while significant programmes of silvicultural treatment and multiple use management are still all-too-rare. Yet case studies are emerging that suggest that economically viable and ecologically sound management can be achieved, given the right mix of ingredients.

2. Achieving sound management will not be easy, and will depend on the concerted efforts of national governments, management agencies, research institutions and non-governmental groups in the tropical countries themselves. The broader international community also has a role to play in providing expertise, cooperation and financial assistance, working through frameworks such as the Tropical Forestry Action Plan, coordinated by FAO, and Unesco's Action Plan for Biosphere Reserves. There is increasing support for natural forest management in scientific and conservation communities, and this should be drawn upon to generate support for management and research projects. As Oldeman (1987) has written, good forest management of existing forests is economically much more interesting and profitable than the recuperation of degraded lands by means of afforestation. Prevention not only is better than healing, it is cheaper too.

3. From the research viewpoint, it is recognized that many of the management problems are not ecological problems as such, or at least are not amenable to an ecological solution. Increased effort should be made to define areas where ecological inputs can be put to good use in management, to translate existing ecological information on the behaviour of rain forest into forms in which it can be incorporated into the management process, and to tailor future research to provide predictive knowledge of processes inherent in future management options.

4. Much of the earlier ecological research on rain forest ecosystems was descriptive, fragmentary and focussed on "pristine" situations. In future, greater emphasis might usefully be given to prescriptive, cooperative efforts, with a focus on sustained management and multiple use of mixed tropical forest ecosystems as well as on the redevelopment of human impacted and degraded systems. One framework for collaborative research might be provided by the theme of "Forest regeneration and ecosystem rehabilitation in the humid tropics", endorsed by the International Coordinating Council for the MAB Programme at its ninth session in October 1986 (Unesco 1986, Section 3.5 and Annex 9). The elaboration of research hypotheses to be tested in such efforts might take advantage of the experience gained within such programmes as that on Tropical Soil Biology and Fertility (Swift 1985, 1987). Efforts should also be made to extend and reinforce the network of biosphere reserves in the humid tropics as areas for research, education, training and demonstration of sound management practices, including the conservation of genetic materials.

5. Differences in the scale of interest of researcher and manager remain a major stumbling block to the applicability and application of research findings. The focus of much research is at a more detailed scale than those of concern to the planner and manager. Many researchers working on rain forests are interested in processes and phenomena acting at a scale of a few square metres to a few hectares, while management and decision-making take place within a context of several tens, hundreds or thousands of hectares or square kilometres. In designing new research activities, attention might thus be given to ways of increasing the time and space scales that are considered, with a view to linking up with the concerns of the manager and planner. A related aspect is that of assessing

the interrelations and conflicts between ecological, social and economic processes and of seeking ways of "internalizing" dimensions that are presently considered as "externalities". Such measures might help in building bridges between scientist and manager, as well as in exploring how "fixed variables" might be transformed into variables that are no longer fixed.

6. At the same time as relating research to larger space and time frameworks, there is also need for new research initiatives at a more fundamental, finer scale, designed to gain a better understanding of the mechanisms and processes that underpin rain forest regeneration. This would be in line with what could be called a hierarchical view of life - the notion that the natural world can be profitably viewed as a multi-layered system, hierarchical in space and time, and that one needs to look up a step in the hierarchy (e.g. in terms of space and time) to understand the constraints under which a phenomena occurs and descend a step to determine causality (Allen and Starr 1982, O'Neill et al. 1986, Salthe 1985). An example of switching scale in rain forest regeneration is the detailed, fine-scale study by Smits (1985) of the role of mycorrhizae in dipterocarp regeneration, and the subsequent testing of the insights gained within large-scale reafforestation schemes in East Kalimantan.

7. Improved communication between researchers and managers is needed for putting the results of research into practice. The primary channel for the communication of the results of much scientific research remains the scholarly or professional journal, with contributions subject to rigorous peer review. At the same time, there is need to encourage scientists to make available their findings in a form comprehensible to and useable by those responsible for land use planning and resource management. For example, a detailed scientific paper in an international journal might be complemented by a shorter communication geared to the local forest-planner - what Salleh (1986) has called a policy of "double publishing".

8. Field workshops on tropical forest management, that bring together researchers and managers - as equal partners, present in approximately equal numbers - also have a role to play, at the national and regional level. Such workshops can serve to acquaint researchers with the practical problems and constraints of tropical forest management, and familiarize forest managers with recent ecological findings and scientific methodology. Personal interaction may be fostered by focussing on problems as perceived within local, national and regional contexts. In seeking out a dialogue and interface between researcher and manager, discussion should generally focus on topics and terms that impinge on the daily concerns of the forest manager and planner. For example, an examination of the effect of logging damage on trees and soil is likely to be of greater interest to the manager than a discussion on gap phase dynamics.

9. In concluding, and borrowing from Schmink (1987), the challenge of seeking sustainable development in the humid tropics depends on the best creative efforts of people in many different fields, willing to work together on the practical task of designing feasible policies and land management systems. Given a willingness to acknowledge the complexity of the problems involved - and to search for broad principles as well as small, incremental solutions - there is still room for optimism.

## REFERENCES CITED


Alexandre, D.H.; Guillaumet, J.L.; Kahn, F.; Namur, C. de; Moreau, R. 1978. Observations sur les premiers stades de la reconstitution de la forêt dense humide (Sud-ouest de la Côte d'Ivoire). Cahiers ORSTOM, sér. Biol., 8 (3), 189-270.

Allen, T.F.H.; Starr, T.B. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago.

Amo, S. R. del. Management of secondary vegetation for artificially creating useful rain forest in Uxpanapa, Veracruz, Mexico - an intermediary alternative between transformation and modification. (in press)*

Anderson, A.B. Forest management strategies by rural inhabitants in the Amazon estuary. (in press)*

Appanah, S.; Salleh, M. N. Natural regeneration and its implications for forest management in the Malaysian dipterocarp forests. (in press)*

Baker, H.G. 1965. Characteristics and modes of weeds. In: H.G. Baker; G.L. Stebbins (Eds), The genetics of colonizing species, 347-356. Academic Press, New York

Bawa, K.S.; Krugman, S.L. Reproductive biology and genetics of tropical forest trees in relation to conservation and management. (in press)*

Bazzaz, F.A. 1984. Dynamics of wet tropical forests and their species strategies. In: E. Medina; H.A. Mooney; C. Vazquez-Yanes (Eds), Physiological ecology of plants of the wet tropics, 233-243. Junk, The Hague.

Bazzaz, F.A. Regeneration of tropical forests: physiological responses of secondary species (in press)*

Bazzaz, F.A.; Pickett, S.T.A. 1980. Physiological ecology of tropical succession: a comparative review. Ann. Rev. Ecol. Syst., 11, 287-310.

Boojh, R.; Ramakrishnan, P.S. 1982. Growth strategy of trees related to successional status. I - Architecture and extension growth. II - Leaf dynamics. Forest Ecology and Management, 4, 359-374, 375-386.

Brown, S.; Lugo, A.E.; Silander, S.; Liegel, L. 1983. Research history and opportunities in the Luquillo Experimental Forest. US Forest Service, New Orleans.

Brünig, E.F.; Bossel, H.; Elpel, K.-P.; Grossmann, W.-D.; Schneider, T.W.; Wang Zhu-hao; Yu, Zuo-yue (Eds). 1986. Ecologic-socio-economic system analysis and simulation: a guide for application of system analysis to the conservation, utilization and development of tropical and subtropical land resources in China. Institute for World Forestry and Ecology, Hamburg.

Coley, P.D. 1983. Rates of herbivory on different tropical trees. In:E.G. Leigh; S.A. Rand; D.M. Windsor (Eds), The ecology of a tropical forest. Seasonal rhythms and long-term changes, 123-132. . Smithsonian Institution and Oxford University Press, Oxford.

Crome, F.H.J. 1985. Problems of wildlife management in relation to forestry practices in the southern hemisphere. In: J. Kikkawa (Ed.), Wildlife management in the forests and forestry controlled lands in the tropics and the southern hemisphere, 15-21. IUFRO, University of Queensland, St. Lucia, Brisbane.

Crome, F.H.J. Wildlife conservation and rain forest management examples from north east Queensland. (in press)*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* References to papers presented at the Guri workshop. Book based on the workshop edited by A. Gomez-Pompa, T.C. Whitmore and M. Hadley, proposed for publication in the newly launched Man and Biosphere Book Series of Cambridge University Press and Unesco.

CTFT-ORSTOM. 1983. Journées ECEREX. ORSTOM, Cayenne.
Cuevas, E.; Medina, E. 1986. Nutrient dynamics within Amazonian forest ecosystems. I. Nutrient flux in fine litterfall and efficiency of nutrient utilization. Oecologia, 68, 466-472.
Dosso, H.; Guillaumet, J.L.; Hadley, M. 1981. The Tai project: land use problems in a tropical rain forest. Ambio, 10(2-3), 120-125.
FAO. 1985. Forest product prices. 1965-1984. FAO Forestry Paper 61. FAO, Rome.
FAO. 1986. Tropical Forestry Action Plan. Committee on Forest Development in the Tropics. FAO, Rome.
FAO. 1987. Tropical Forestry Action Plan. FAO, Rome.
FAO/UNEP. 1981. Tropical Forest Resources Assessment Project. FAO, Rome.
Fernside, P.M.; Rankin, J.M. 1985. Jari revisited: changes and the outlook for sustainability in Amazonia's largest silvicultural estate. Interciencia, 10(2), 121-129.
Gautier-Hion, A. 1984. La dissémination des graines par les Cercopithécidés forestiers africains. Rev. Ecol. (Terre Vie), 39, 159-165.
Gomez-Pompa, A. 1987. On Maya agriculture. Mexican Studies/Estudios Mexicanos, 3 (1). University of California, Riverside.
Gomez-Pompa, A.; Amo, S.R. del (Eds). 1985. Investigaciones sobre la regeneracion de selvas altas en Veracruz (Mexico). Volumen II. Instituto Nacional de Investigaciones sobre Recursos Bioticos, Xalapa.
Gomez-Pompa, A.; Burley, W. The management of natural tropical forests. (in press)*
Graaf, N.R. de. 1986. A silvicultural system for natural regeneration of tropical rain forest in Suriname. Agricultural University, Wageningen.
Graaf, N.R. de. Managing natural regeneration in Suriname: the Celos Silvicultural System. (in press)*
Guillaumet, J.L.; Couturier, G.; Dosso, H. (Eds). 1984. Recherche et aménagement en milieu forestier tropical humide: le Projet Taï de Côte d'Ivoire. Notes techniques du MAB 15. Unesco, Paris.
Gunatilleke, C.V.S.; Gunatilleke, I.A.U.N. 1985. Phytosociology of Sinharaja - a contribution to rainforest conservation in Sri Lanka. Biological Conservation,31, 21-40.
Hadley, M.; Lanly, J.P. 1983. Tropical forest ecosystems: identifying differences, seeking similarities. Nature and Resources, 19 (1), 2-19.
Hendrison, J. Damage-controlled logging in managed tropical rain forest in Suriname. Agricultural University, Wageningen. (in press)
Herrera, R.; Jordan, C.F.; Klinge, H.; Medina, E. 1978. Amazon ecosystems. Their structure and functioning with particular emphasis on nutrients. Interciencia, 3, 223-232.
Herrera, R.A.; Capote, R.P.; Menendez, L.; Rodriguez, M.E. Silvigenensis stages and the role of mycorrhizae in natural regeneration in Sierra del Rosario, Cuba. (in press [a])*
Herrera, R.A.; Menendez, L.; Rodriguez, M.E. 1986. Ecologia de los bosques tropicales de la Sierra del Rosario, Cuba. Proyecto MAB 1. 1974-1986. Libro de Resumenes. Academia de Ciencias de Cuba, Havana.
Herrera, R.A.; Menendez, H.; Rodriguez, M.E. (Eds). Ecologia de los bosques tropicales de la Sierra del Rosario, Cuba. 2 vols. Unesco, Montevideo. (in press [b])
Hladik, A.; Blanc, P. 1987. Croissance des plantes en sous-bois de forêt dense humide (Makokou, Gabon). Rev. Ecol. (Terre Vie), 42, 209-234.
IRET; ECOTROP (CNRS); Unesco. 1987. Makokou (Gabon). Une station de recherche en écologie forestière tropicale. Présentation et publications (1962-1986)/A research station in tropical ecology. Overview and publications (1962-1986). Unesco, Paris.
Janzen, D.H. 1986. Guanacaste National Park: ecological and cultural restoration. Editorial Universidad Estatal a Distancia, San José.
Janzen, D.H.; Vasquez-Yanes, C. Aspects of tropical forest seed ecology of relevance to management of tropical forested wildlands. (in press)*
Jordan, C.L. Nutrient cycling processes and tropical forest management. (in press)*
Kahn, F. 1982. La reconstitution de la forêt tropicale humide, Sud-Ouest de la Côte d'Ivoire. Collection Mémoires No. 97. ORSTOM, Paris.
Koyama, H. 1978. Photosynthesis studies in Pasoh forest. Malayan Nature Journal, 30, 253-278.
Ladrach, W.E. 1985. Forest research in the Bajo Calima concession. Ninth Annual Report. Celulosa y Papel de Columbia S.A., Cali.

Landsberg, J.J. 1984. Physical aspects of the water regime of wet tropical vegetation. In: E. Medina; H.A. Mooney; C. Vazquez-Yanes (Eds), Physiological ecology of plants of the wet tropics, 13-26. Junk, The Hague.

Lanly, J.P. 1982. Tropical forest resources. FAO Forestry Paper No. 30. FAO, Rome.

Leigh, E.G. Jr.; Rand, A.S.; Windsor, D.M. (Eds). 1982. The ecology of a tropical forest. Seasonal rhythms and long-term changes. Smithsonian Institution and Oxford University Press, Oxford.

Leslie, A.J. 1977. Where contradictory theory and practice co-exist. Unasylva, 29 (115), 2-17.

Leslie, A.J. 1987. A second look at the economics of natural management systems in tropical mixed forests. Unasylva, 39 (155), 46-58.

Lieberman, D.; Lieberman, M. 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982). Journal of Tropical Ecology, 3 (4), 347-358.

Lieberman, D.; Lieberman, M.; Hartshorn, G.; Peralta, R. 1985, Growth rates and age-size relationships of lowland tropical wet forest trees in Costa Rica. Journal of Tropical Ecology, 1, 97-109.

Lugo, A.E. 1986. Outline of a proposal to study human-impacted tropical ecosystems in the context of the Man and the Biosphere Program. Paper presented to MAB General Scientific Advisory Panel. Paris, 21-24 April 1986.

Maître, H.F. 1986. Recherches sur la dynamique et la production des peuplements naturels en forêt dense tropicale d'Afrique de l'Ouest. Proceedings of the 18th World Congress of IUFRO (Ljublijana, September 1986), Division I, Vol. 2, 438-450. Yugoslav IUFRO World Congress Organizing Committee, Ljubljana.

Maître, H.F. 1987. Natural forest management in Côte d'Ivoire. Unasylva, 39(157/158), 53-60.

Maître, H.F. Silvicultural interventions and their effects on forest dynamics and production in some Côte d'Ivoire rain forests. (in press)*

Maître, H.F.; Hermeline, M. 1985. Dispositifs d'étude de l'évolution de la forêt dense ivoirienne suivant différentes modalités d'intervention sylvicole. Présentation des principaux résultats après quatre années d'expérimentation. SODEFOR, Abidjan, and CTFT, Nogent and Abidjan.

Manokaran, N.; Kochummen, K.M. 1987. Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. Journal of Tropical Ecology, 3, 315-330.

Maury-Lechon, G. 1982. Régénération forestière en Guyane française: recrû sur 25 ha de coupe papetière en forêt dense humide (Arbocel). Bois et Forêts de Tropiques, 197(3) 3-21.

Maury-Lechon, G. Comparative dynamics of tropical rain forest regeneration in French Guyana. (in press)*

Medina, E.; Cuevas, E. 1987. Patterns of nutrient accummulation and release in Amazonian forests of the Upper Rio Negro basin. Paper presented to international symposium on mineral nutrition in tropical forest and savanna, ecosystems. Stirling (UK), September 1987.

Molofsky, J.; Hall, C.A.S.; Myers, N. 1986. A comparison of tropical forest surveys. Office of Energy Research, United States Department of Energy, Washington, D.C.

Myers, N. 1980. Conversion of moist tropical forests. National Academy of Sciences, Washington, D.C.

Nair, C.T.S. Management of the tropical wet evergreen forests in India: a comparative account of the silvicultural practices in Kerala, Andaman islands and Assam. (in press)*

Oberbauer, S.T.; Strain, B.S. 1984. Photosynthesis and successional status of Costa Rican rain forest trees. Photosynthesis Research, 5, 227-232.

Okali, D.U.U. (Ed.). 1979. The Nigerian rain forest ecosystem. Nigerian MAB National Committee, Ibadan.

Okali, D.U.U.; Ola-Adams, B.A. 1987. Tree population changes in treated rain forest at Omo Forest Reserve, south-western Nigeria. Journal of Tropical Ecology, 3, 291-313.

Okali, D.U.U.; Onyeachusim, H.D. The ground flora and rain forest regeneration at Omo Forest Reserve, Nigeria. (in press)*

Oldeman, R.A.A. 1983. Tropical rain forest, architecture, silvigenesis and diversity. In: S.L. Sutton; T.C. Whitmore; A.C. Chadwick (Eds), Tropical rain forest: ecology

and management, 139-150. Blackwell, Oxford.
Oldeman, R.A.A. 1986. Forest modelling without maths. IUCN Bulletin, 16 (4-6), 61-63.
Oldeman, R.A.A. 1987. Tropical forest: the ecosystems. In: C.F. van Beusekom; C.P. van Goor; P. Schmidt (Eds), Wise utilization of tropical rain forest lands, 46-67. Tropenbos Scientific Series 1. Tropenbos, Ede.
O'Neill, R.V.; DeAngelis, D.L.; Waide, J.B.; Allen, T.F.H. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton.
Palmer, J.R. Jari - lessons for land managers in the tropics. (in press)*
Peters, C.M. Plant demography and the management of tropical forest resources: a case study of *Brosimum alicastrum* in Mexico. (in press)*
Pickett, S.T.A. 1983. Differential adaptations of tropical tree species to canopy gaps and its role in community dynamics. Trop. Ecol., 24 (1), 68-84.
Ramakrishnan, P.S. 1985. Research on humid tropical forests. Paper presented by MAB-India to Regional Meeting of the MAB National Committees of Central and South Asian countries. New Delhi, 18-20 March 1985. Department of Environment, New Delhi.
Ramakrishnan, P.S. Rain forest ecosystem function and its management in north-east India. (in press)*
Räsänen, M.E.; Salo, J.S.; Kalliola, R.J. 1987. Fluvial perturbance in the Western Amazon Basin: regulation by long-term sub-Andean tectonics. Science, 238, 1398-1401.
Repetto, R. 1987. Creating incentives for sustainable forest development. Ambio, 16(2-3), 94-99.
Riswan, S.; Kartawinata, K. Regeneration after disturbances in a lowland mixed dipterocarp forest in East Kalimantan, Indonesia. (in press)*
Riswan, S.; Kenworthy, J.R.; Kartawinata, K. 1985. The estimation of temporal processes in tropical rain forest: a study of primary mixed dipterocarp forest in Indonesia. Journal of Tropical Ecology, 1, 171-182.
Rollet, B. 1980. Jari: un succès ou échec ? Un exemple de développement agro-sylvo-pastoral et industriel en Amazonie brésilienne. Bois et Forêts des Tropiques, 192, 3-34.
Saldarriaga, J.G.; Uhl, C. Forest succession in the Upper Rio Negro region of Colombia and Venezuela. (in press)*
Salleh, M. N. 1986. The need for a common interface. In: Proceedings of Tropenbos consultation on a united approach for research in humid tropical forests, 82-90. Tiel, 27-31 October 1986. Tropenbos, Ede.
Salleh, M.N.; Baharudin, J. 1985. Silvicultural practices in Peninsular Malaysia. In: J. Davidson; Tho Yow Pong; M. Bijleveld (Eds), Future of tropical rain forests in South East Asia, 85-90. Commission on Ecology Papers No. 10. IUCN, Gland.
Salo, 1987. Pleistocene forest refuges in the Amazon: evaluation of the biostratigraphical, lithostratigraphical and geomorphological data. Ann. Zool. Fennici, 24(3), 203-211.
Salo, J.S.; Kalliola, R.J. River dynamics and natural regeneration in the Peruvian Amazon. (in press)*
Salo, J.; Kalliola, R.; Häkkinen, I.; Mäkinen, Y.; Niemelä, P.; Puhakka, M.; Coley, P.D. 1986. River dynamics and the diversity of Amazon lowland forest. Nature, 322, 254-258.
Salthe, S.N. 1985. Evolving hierarchical systems: their structure and representation. Columbia University Press, New York.
Sanford, R.L. Jr.; Saldarriaga, J.; Clark, K.E.; Uhl, C.; Herrera, R. 1985. Amazon rain forest fires. Science, 227, 53-55.
Sarrailh, J.M. 1980. L'écosystème forestier guyanais. Etude écologique de son évolution sous l'effet des transformations en vue de sa mise en valeur. Bois et Forêts des Tropiques, 189, 31-36.
Saulei, S. 1984. Natural regeneration following clear-fell logging operations in the Gogol Valley, Papua New Guinea. Ambio, 13(5-6), 351-354.
Saulei, S.; Lamb, D. Regeneration following pulpwood logging in lowland rain forest in Papua New Guinea. (in press)*
Schmidt, R.C. 1987. Tropical rain forest management: a status report. Unasylva, 39(156), 2-17.
Schmidt, R.C. Current programmes of tropical rain forest management. (in press)*
Schmink, M. 1987. The rationality of tropical forest destruction. In: J.C. Figueroa;

F.H. Wadsworth; S. Branham (Eds), Management of the forests of tropical America: prospects and technologies, 22-27. US Department of Agriculture Forest Service, Institute of Tropical Forestry, Rio Piedras, Puerto Rico.

Shukla, R.P.; Ramakrishnan, P.S. 1984. Biomass allocation strategies and productivity of tropical trees related to successional status. Forest Ecology and Management, 9, 315-324.

Smits, W. 1985. Dipterocarp mycorrhiza. In: J. Davidson; Tho Yow Pong; M. Bijleveld (Eds), The future of tropical rain forests in South East Asia, 51-54. Commission on Ecology Papers No. 10. IUCN, Gland.

Swift, M.J. (Ed.). 1985. Tropical Soil Biology and Fertility (TSBF). Planning for research. Biology International - Special Issue 9. IUBS, Paris.

Swift, M.J. (Ed.). 1987. Tropical Soil Biology and Fertility (TSBF). Inter-Regional Planning Workshop. Biology International - Special Issue 13. IUBS, Paris.

Toky, O.P.; Ramakrishnan, P.S. 1983. Secondary succession following slash and burn agriculture in north-eastern India. I. Biomass, litterfall and productivity. Journal of Ecology, 71, 735-745.

Tropenbos. 1986. Proceedings of consultation on a united approach for research in the humid tropical forests. Tiel, 27-31 October 1986. Tropenbos, Ede.

Unesco. 1978. Tropical forest ecosystems. A state-of-knowledge report prepared by Unesco, UNEP and FAO. Natural Resources Research Series 14. Unesco, Paris.

Unesco. 1979. MAB-IUFRO International Workshop on Tropical Rain Forest Ecosystems. MAB Report Series No. 44. Unesco, Paris.

Unesco. 1984. Action Plan for Biosphere Reserves. Nature and Resources, 20(4), 112.

Unesco. 1986. International Coordinating Council of the Programme on Man and the Biosphere (MAB). Ninth Session. Paris, 20-25 October 1986. MAB Report Series No. 60. Paris, France.

van Beusekom, C.F.; van Goor, C.P.; Schmidt, P. 1987a. Tropical forests: use or abuse? Tropenbos Information Series 4. Tropenbos, Ede.

van Beusekom, C.F.; van Goor, C.P.; Schmidt, P. (Eds). 1987b. Wise utilization of tropical rain forest lands. Tropenbos Scientific Series 1. Tropenbos, Ede.

van Dijk, J. 1987. The ecological characteristics of architectural and crown characteristics of juvenile trees in a Venezuelan cloud forest. Agricultural University, Wageningen.

Vitousek, P. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology, 65, 285-298.

Vooren, A.P. 1987. Development versus forest conservation: avoiding a conflict in the Taï region (Côte d'Ivoire). In: C.F. van Beusekom; C.P. van Goor; P. Schmidt (Eds), Wise utilization of tropical rain forest lands, 130-137. Tropenbos Scientific Series 1. Tropenbos, Ede.

Webb, L.J. 1977. Ecological considerations and safeguards in the modern use of tropical lowland rain forests as a source of pulpwood: example, the Madang Area, PNG. Office of Environment and Conservation, Papua New Guinea.

Whitmore, T.C. 1975. Tropical rain forests of the Far East. Clarendon, Oxford.

Whitmore, T.C. 1983. Secondary succession from seed in tropical rain forests. Forestry Abstracts, 44, 767-779.

Whitmore, T.C. Tropical rain forest dynamics and its implications for management. (in press)*

Whitney, G.G. 1976. The bifurcation ratio as an indicator of adaptive strategy in woody plant species. Bulletin of the Torrey Botany Club, 103, 67-72.

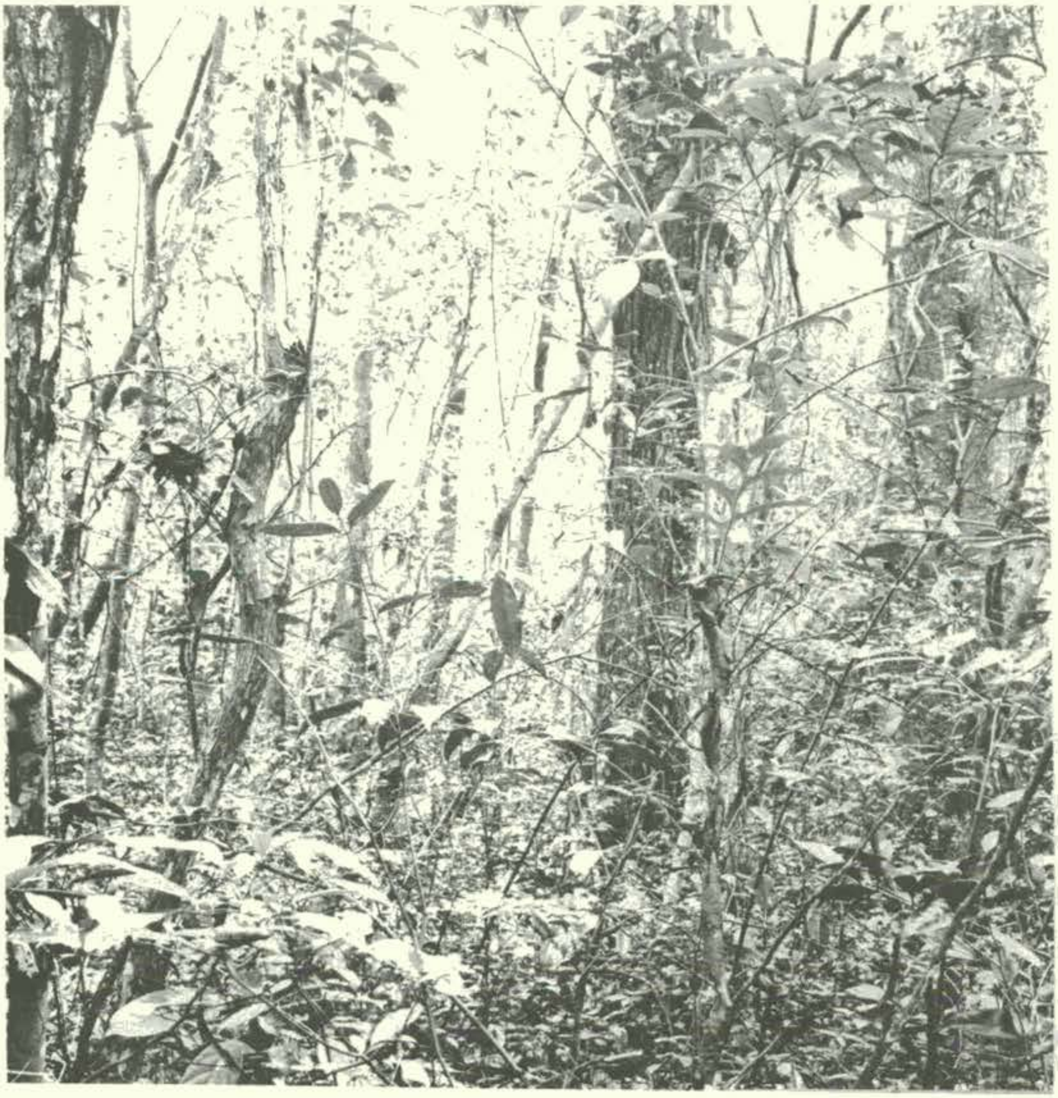
World Resources Institute. 1986. Tropical forests: a call for action. WRI, Washington, D.C.

Wyatt Smith, J. 1966. Ecological studies in Malayan forests. Forest Research Pamphlet No. 52. Forest Research Institute, Kepong.

Zoysa, N. de; Gunatilleke, C.V.S.; Gunatilleke, I.A.U.N. Comparative Phytosociology of Natural and modified rain forest sites in Sinharaja MAB Reserve in Sri Lanka. (in press)*

**Dry evergreen forest at Sakaerat, Thailand**

The 7200 ha biosphere reserve at Sakaerat Environemental Research Station in northeastern Thailand includes both dry dipterocarp and evergreen dipterocarp forests. The dry evergreen forest shown here is characterized by a rather dense spiny undergrowth with many vines. Dominant species are *Hopea ferrea, Walsura trichostemon*, two species of *Hydnocarpus* and at least two species of *Memecylon*, giving the forest a quite different composition from lowland and hill rain forests. Sakaerat provides an important facility for training and demonstration, for use by such groups as teachers, undergraduates, forest managers, etc. It is regularly used as a site for field training by the Faculty of Forestry of Kasetsart University, the Royal Forest Department and other national institutions, while a regional training seminar on forest habitat matching was held there in January 1986. Photo: B. Rollet.



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# ANNEX 2

## PAPERS PRESENTED AT THE WORKSHOP*

SETTING THE SCENE: INTRODUCTION

The management of natural tropical forests. **A. Gomez-Pompa and W. Burley**

TOPICAL REVIEWS

The characteristics, sylvigenesis and architectural diversity in tropical rain forests. **R. A.A. Oldeman and J. van Dijk**

Tropical rain forest dynamics and its implications for management. **T.C. Whitmore**

Regeneration of tropical forests: physiological responses of secondary species. **F.A. Bazzaz**

Reproductive biology and genetics of tropical forest trees in relation to conservation and management. **K.S. Bawa and S.L. Krugman**

Aspects of tropical forest seed ecology of relevance to management of tropical forested wildlands. **D.H. Janzen and C. Vasquez Yanes**

Nutrient cycling processes and tropical forest management. **C.L. Jordan**

Current programmes of tropical rain forest management. **R.C. Schmidt**

CASE STUDIES

Silvigenesis stages and the role of mycorrhizae in natural regeneration in Sierra del Rosario, Cuba. **R.A. Herrera, R. P. Capote, L. Menéndez and M.E. Rodriguez**

Phytosociological comparison of modified and undisturbed forest sites at Sinharaja, Sri Lanka. **N.D. de Zoysa, C.V.S. Gunatilleke and I.A.U.N. Gunatilleke**

Pattern and structure along gradients in natural forests in Borneo and in Amazonia: their significance for the interpretation of stand dynamics and functioning. **E.F. Bruenig**

River dynamics and natural forest regeneration in the Peruvian Amazon. **J.S. Salo and R.J. Kalliola**

Floristic differences in natural gaps and man-made secondary growth areas through the first 26-years of forest regeneration in Colombian Amazonia. **T. Walschburger and P. von Hildebrand**

Plant demography and the management of tropical forest resources: a case study of *Brosimum alicastrum* in Mexico. **C.M. Peters**

The ground flora and rain forest regeneration at Omo Forest Reserve, Nigeria. **D.U.U. Okali and H.D. Onyeachusim**

Comparative dynamics of tropical rain forest regeneration in French Guyana. **G. Maury-Léchon**

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* Not all papers indicated here are included in the book based on the workshop, since certain have already been published substantively elsewhere. On the other hand, the list of case studies also includes a couple of papers not presented at Guri, but commissioned for inclusion in the book.

Regeneration after disturbances in a lowland mixed dipterocarp forest in East Kalimantan, Indonesia. **S. Riswan and K. Kartawinata**

Recovery of forest vegetation following slash-and-burn agriculture in the Upper Rio Negro. **J.G. Saldarriaga and C. Uhl**

Regeneration following pulpwood logging in lowland rain forest in Papua New Guinea. **S. Saulei and D. Lamb**

Guanacaste National Park: a case study in restoration ecology. **D. H. Janzen**

Rain forest ecosystem function and its management in northeast India. **P.S. Ramakrishnan**

Management of secondary vegetation for artificially creating useful rain forest in Uxpanapa Veracrux, Mexico - an intermediary alternative between transformation and modification. **S. del Amo**

Forest management strategies by rural inhabitants in the Amazon estuary. **A.B. Anderson**

Natural regeneration and its implications for forest management in the Malaysian dipterocarp forests. **S. Appanah and Salleh Mohd. Nor**

Management of the tropical wet evergreen forests in India: a comparative account of the silvicultural practices in Kerala, Andaman islands and Assam. **C.T.S. Nair**

Silvicultural interventions and their effects on forest dynamics and production in some Côte d'Ivoire rain forests. **H.F. Maître**

Managing natural regeneration in Suriname: the Celos Silvicultural System. **N.R. de Graaf**

Wildlife conservation and rain forest management - examples from north east Queensland. **F.H. G. Crome**

Jari: lessons for land managers in the tropics. **J.R. Palmer**

The present status of research into management of the rain forests of Amazonian Brazil. **J.C.L. Dubois**

Scientific research and management of the Caroni River Basin, Venezuela. **L. Castro-Morales and S. Gorzula.**

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ROMANIA - Academy of the Socialist Republic of Romania
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