POTENTIAL ECOLOGICAL IMPACT OF INCREASED INTENSITY OF TROPICAL FOREST UTILIZATION

John Ewel & Louis F. Conde

Special Publication No. 11

ISSN 0125 — 975 X

BIOTROP
SEAMEO Regional Center
for Tropical Biology

ISSN 0125–975 X

POTENTIAL ECOLOGICAL IMPACT OF INCREASED INTENSITY OF TROPICAL FOREST UTILIZATION

John Ewel and Louis F. Conde[1]

Department of Botany
University of Florida
Gainesville, Florida 32611
U.S.A.

[1] Present address: School of Forest Resources and Conservation, University of Florida, Gainesville, F1 32611, U.S.A.

TABLE OF CONTENTS

PREFACE

In 1974 the U.S. Agency for International Development (AID) contracted with the Forest Products Laboratory (FPL) of the U.S. Forest Service to try to determine the technical feasibility of using the broad range of species found in tropical forests in an integrated manufacturing scheme. From the start of the project both AID and FPL staff members expressed concern that consideration be given to the potential environmental impact of such increased utilization intensity. Accordingly, in 1975 the FPL contracted J. Ewel, as a member of the project's Steering Committee, to review the available literature and thereby attempt to identify potential environmental impacts, both detrimental and positive, that might result from increased tropical forest utilization.

A brief literature search of this sort is not, of course, intended to produce final answers. Rather, its function is to identify potential problems, such that proper study and consideration can be given them prior to adoption of new utilization technology. Because we were attempting to assess the possible impact of a process that does not yet exist, i.e., the capability to use a much broader range of species than is currently done, it is not surprising that we found almost no literature that addressed the subject directly. We expected this, and from the start planned to concentrate our efforts on a review of literature dealing with the ecological impacts of current types of tropical forest utilization. We carefully examined nearly 400 publications, of which about 200 turned out to have some direct relevance to this project. This can be compared with a study by the U.S. Environmental Protection Agency (1976) concerning forestry practices and their impact on water quality in Oregon, Washington, Idaho, and Alaska. In spite of the narrower geographical and topical scope of that review, it contains a bibliography of over 550 references! Whitmore's (1975) outstanding book on "Tropical Rain Forests of the Far East" contains a concise, but surprisingly thorough, evaluation of the impact of modern society on tropical Asian vegetation and wildlife, yet his treatment covers only six pages. Clearly, the tropical data gap is huge and its most glaring holes must be filled before environmental impacts can be properly assessed.

Not only is the amount of tropical data limited, but its geographic distribution is highly skewed toward the Far East. Over half of the relevant papers and probably 90 percent of the useful data we found came from studies conducted in Asian forests. Latin America, which contains far more tropical forest than any other part of the world, is almost virgin territory for the study of the ecological impact of forest utilization.

The original version of this report was prepared in 1976. We were extremely pleased when, in 1979, BIOTROP expressed interest in publishing this report as part of their Special Publications series. The bibliography contains more entries than are cited in the text, and has been updated through early 1980. Although metric units were used in the text whenever possible, tables and figures from the works of others contain the original units.

We thank V. Millsip and B. Brown for assistance with library searches, B. Fischer for typing, G. Fuller and A. Lugo for illustrations, and the following publishers for permission to reproduce tables and figures: BIOTROP; Cambridge University Press; Commonwealth Forestry Association; East African Agricultural and Forestry Journal; Ghana Council for Scientific and Industrial Research; Instituto Nacional de Pesquisas da Amazonia; International Union for Conservation of Nature and Natural Resources; John Wiley & Sons, Ltd.; Journal of Tropical Geography; S. Karger AG; Drs. K. A. Longman and J. Jenik; Malayan Nature Society; Malaysian Forest Research Institute; Nigerian Federal Department of Forestry; Noord-Hollandsche Uitg-Mig., B.V.; Oxford University Press; Pergamon Press, Ltd.; and Dr. H. Popenoe.

John Ewel and Louis Conde
Gainesville, Florida, U.S.A.
June, 1980

INTRODUCTION

Until recently, the logging of tropical forests was a relatively selective process. A handful of high-value species was harvested and the rest were left, often to be felled and burned by the shifting agriculturists who follow logging roads as access routes to new land. Past logging frequently resulted in the loss of residual trees, either because of strict size and quality restrictions, or because the species left were unacceptable at the manufacturing end. These kinds of use restrictions, although slackening, still result in the utilization of a relatively small portion of the total number of tree species available. In West Malaysia, for example, there are more than 2500 tree species, 700 of which reach sizes suitable for logging, yet fewer than 150 of these are regularly used (Burgess 1971). The situation in Africa is similar. Mensah (1966) reports that only 16 out of 175 species of large trees are regularly harvested in Ghana. The ratio of species-used to species-available is likely to be even smaller in the American tropics than it is in the Far East and Africa.

Wood demands continue to rise rapidly, however, and one result has been a tremendous increase in the rate of logging of tropical forests in the past decade. Because relatively few species are harvested, the demand is satisfied by logging tremendous areas. In some cases the high-graded residual forests are subjected to silvicultural treatment, but more often than not the land is either abandoned to let nature do the work of forest recovery or else it is taken over by agriculturists. If the world demand for wood is to be met while avoiding the degradation and destruction of all tropical forests the only alternative seems to be that of increasing our technical capability to use a wider range of species. Intensive forest utilization and management applied to smaller areas can provide a means for taking the pressure off of other lands while permitting developing tropical nations to tap the high potential productivity of their forests. In the hands of the greedy, the technical capability to utilize any and all species could lead to unprecedented ecological destruction of tropical forests. Used wisely, however, it could provide us with an ecologically beneficial silvicultural tool, one that could be used to maintain tropical forests as highly productive, diverse ecosystems - a truly renewable tropical resource.

The review is divided into sections dealing with potential ecological impacts on vegetation, soil, water, and animals, followed by research needs and conclusions.

IMPACT ON VEGETATION

The main impact of utilization on vegetation is obvious: it is the vegetation itself which is the raw material being harvested, and presumably if the use of the vegetation is an unsupportable ecological loss this would be determined prior to initiating the utilization scheme. Assuming that a given forest is appropriate for utilization, then the problem becomes one of assessing the impact on the potential of that vegetation to recuperate, thus assuring that the forest is indeed a renewable resource. The potential impact on the vegetation must consider all of the vegetation: not only commercial species, but non-commercial trees, shrubs, vines, herbs, and epiphytes as well. Each of these plays a role in the natural ecosystem and disregard for their functions may result in reduced capacity for the land to produce sustained yields of forest products.

Four aspects of the impact of utilization on tropical forest vegetation are discussed below. First, there is the felling operation, closely followed by log extraction. These two processes are closely coupled, both chronologically and in terms of their impact on the forest. They are the most conspicuous, and probably the best studied, of the effects of utilization on tropical forest vegetation. The third impact discussed involves changes in the forest ecoclimate resulting from utilization. This primarily involves changes in light quantity and quality, temperature, and moisture, all of which directly affect the rate and floristic composition of forest regeneration. Finally, the less visible and less studied effects of the potential impact of utilization on the gene pool of the world's most complex ecosystem are discussed.

Felling

Felling damage includes breakage of saplings and residual stems, bark "skinning" of residuals which increases the infection rate of pathogens (Nicholson 1958a), and topping of seedling regeneration by the crowns of felled trees. Such damage is likely to be greater in tropical forests than in temperate forests because, with current utilization schemes, most of the trees felled are large emergents (Burgess 1971) rather than smaller trees found in the main canopy. Felling damage is related to both the size of the individual trees felled and the volume of wood extracted per unit area. Mensah (1966), for example, found that forests in Ghana were less severely damaged by felling than were forests in Sabah (North Borneo) studied by Nicholson (1958a). This difference was due, in part, to the smaller trees being felled in Ghana and, in part, to the greater volume extracted in Sabah. Nicholson (1958a) developed regression lines which show the relationship between volume extracted and stand damage. These relationships were used by Redhead (1960) and Mensah (1966) to compare data from Nigeria and Ghana, respectively, with those from Sabah, and are reproduced as Figure 1. The data from Africa fell very close to Nicholson's predicted values, even though less than half the volume was extracted from the forests in Africa than was extracted from most of Nicholson's plots.

In addition to the studies by Nicholson (1958a), Redhead (1960), and Mensah (1966) mentioned above, three other studies have included a quantitative assessment of felling damage in tropical forest harvesting operations. Wyatt-Smith & Foenander (1962) conducted one such study in Malaya, Fox (1968b) reported results from Sabah, and Tinal & Palenewen (1975) studied a selectively logged site in East Kalimantan. Nicholson's (1958a) data (Table 1) are typical of those observed in most of the earlier studies; he found that about 45 percent of the residual stand was damaged, mostly by being "unavoidably' felled or broken off. Wyatt-Smith & Foenander (1962), however, cautioned that Nicholson's data did not include trees that were completely destroyed during felling and road making. In a later study also conducted in Sabah, Fox (1968e) found that felling damage was greater than that measured by Nicholson (1958a). He suggested that the increased damage resulted from the use of larger logging equipment. Serevo (1949) reached similar conclusions

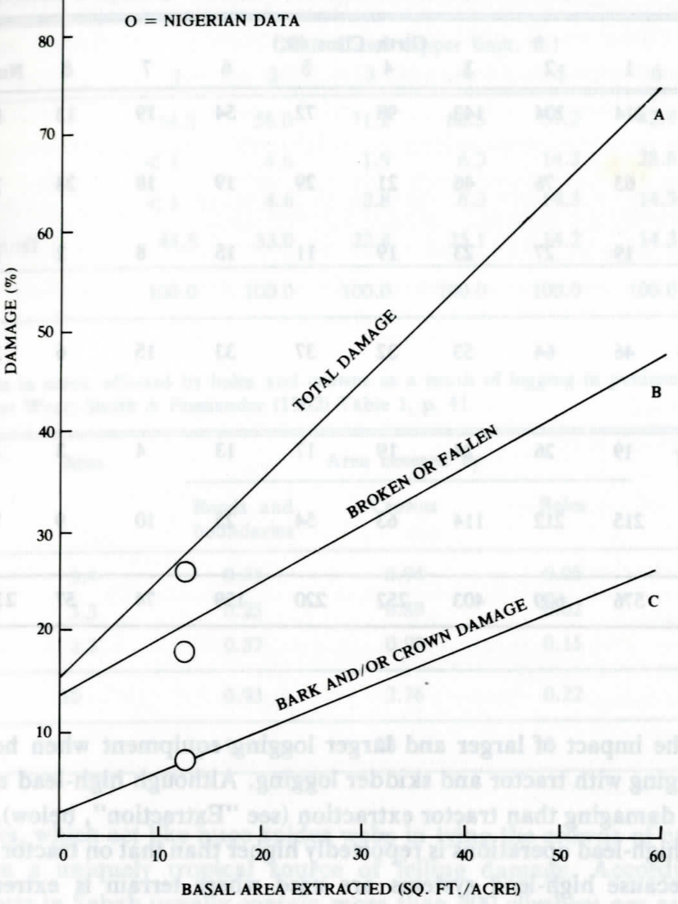

Fig. 1. Relationship between logging damage and volume extracted. Only stems >3 m tall and >9.7 cm DBH assessed for damage. After Redhead (1960), Fig. I, p. 13 based on relationships developed by Nicholson (1958a) in Sabah.

Table 1. Damage to the residual stand as a result of logging in Sabah. Values are trees per 100 acres. After Nicholson (1958a) Table 1 p. 238.

Damage Type	Girth Class (ft.) 1	2	3	4	5	6	7	8	Total Number	Percent
No damage (Good form)	214	204	143	98	72	54	19	13	817	34.8
No damage (Bad form)	63	76	46	21	29	19	18	24	296	12.6
Bark damage (No crown damage)	19	27	23	19	11	15	8	2	124	5.3
Crown damage (No bark damage)	46	64	53	32	37	33	15	6	286	12.2
Both bark and crown damage	19	26	24	19	17	13	4	3	125	5.3
Fallen or broken off	215	212	114	63	54	25	10	9	702	29.8
Total	576	609	403	252	220	159	74	57	2350	100.0

regarding the impact of larger and larger logging equipment when he compared carabao logging with tractor and skidder logging. Although high-lead extraction is usually less damaging than tractor extraction (see "Extraction", below), the felling damage on high-lead operations is reportedly higher than that on tractor operations, probably because high-lead systems are used where terrain is extremely steep, resulting in considerable down-slope rolling of felled trees which damage the residual stand (Blanche 1978, Rapera 1978).

Much of the damage resulting from felling consists of covering the regeneration with logging debris. Redhead (1960), for example, found that about 44 percent of the residual stand was damaged by logging debris alone (Table 2) and that most of the damage was inflicted on the smaller size classes. Likewise Wyatt-Smith & Foenander (1962) found that 30 percent of the logged area they studied in Malaya was covered by the crowns and residual boles of felled trees (Table 3). If additional species are harvested more logging debris is likely to accumulate, particularly if tops are left in the forest as will probably be necessary to avoid excessive nutrient export from the site. Although the debris damages the pre-harvest regeneration, its impact on subsequent regeneration has not been studied. It is possible that logging debris will offer some soil protection and ameliorate microclimatic conditions at the soil surface, thus benefitting seedling restablishment.

Table 2. Damage due to felling debris resulting from logging in Nigeria. Values are per cent of individuals sampled (n = 1005). After Redhead (1960) Table V p. 10.

Damage Type	Girth Clases (upper limit, ft.) 1	2	3	4	5	6	Total
No damage	54.8	58.0	71.2	62.5	57.2	42.9	56.0
Bark damage	< 1	4.6	1.9	6.3	14.3	28.6	1.3
Crown damage	< 1	4.6	3.8	6.3	14.3	14.3	1.2
Fallen or broken off	44.5	33.0	23.4	25.1	14.2	14.3	41.5
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 3. Area in acres, affected by boles and crowns as a result of logging in peninsular Malaysia. After Wyatt-Smith & Foenander (1962) Table 1, p. 41.

Sample	Area	Area covered by Roads and boundaries	Crowns	Boles	Total area damaged
1	3.4	0.31	0.94	0.05	1.30
2	3.3	0.25	0.89	0.02	1.16
3	3.3	0.37	0.93	0.15	1.45
Total	10	0.93	2.76	0.22	3.91
% damage		9	28	2	39

Climbers, which act like huge spider webs in tying the crowns of canopy trees together, are a uniquely tropical source of felling damage. According to Fox (1968e), forests in Sabah usually contain more than 800 climbers per acre (c. 2000 per hectare); of these, almost 20 percent are strong enough to remain unbroken when a tree is felled. This then requires that one or more additional trees be cut to get the desired stem on the ground. In other cases the desired tree does fall, but the climbers pull other trees to the ground as well. As Davis & Richards (1933) pointed out, the felling of a live canopy tree is different than most of the natural tree fall which commonly occurs in tropical forests. In most cases, natural fall consists of dead trees with rotten branches; these break when the tree topples, so little additional vegetation comes down with it. In some felling operations in Southeast Asia trees to be felled are killed by poisoning prior to harvest. This reduces the crown volume and facilitates limb breakage, thus lowering the probability that a cut tree will be hung up with climbers. Another way to cope with the climber problem is to cut and poison climbers prior to felling. Fox (1968e) found that pre-harvest climber cutting and poisoning resulted in 16 percent less damage to the residual stand (Table 4). The presence of climbers complicates attempts to develop silvicultural schemes for tropical forests because the silviculturist can never be certain which trees will be felled as part of a harvest. Technology that permits utilization of more species will likely reduce wood loss due to climbers by facilitating utilization of trees which are unavoidably felled.

Table 4. Effect of climber cutting prior to harvest on amount of logging damage. Values are numbers of trees per 100 acres. After Fox (1968e), Table 3, p. 333.

Damage Type	Climbers cut		Control	
	Number	Percentage	Number	Percentage
Fallen or broken off	695	43.7	1145	61.7
Bark damage without severe crown damage	15	0.9	10	0.5
Bark damage with severe crown damage	160	10.1	155	8.4
Severe crown damage only	45	2.8	60	3.2
Total, Damaged	915	57.5	1 370	73.8
Trees with little crown damage and free of bark damage	170	10.7	205	11.0
Undamaged trees	505	31.8	280	15.1
Total, little or no damage	675	42.5	485	26.1
GRAND TOTAL	1590	100	1855	100

Fox (1968b) has made several suggestions to reduce residual stand damage. Two of these — climber cutting and directional felling — are aimed at reducing felling damage. However, in discussing natural regeneration of Dipterocarp forests, Nicholson (1965) said:

> "Probably the most pressing need is to curtail logging damage. Experiments have shown that there is little hope of making a significant improvement in this regard either by marking for felling or for retention, though the former has shown the most promise, probably because trained forest workers are better able to judge the worth of groups of poles and to direct a tree in the least damaging direction."

Felling damage will continue to be a significant problem in any kind of tropical forest utilization scheme, but the utilization of more species will offer additional flexibility which can be used to reduce the inevitable damage below current levels which affect half or more of the residual stand.

Extraction

Extraction of logs from the forest may be the single most damaging aspect of utilization on tropical forest vegetation. All of the impacts of felling, including damage to seedlings and residual trees, are also incurred during extraction. In addition, however, extraction is more likely to expose the mineral soil and disturb large expanses of forest floor. As the size of extraction equipment and the volumes extracted per unit area have increased in recent years the damage due to extraction has likewise increased (Fox 1972a). Today it is one of the most important causes for ecological concern with respect to tropical forest utilization, and ways to minimize its potentially devastating impact are clearly called for.

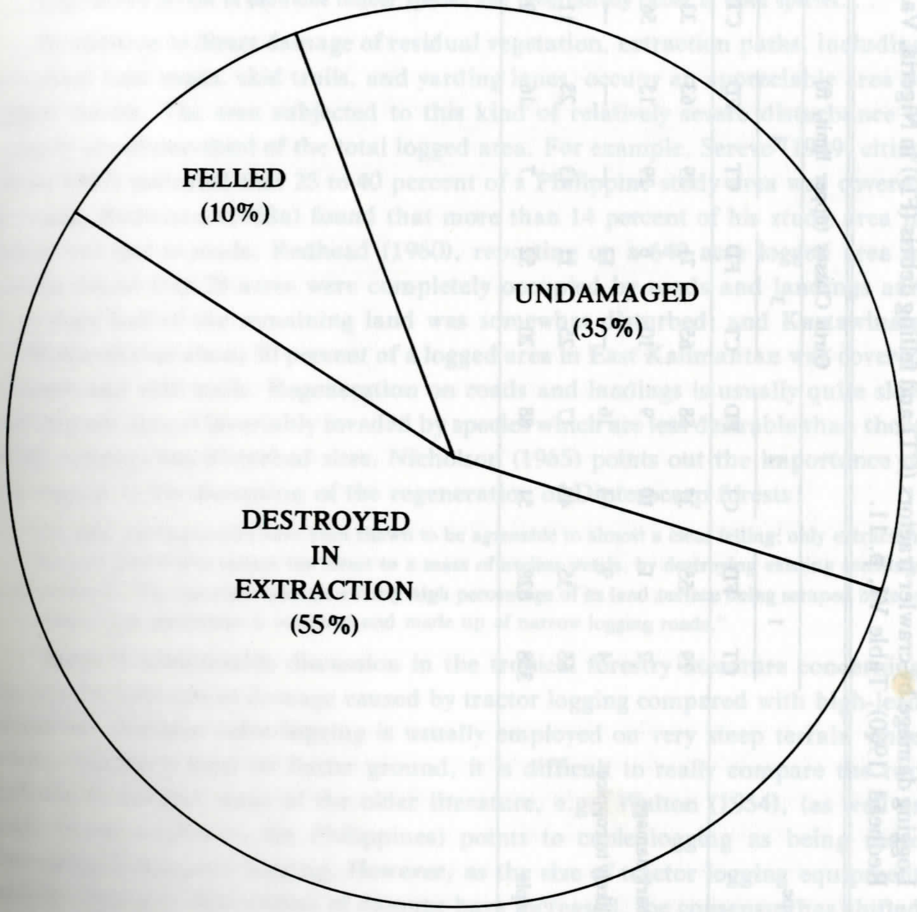

Fig. 2. Impact of logging on stand basal area (stems > 10 cm DBH) in West Malaysia. After Burgess (1971), Fig. 1, p. 232.

Table 5. Logging damage by crawler tractors (CT) and felling debris (FD) in Nigeria, Values are per cent of individuals. After Redhead (1960), Table VI, p. 11.

Damage Type	Girth Classes (upper limit, ft) 1		2		3		4		5		6		Total	
	CT	FD	CT	FD	CT	FD	CT	FD	CT	FD	CT	FD	CT	FD
No damage	29	55	37	58	65	71	29	63	33	57	100	43	32	56
Crown and bark damage	2	1	10	9	10	6	29	13	56	29	—	43	4	2
Broken but likely to coppice	4	9	4	16	—	12	—	—	—	—		—	3	9
Destroyed	65	35	49	17	25	11	43	25	11	14	—	14	59	32
Stems in sample	358	828	51	88	20	52	7	16	9	14	2	7	447	1,005

A review of numerous studies of the impact of harvesting on residual vegetation indicates that usually about 50 percent of the residual stand is damaged (see, for example, Fig. 2). As illustrated by a typical study (Table 5) much of the damage coincident with harvesting results from the extraction process. Losses due to felling and extraction might be salvaged if greater latitude of utilization — in terms of both species and size classes — were feasible. It is important, however, that all of the extraction be accomplished by a single pass through the forest because several investigators have pointed out that repeated entry of logging equipment further disturbs the site and retards the process of succession and recovery. The following quote from Burgess (1971) is typical:

> "Relogging of exploited forest is a most undesirable process silviculturally, since the whole plant succession process is set back every time the forest is disturbed, and the forest becomes progressively poorer in desirable timber species and progressively richer in weed species. . ."

In addition to direct damage of residual vegetation, extraction paths, including secondary haul roads, skid trails, and yarding lanes, occupy an appreciable area of logged forests. The area subjected to this kind of relatively severe disturbance is typically about one-third of the total logged area. For example, Serevo (1949, citing Munn 1947) indicated that 25 to 40 percent of a Philippine study area was covered by roads; Nicholson (1958a) found that more than 14 percent of his study area in Sabah was lost to roads; Redhead (1960), reporting on a 640 acre logged area in Nigeria found that 29 acres were completely occupied by roads and landings and more than half of the remaining land was somewhat disturbed; and Kartawinata (1978) found that about 30 percent of a logged area in East Kalimantan was covered by roads and skid trails. Regeneration on roads and landings is usually quite slow and they are almost invariably invaded by species which are less desirable than those which colonize less disturbed sites. Nicholson (1965) points out the importance of this impact in his discussion of the regeneration of Dipterocarp forests:

> "All other limiting factors have been shown to be agreeable to almost a clear felling; only extraction has the potential to reduce the forest to a mass of useless weeds, by destroying existing seedlings and poles. The forest can tolerate a fairly high percentage of its land surface being scraped bare so long as this percentage is scattered and made up of narrow logging roads."

There is considerable discussion in the tropical forestry literature concerning the relative amounts of damage caused by tractor logging compared with high-lead extraction. Because cable logging is usually employed on very steep terrain while tractor logging is used on flatter ground, it is difficult to really compare the two systems. In general, most of the older literature, e.g., Walton (1954), (as well as some recent studies in the Philippines) points to cable logging as being more damaging than tractor logging. However, as the size of tractor logging equipment and the quality of field studies of damage have increased, the consensus has shifted toward the view that high-lead logging is less damaging than tractor logging (e.g., see Fox 1969, Russell 1974). Burgess' (1971) comment is typical of recent evaluations:

> "All cable logging methods give an impression of catastrophic damage near the spar tree and landings (and this is all the visitor usually sees), but on the balance they are less likely to cause damage than tractor logging."

Nicholson (1963) found that an area subjected to high-lead logging had 811 adequately stocked milliacre regeneration plots per acre prior to logging, and 528 after logging (Table 6). He noted, however, that this was better than the stocking observed on many tractor-logged areas. In two recent studies in the Philippines, however, Blanche (1978) and Rapera (1978) reported that high-lead logging was more damaging than tractor logging. The Philippine forests are managed by a selection system, whereas other tropical forests in Southeast Asia are managed according to the Malaysian Uniform System; the difference in silvicultural practices may account for part of the difference in view toward high-lead extraction.

Table 6. Regeneration stocking before and after high lead logging in Sabah. One chain = 66 ft. = 20.3 m. Values are numbers of stocked milliacre plots per acre. After Nicholson (1963), p. 295.

Distance from spar tree (chains)	No. of Observ.	Before logging	After logging
0 — 1	9	855	35
1 — 2	9	888	56
2 — 3	9	922	312
3 — 4	9	866	344
4 — 5	9	877	578
5 — 6	9	900	623
6 — 7	9	800	368
7 — 8	8	809	600
8 — 9	8	779	638
9 — 10	7	700	630
Total		8396	4184

There is no doubt that areas where the soil is severely disturbed by machinery recover very differently from relatively undisturbed logged areas. Main haul roads, landings, and spar tree surroundings are prime examples of such sites. Nicholson (1965), for example, points out that:

> "It is probably inevitable that large bare areas will be found in most logged areas and this applies to high-lead logging as well, where up to two chains from the spar tree can be bared. Experiments are in hand and will be intensified to find the best means of restoring these to forest production. These very inhospitable sites are slow to regenerate naturally and probably it will be necessary to raise and plant hardy species on them. Work on the screening of potential species should be pushed ahead; it is not expected that many will qualify in both hardiness and ease of seed collection."

A disturbed, exposed mineral soil is often a more favorable seedbed for weed species than for desirable tree species. Thus, soil disturbance can result in site capture by undesirable weeds such as *Imperata* grass, bamboos, or very low density pioneer tree species; recolonization of such areas by desirable woody species is slow (Fox 1968a). There are several examples cited in the literature in which the presence of site disturbance was still evident many years later because of the particular kind of vegetation which colonized the most heavily disturbed areas. In one well-documented case, Meijer (1970) (see also Fox 1968d) found that spar tree locations could easily be detected more than forty years after logging. The disturbed soil at these points was colonized by *Anthocephalus*, a fast-growing invader with a relatively long life span. The *Anthocephalus* extended outward from the spar tree location like spokes from a hub as it colonized the haul lines. Meijer (1970) found that, forty years after logging, heavily disturbed portions of the forest had not yet returned to their original species composition nor to half their probable original volume.

In addition to direct damage to seedlings and saplings, as well as the effects caused by exposing the mineral soil, extraction can result in additional site modification. Kartawinata (1978), for example, pointed out that damage frequently results from the ponding of water behind blocked water courses. This sort of damage, however, should certainly be amenable to a simple engineering solution and should be considered quite independently of those kinds of impacts which are less easily dealt with.

The utilization of a broader range of species and size classes certainly offers potential for retrieval of that wood volume which might otherwise be destroyed and unharvested as part of the extraction operation. Although, properly used, the potential for harvesting material which would otherwise be lost can be a very useful silvicultural tool, we must also recognize that such utilization could result in increased environmental damage if abused. Damage due to extraction increases with the volume removed and might reach unsupportable levels if the capability to use all species and sizes were employed unwisely.

Ecoclimate

The ecoclimate—the climate at the habitat level to which whole organisms are exposed — changes as a result of utilization of tropical forests. These changes are evident to even the most casual observer: the mature, undisturbed forest is dark, moist, cool, and wind-free, whereas forest clearings are well-lighted, relatively dry, hot at midday, and exposed to air movement. These changes directly affect the vegetation: both the residual trees and saplings, and the new seedlings. The ecoclimate directly governs the survival of the residual stand as well as the kind of regeneration which reoccupies the site, so is of great importance in assessing the potential impact of tropical forest utilization. Great expanses of lowland, wet tropical forests tend to be well-buffered climatically, but after logging even large unlogged tracts within a logged landscape may experience internal changes in ecoclimate. Chew (1968) for example studied a 184 acre (75 ha.) forest remnant within a logging concession and found that the internal forest climate had been modified considerably by the removal of the surrounding forest. He noted that the former vertical patterns of temperature and moisture from the forest floor up through the canopy were modified by the surrounding clearings. Because logging can potentially change the ecoclimate of adjacent, unlogged stands, this will have to be considered in determining the size and location of forest preserves which are to be left within a mosaic of managed forest lands.

Solar energy is the driving force behind other environmental variables so it is perhaps appropriate to consider it first. Its importance is emphasized by Whitmore & Wong (1958) in their discussion of the effects of felling a tropical forest:

> "Perhaps the most important single factor which is changed is the light. The hig trees which have been arrested at the sapling or pole stage are able to renew growth, but have to compete with a host of light-loving herbs, ferns, bushes, small trees and climbers. If these plants of secondary forest compete successfully, the reforming of high forest may be a long operation and ***belukar***, the dense impenetrable jungle of popular imagination, forms a biotic climax."

Less than two percent of the visible light which strikes the canopy of a dense tropical forest reaches the forest floor and almost half of the light energy input to the forest floor consists of sunflecks, the meandering, ephemeral bursts of direct light which penetrate the canopy. After clearing there is a significant change in the quality of the light regime (Table 7), notably a proportionally greater increase in infrared radiation than visible. This difference in light quality, however, is probably less important than the change in intensity; there are nearly two orders of magnitude more light in a clearing than on the shaded floor of a tropical forest (Fig. 3).

Table 7. Light quality in a clearing and under forest in Suriname. Values are per cent of total illumination, 350 — 850 nanometers. After Schulz (1960), Table III, p. 49.

Spectral region (nanometers)	Open	Forest
violet + blue (350 — 500)	20	25
green + yellow (460 — 610)	38	32
green + yellow (500 — 610)	33	26
500 — 850	80	75
orange + red + infrared (610 — 850)	47	40

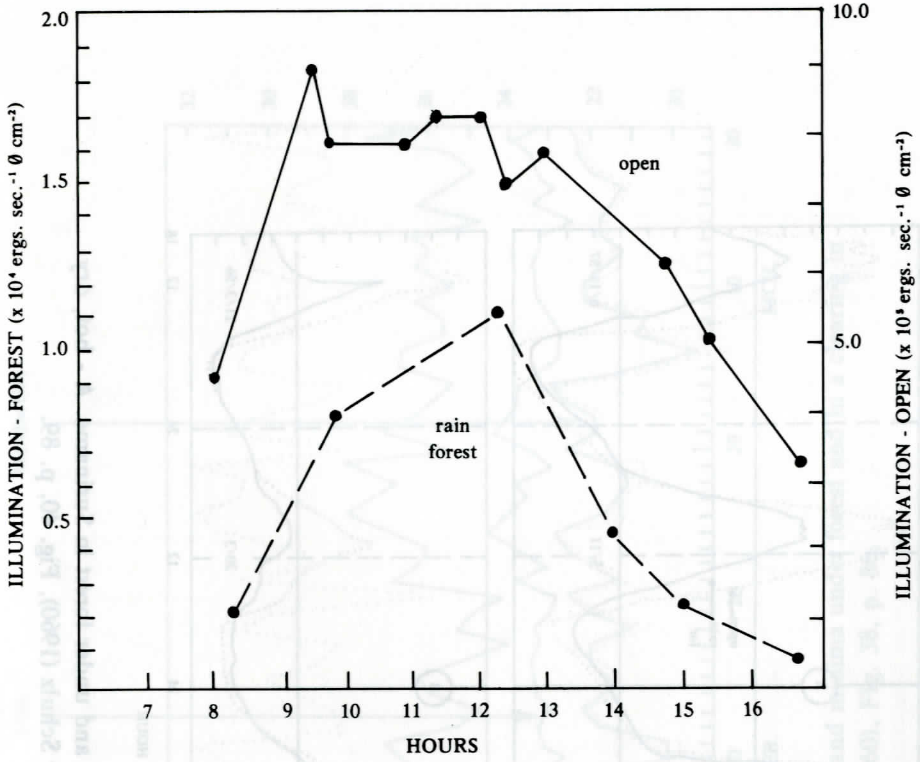

Fig. 3. Light intensity in a clearing and under forest in Suriname. Note scale differences. After Schulz (1960), Fig. 17, p. 46.

Increased solar radiation intensity results in higher air and soil temperatures. Figure 4 shows the daily march of air temperature in a forest compared with that in a nearby clearing. The minimum daily temperatures are not very different, but the maxima are consistently about 4°C higher in the clearing than in the forest (see also Figure 5). Similar effects are observed for soil temperatures. Mean monthly soil temperature at two depths under a forest and in a clearing are shown from Schulz' (1960) detailed Suriname study in Figure 6 which shows consistently higher soil temperatures in the clearing, as well as much greater month-to-month variation. The increased temperature variation in clearings is illustrated on a daily basis in Figure 7, which shows that, at a depth of 2 cm, soil in a clearing can experience a diurnal temperature range of 14°C, whereas the forest soil varies only about 1°C during the same time interval. Uniform, unvarying temperatures are a key characteristic of the forest climate; clearing not only markedly increases the temperatures of the soil and air, but results in increased diurnal and seasonal temperature variation as well.

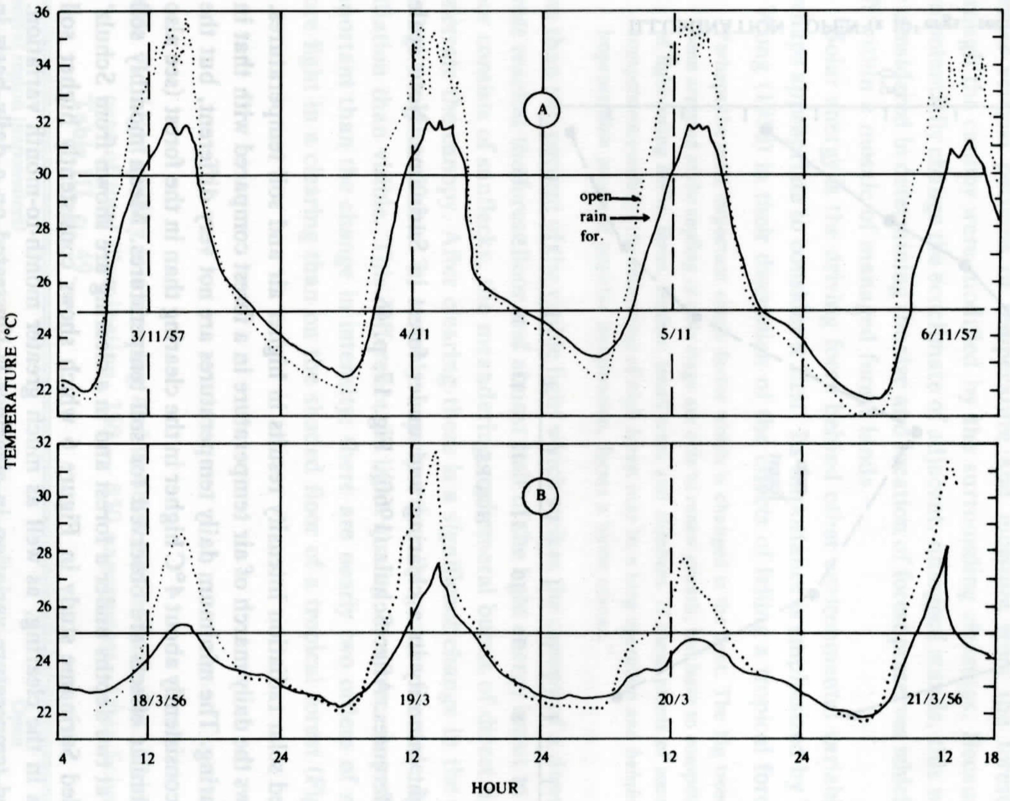

Fig. 4. Air temperature in a clearing and under forest in Suriname. A - hot, dry season; B - wet season. After Schulz (1960), Fig. 40, p. 89.

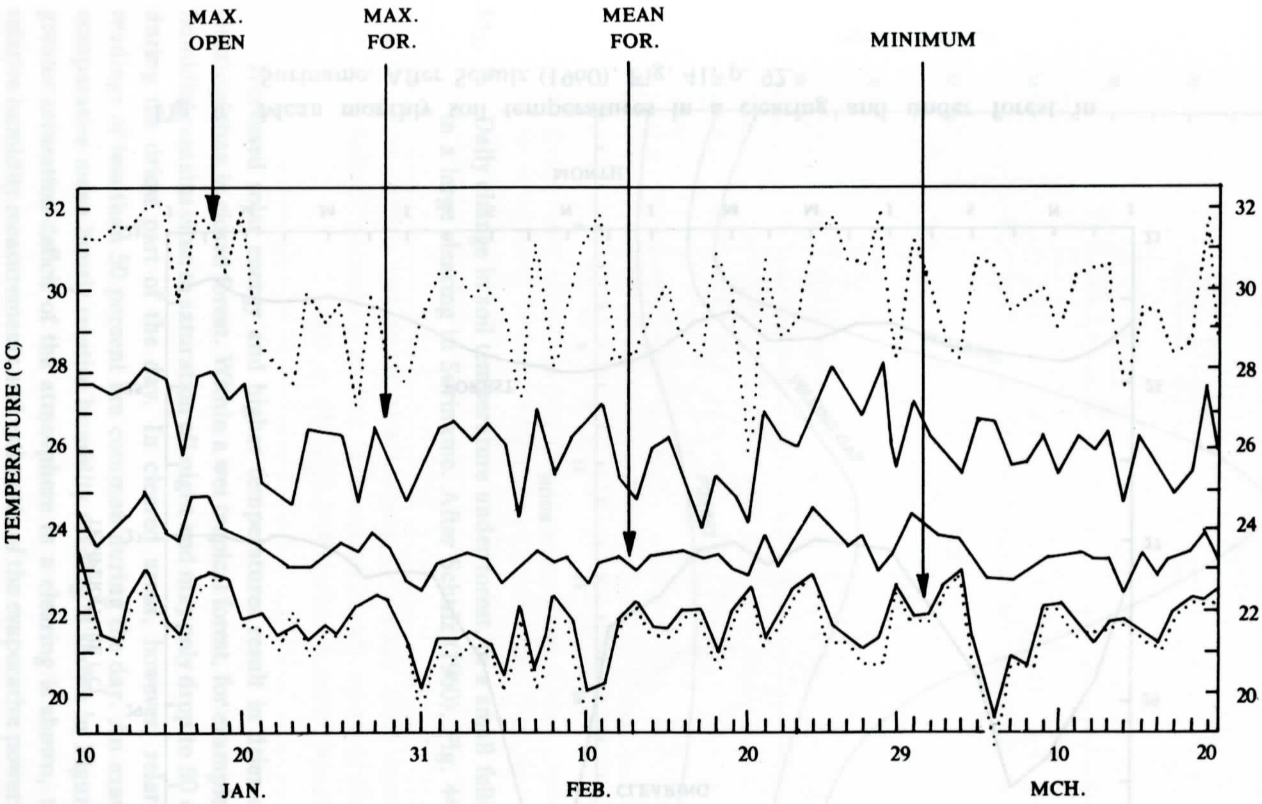

Fig. 5. Daily temperature maxima and minima under forest and in a clearing in Suriname. After Schulz (1960), Fig. 38, p. 86.

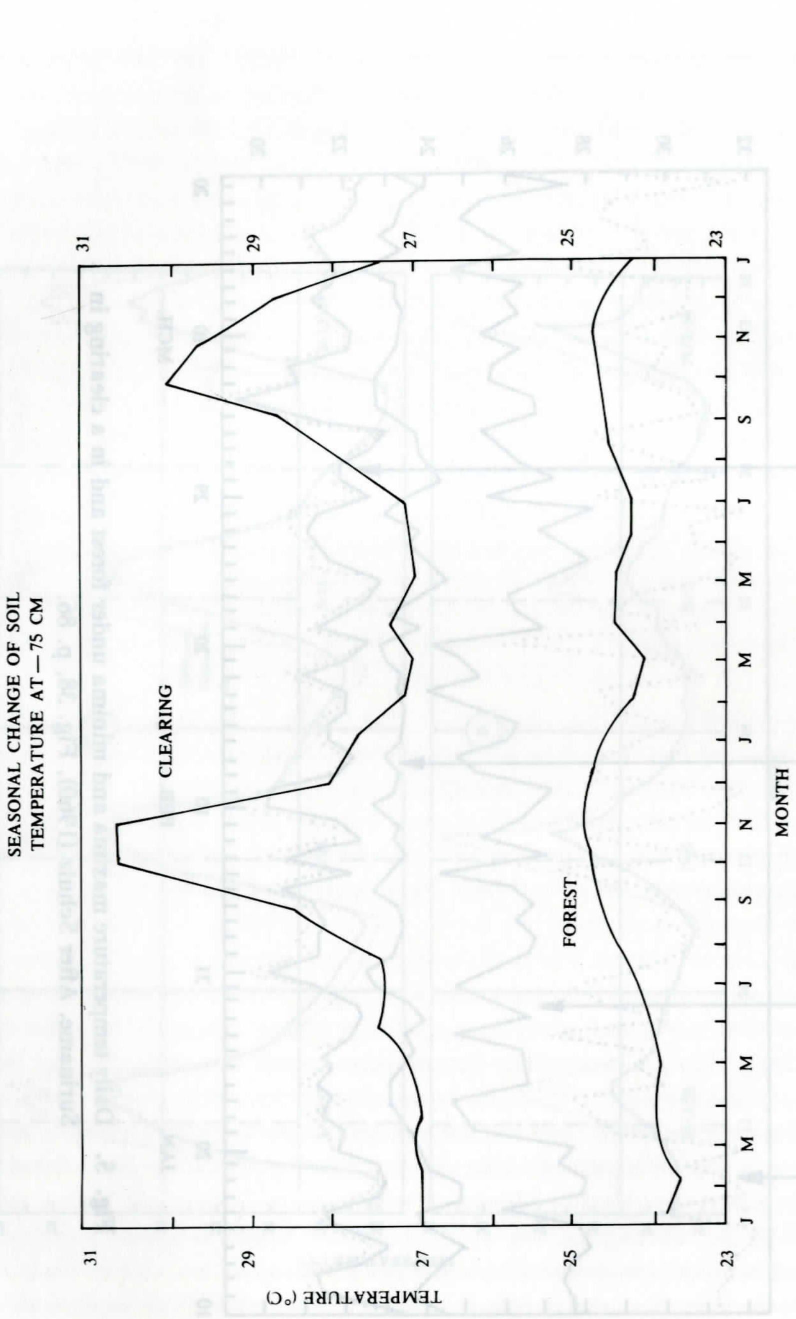

Fig. 6. Mean monthly soil temperatures in a clearing and under forest in Suriname. After Schulz (1960), Fig. 41, p. 92.

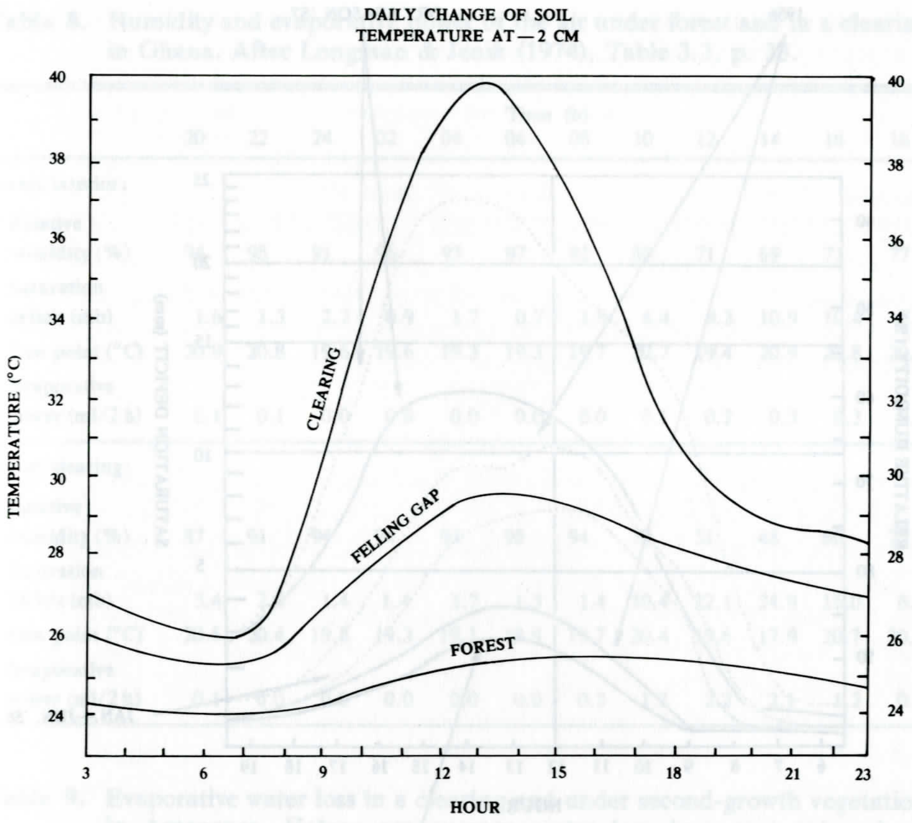

Fig. 7. Daily change in soil temperature under forest, in a small felling gap, and in a large clearing in Suriname. After Schulz (1960), Fig. 44, p. 95.

Increased solar energy and higher temperatures result in drier conditions in clearings than in closed forest. Within a wet tropical forest, for example, the relative humidity remains close to saturation all night and may only drop to 80 or 90 percent during the driest part of the day. In cleared areas, however, relative humidity readings of less than 50 percent are common during the day. An example of such comparative mean hourly relative humidity reading is shown in Figure 8, and the greater saturation deficit of the atmosphere in a clearing is shown, together with relative humidity measurements and estimates of the evaporative power of the air, in Table 8. Even second-growth vegetation does much to retard water loss after clearing. Brinkmann (1972), for example, found that air in a clearing had about three times the evaporative power of air under secondary vegetation (Table 9). The

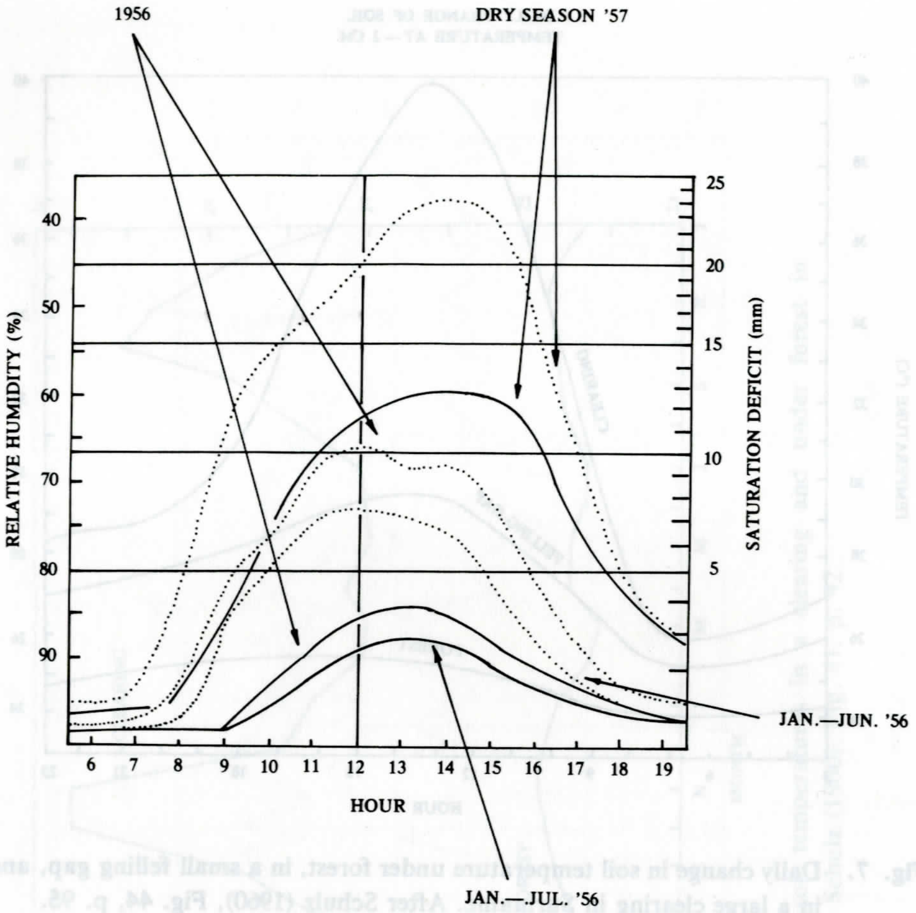

Fig. 8. Average daily march of atmospheric saturation deficit and relative humidity under forest (solid lines) and in a clearing (dotted lines) in Suriname. After Schulz (1960), Fig. 23, p. 60.

atmospheric water deficit and increased soil temperature increases water loss from the soil under clearings, as illustrated by Cunningham's (1963) data shown in Table 10.

What are the impacts of these changes in light, temperature, and moisture on residual vegetation and its ability to regenerate? Trees left standing after a logging operation respond in a variety of ways, depending on the species, the site, and the condition of the forest prior to logging. Logging of extremely dense, mature tropical forest frequently results in the death of residual trees due to changes in the ecoclimate, which can produce crown dieback, sunscalding of the trunk and branches, and possibly water stress (e.g., see Blanche 1978). In forests which are more open, and in some major community types, such as certain Southeast Asian Dipterocarp forests, however, the residual trees frequently respond to logging with a positive growth response (Nicholson 1965). There is evidence, however, that advance growth in some Dipterocarp forests is subject to insect attack (Fox 1968^{a}) and that residual trees are subject to attack by a wood-boring Cerambicid (Nicholson 1965).

Table 8. Humidity and evaporative power of the air under forest and in a clearing in Ghana. After Longman & Jenik (1974), Table 3.3, p. 33.

	Time (h)											
	20	22	24	02	04	06	08	10	12	14	16	18
Forest interior:												
Relative humidity (%)	94	95	91	96	93	97	92	85	71	69	71	77
Saturation deficit (mb)	1.6	1.3	2.2	0.9	1.7	0.7	1.9	4.4	9.3	10.9	10.4	7.4
Dew point (°C)	20.9	20.8	19.6	19.6	19.3	19.3	19.7	20.7	19.4	20.9	20.8	20.8
Evaporative power (ml/2 h)	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.3	0.3	0.2
Forest clearing:												
Relative humidity (%)	87	91	94	94	93	95	94	70	51	45	60	75
Saturation deficit (mb)	3.4	2.4	1.4	1.4	1.7	1.3	1.4	10.4	22.1	24.9	16.0	8.0
Dew point (°C)	20.5	20.4	19.5	19.3	19.1	18.9	19.7	20.4	19.6	17.9	20.7	20.2
Evaporative power (ml/2 h)	0.1	0.0	0.0	0.0	0.0	0.0	0.3	1.2	2.2	2.1	1.2	0.4

Table 9. Evaporative water loss in a clearing and under second-growth vegetation in Amazonas. Values are average water loss (per cent volume) of spherical ceramic bulbs. After Brinkmann (1972), Table 1, p. 36.

	clearing	below cover
dry season	76	27
rainy season	49	13

Seedling regeneration responds similarly to the changed environmental conditions resulting from harvesting: this ranges the gamut from death to positive growth responses. Brown & Matthews (1914), Serevo (1949), and Asiddao (1950) pointed out that much regeneration is lost because of the shock resulting from canopy opening. Part of this seedling loss may be due to dessication of the litter and

Table 10. Soil temperature and moisture under three conditions of exposure in Ghana. After Cunningham (1963), Table I, p. 337.

Treatment	Mean daily soil temperatures at 3 in. (°C) Max.	Min.	Mean weekly soil moisture 0-6 in. (per cent on oven-dry basis)
Shade	27	24	32.7
Half-exposure	32	24	28.2
Full-exposure	38	24	21.0

surface soil (Kartawinata 1978). Seedlings of many valuable species respond favorably to some shade; Nicholson (1960), for example, found that many species of Dipterocarp seedlings grew best under partial shade. This is true for many commercial tree species in the tropics: desirable species are frequently intermediate in tolerance and are neither pioneers which invade completely exposed, disturbed sites, nor species which reproduce in the dense shade of mature, undisturbed forest. Liew & Wong (1973) found that larger seedlings responded most vigorously to canopy opening and that, although logging killed many seedlings, the survivors responded with increased growth. Light-loving species of all kinds, both desirable and undersirable, respond favorably to increased light on the forest floor. Canopy opening frequently results in a burst of growth of undesirable weeds, both from seed storage in the soil and from rapid seed colonization from nearby disturbed areas. The weeds can , in fact, sometimes use the residual vegetation to good advantage in taking over a site. Nicholson (1965) aptly refers to some residual trees as "living climber towers", from which climbers are able to spread out over a site as well as gain a vertical advantage for seed dispersal.

There is a fine line between the positive and negative effects of forest utilization on the ecoclimate and its impact on vegetation. If manipulated properly, there is a potential to realize positive growth responses, high regeneration survival, and favorable species composition. If disregarded, however, the results can include loss of the residual stand, seedling death, and takeover of the site by undesirable climbers, herbaceous weeds, and short-lived pioneer trees.

Gene Pool

In the last few years numerous tropical scientists (e.g., Gómez-Pompa *et al.* 1972; Richards 1973; several sections in the volume edited by Farnworth & Golley 1974; Whitmore 1975; Myers 1976, 1979) have called attention to the potential loss and/or degradation of genetic material due to destruction of tropical forests. These are not ill-informed preservationists getting excited about some wood harvesting.

Rather, they are internationally known scholars who base their warnings on sound observations. The potential dangers they call attention to are very real and must not be disregarded in planning for the wise management and utilization of tropical forests.

Gene pool degradation can be broken down into two types. First, there is the "genetic erosion" which occurs when trees with sound boles and good form are selectively harvested in preference to individuals with undesirable characteristics which are left to provide the seed for the next crop. Blanche (1978) has warned against this problem with respect to the Dipterocarp forests of the Philippines and it is likely to occur in other tropical areas as well. If utilization of more kinds and sizes of trees becomes a possibility, then it offers a means of protecting against such genetic erosion. As long as we continue to high-grade tropical forests, however, the quality of the gene pool will continue to decrease.

Perhaps more serious a problem than the potential for genetic erosion is the possibility that entire species, many unknown to science, can be lost forever by mismanagement of the forest resource. The material subject to loss consists not only of the species harvested (these, in fact, are probably the least likely to disappear), but the myriad of other species found in diverse tropical forests. For example, one common post-harvest silvicultural practice is that of girdling and poisoning remnant trees which, for one reason or another, were not harvested. Meijer (1968) points out that this common practice may not only result in the irrevocable loss of species whose potentially useful characteristics are presently unknown, but that it is probably a treatment of dubious silvicultural value as well. Removal of the remnant trees opens the site to increased invasion by undesirable weedy species and creates and unfavorable environment for seedlings of many high-value species.

The loss of species is potentially an unusually severe problem in tropical forests for two reasons. First, the tropical forests contain so many species that loss of a tropical forest is likely to result in the loss of more species than would be the case if an equal area of temperate forest were lost. Second, species are packed into tropical environments and the resources for plant growth are so subdivided that the forests are much less uniform in space than are temperate forests. Thus, removal of a patch of forest is not only likely to destroy the individuals living there, but that combination of species is much less likely to reoccur in space than would be the case in temperate forests. There can be no doubt that increasing our incomplete knowledge of the characteristics of the species found in tropical forests is certain to result in the discovery of processes and products of benefit to mankind. Myers (1976), in a commentary on the possible loss of tropical species, states:

> "Despite limited knowledge about genetic reservoirs, it seems a statistical certainty that tropical forests contain source materials for many pesticides, medicines, contraceptive and abortifacient agents, potential foods, beverages, and industrial products. Of particular value for human purposes are the specialized genetic characteristics of many localized species — yet these attributes are associated in many instances with restricted range, precisely the factor that makes them vulnerable to destruction."

Any research program which increases our potential for species utilization must consider possible effects on the gene pool of tropical forests. One positive result may be that, by increasing the numbers of species which can be utilized, fiber demands might be met from smaller areas of forest. Indiscriminant harvest of all species, however, regardless of our knowledge of their characteristics, could potentially lead to an irrevocable loss of valuable genetic information.

IMPACT ON SOILS

Deep, well-weathered tropical soils, which form under conditions of high rainfall; high, uniform temperatures; and high rates of organic matter turnover, are tightly linked to the vegetation growing upon them. When that link is broken, as through harvesting the vegetation, the soil characteristics change. Under conditions of moderate, short-term disturbance those changes are usually temporary, but if the disturbance is severe and prolonged the changes are sometimes irreversible. Tropical soils are infinitely more varied than the uniform bands of red which often depict them on the maps included as end flaps of introductory geography texts. It is, therefore, impossible to describe a "typical" tropical soil and describe its susceptibility to damage due to forest utilization. Some tropical soils can withstand tremendous physical abuse and still respond by supporting a luxuriant vegetation. Others are extremely sensitive and, if disturbed, become the substrate for a different vegetation, often one which is less productive and diverse than the original forest. In all cases, however, the soils must always support the forests and because of the potential irreversibility of the changes which can occur in them, they are perhaps the key objects of concern in maintaining long-term site quality.

The following sections discuss three kinds of soil impacts. First, physical properties, including losses due to erosion, are described. Next, chemical characteristics are discussed. An estimate of nutrient losses due to harvesting in tropical forests is included in this section because we traditionally think of the soil as the chemical warehouse of the ecosystem, even though this is not always the case in tropical forests. Finally, the possible impacts on soil microorganisms — the creatures that make the soil a complex living system rather than just an inert mass of silicon, iron, oxygen, and aluminum — are discussed.

Physical Properties

Erosion is one of the most conspicuous physical results of humid tropical forest utilization, but should not be an insurmountable engineering problem. All studies of erosion and its relation to logging of humid tropical forests indicate that erosion does increase during and after logging (Wyatt-Smith 1949, Pernet 1952, Kellman 1969, Burgess 1971, Anderson 1972, Liew 1974). If logging is followed by fire, erosion is even greater (Table 11). Some authors indicate an alarming increase of soil loss after logging. Anderson (1972), for example, stated that losses from one hectare in Brazil increased from two pounds per year before logging to 34 tons per year after logging. Most studies do not indicate such high initial loss rates and do indicate a general decline in erosion as regrowth develops (compare Table 12 & 13) although erosion may continue in local highly disturbed areas for many years

Table 11. Soil erosion or accretion (inches) under slashed, slashed and burned, and unslashed vegetation in peninsular Malaysia. After Wyatt-Smith (1949), Table 1, p. 85.

Treatment	Time (days)	
	112	554
Slashed and burned		
1	- 0.25	- 0.25
2	nil	- 0.25
3	- 1.0	- 0.8
4	nil	nil
5	- 0.5	- 2.5
Slashed		
6	- 1.25	- 1.0
7	- 1.25	- 0.6
8	nil	nil
9	nil	nil
10	nil	nil
Unslashed		
11	nil	+ 0.7
12	nil	nil
13	nil	- 0.8
14	nil	nil
15	nil	+ 0.5

Table 12. Sediment losses under different permanent cover types in the Philippines. Values are averages for a 197-day sample period. After Kellman (1969), Table 8, p. 49.

Location	Sediment Loss (gm/day)
Primary forest	0.20
Softwood tree fallow	0.29
Imperata grassland	0.40
New abaca plantation	0.47
10 yr. old abaca plantation	0.59

Table 13. Sediment losses from swidden cropping in the Philippines. The post-harvest sampling period was 29 days. After Kellman (1969), Table 9, p. 49.

Location	Cropping Period Period (days)	 Mean Loss (gm/day)	Post-Harvesting Period (gm/day)
New corn swidden	138	3.03	0.65
New rice swidden	158	1.45	0.37
2 yr. old corn swidden	100 of 121	12.05	9.81
12 yr. old rice swidden	175	119.31	6.32

Table 14. Post-logging erosion and accretion in Sabah. Values are change in soil depth in inches. Numbers in parenthesis are number of belian pegs affected. After Liew (1974), Table 2, p. 25.

Time after establishment (months)	In Tractor Paths			Off Tractor Paths		
	Erosion	Accretion	No Change	Erosion	Accretion	No Change
1	- 14 (11)	+ 4 (2)	(10)	- 33 (22)	+ 27 (13)	(21)
2	- 12 (9)	+ 4 (7)	(7)	- 16 (16)	+ 17 (17)	(23)
3	- 6 (9)	+ 3 (6)	(8)	- 24 (29)	+ 4 (9)	(18)
4	- 5 (11)	+ 4 (7)	(5)	- 12 (20)	+ 11 (18)	(18)
5	- 3 (6)	+ 2 (3)	(4)	- 3 (7)	+ 4 (10)	(39)
6	- 5 (10)	+ 2 (2)	(11)	- 99 (20)	+ 4 (8)	(28)
14	- 24 (10)	+ 11 (8)	(5)	- 18 (19)	+ 22 (25)	(12)
20	- 19 (12)	+ 5 (4)	(7)	- 31 (26)	+ 16 (14)	(16)

(Burgess 1971). Most erosion is typically associated with roads and skid trails, i.e., the areas which sustain the most soil damage. One study, however (Liew 1974), indicated less soil movement along tractor paths than away from tractor paths, presumably due to compaction of the soil by the tractors (Table 14).

Other physical effects on soils include loss of structure and compaction (Russell 1974). Undisturbed forest soils tend to have higher values for crumb stability (Coulter 1950) and porosity (Cunningham 1963, Freise 1934) and lower values for bulk density (Popenoe 1959) than soils that have been cleared (Tables 15 & 16). The amount of this type of soil damage depends, in part, on the harvesting techniques used. Animal logging results in the least total damage (Brown 1955) while tractor logging tends to cause more damage than high-lead logging (Russell 1974, U.S. Environmental Protection Agency 1976). Although high-lead logging causes less soil damage than tractor logging, the resulting erosion may be equally severe since high-lead logging tends to be used in steeper terrain.

Table 15. Soil porosity and crumb structure in 0-3 inches under three conditions of exposure in Ghana. After Cunningham (1963), Table 2, p. 337.

Treatment	Porosity (volume %) Capillary pore space	 Non-Capillary pore space	 Total pore space	Water-stable aggregates (% air-dry soil > 3 mm) Total structure	 True crumb structure
Shade	37.0	14.7	51.7	55.3	39.8
Half-exposure	35.0	16.4	51.4	50.2	28.9
Full-exposure	32.6	10.1	42.7	48.7	29.0

Chemical Characteristics

Unlike many temperate soils which derive most of their cation exchange capacity (CEC) from clays, many soils of the humid tropics owe most of their CEC to their colloidal organic matter content. Accordingly, most chemical changes which occur in tropical soils as a result of forest utilization probably reflect changes in the soil organic matter. Contrary to common belief, however, the rate of organic matter breakdown does not increase after clearing. In a study of decomposition in tropical second-growth, mature forest, and clearings one of us (Ewel 1976) reported:

> "Decomposition did. . . occur more slowly in the cleared areas than under vegetation. References are often encountered in the popular literature which point out the danger of clearing tropical soils due to the increased decomposition of organic matter, supposedly because of its rapid oxidation. Although organic matter is reduced by . . . anything . . . which reduces the organic inputs to the system, the results . . . indicate that decomposition is retarded by removal of the vegetation. A cleared area in the tropics is a harsh environment, subject to drying during the day and exhibiting a wide daily range in temperature. Such conditions are undoubtedly more rigorous for decomposer organisms than those found in the litter beneath a vegetative cover."

Because organic matter inputs in the form of leaf and branch fall are cut off when a forest is cleared, the organic matter and CEC decrease after clearing, as shown in Table 17 (Coulter 1950, Riquier 1953, Cunningham 1963, Nye & Greenland 1964, Soerianegara 1970). The drop in CEC releases nutrients into the soil solution, where they are subject to loss through leaching and surface runoff (Cunningham 1963, Nye & Greenland 1964, Kellman 1969). Popenoe's (1959) data give an idea of the magnitude of change in nutrient status following clearing, as do Cunningham's (1963) data for carbon, phosphorus, and nitrogen (Table 18).

Table 16. Soil physical and chemical properties under three stages of shifting cultivation in Guatemala. Values are averages from four locations. After Popenoe (1959), Table 1, p. 74.

Stage	Depth (inches)	bulk density (g/cc)	pH	Nitrogen (%)	Carbon-Nitrogen ratio	Potassium (ppm)	Calcium (ppm.)	Magnesium (ppm)	Exchange Capacity (me/100 g)	Base saturation (%)
Forest	0— 2	—	575	103	159	280	6343	964	943	537
	2— 8	056	574	49	144	97	3264	516	45.2	51.7
	8—16	—	5.93	.23	10.9	51	2143	435	33.7	45.8
Cleared land	0— 2	—	6.37	.74	12.0	406	5615	868	68.4	58.4
	2— 8	0.71	5.69	.35	13.2	154	2757	539	41.9	43.3
	8—16	—	6.14	.19	10.5	84	2782	584	39.3	44.4
2 year 2nd growth	0— 2	—	5.85	.76	15.2	306	5048	667	75.0	53.3
	2— 8	0.70	5.79	.32	11.7	92	3022	347	43.4	45.6
	8—16	—	6.07	.19	9.4	64	3491	324	35.3	50.0

Table 17. Changes in cation exchange capacity, potassium, and pH under three conditions of exposure in Ghana. Values are means of eight plots. After Cunningham (1963), Table 5, p. 341.

		Cation exchange capacity (me/100 g)			Exchangeable K (me/100 g)			pH		
Horizon (inches)	Year	Shade	Half-exposure	Full-exposure	Shade	Half-exposure	Full-exposure	Shade	Half-exposure	Full-exposure
0—2	1957	14.95	15.10	15.25	0.76	0.62	0.72	7.3	7.3	7.3
	1960	13.73	10.99	9.90	0.26	0.20	0.21	6.7	6.9	6.9
2—6	1957	6.40	6.32	6.59	0.28	0.23	0.31	6.9	6.9	7.0
	1960	6.15	6.30	6.22	0.21	0.24	0.24	6.6	6.7	6.7

Table 18. Changes in soil carbon, phosphorus, and nitrogen under three conditions of exposure in Ghana. Values are means of eight plots. After Cunningham (1963), Table 4, p. 339.

Horizon (inches)	Year	Organic C (%)			Organic P (p.p.m.)			Total N (%)		
		Shade	Half-exposure	Full-exposure	Shade	Half-exposure	Full-exposure	Shade	Half-exposure	Full-exposure
0—2	1957	3.48	3.40	3.65	334	340	353	0.432	0.352	0.364
	1960	2.62	1.75	1.56	271	190	176	0.268	0.185	0.171
	% decrease	24.7	48.5	57.3	18.9	44.1	50.1	21.6	47.4	53.0
2—6	1957	1.02	1.06	1.10	194	206	215	0.110	0.118	0.124
	1960	0.85	0.79	0.77	174	158	161	0.099	0.091	0.090
	% decrease	16.7	25.4	30.0	10.3	23.3	25.1	10.0	22.8	27.4

Not all of the nutrient loss due to leaching is permanent. Many studies, including several that deal with shifting agriculture and its associated fallow vegetation, indicate that the nutrients immobilized in regrowth and fallow soil quickly approach the levels found under mature forest (Joachim & Kandiah 1948; Snedaker 1970; Soerianegara 1970; Brams 1973; Harcombe 1973, 1977a&b; Golley *et al.* 1975). Some of the leached nutrients are retrieved by deep-rooted plants, especially on sandy, well-drained soils. Such uptake is much less likely in more typical fine-textured, deeply weathered soils, however. Such soils are often imperfectly drained, nutrient poor, and have 90 percent or more of their plant roots in the upper 10-15 cm. Nutrients leached deeply into such soils are almost irretrievable.

If post-harvest burns are used to reduce logging debris the nutrients tied up in the slash are released and may be lost due to leaching and run-off (Brinkmann & Nascimento 1973). If regrowth is rapid, however, as at the onset of the wet season, many of the released nutrients will be available for the new regrowth, thus insuring that the soil is quickly covered with vegetation.

Another potential loss, but one which has not been well studied, is the removal of nutrients in harvested biomass. This may be of considerable importance in tropical forests where the bulk of the nutrient capital of the site is incorporated in the vegetation, rather than in the soil as in most temperate zone forests. There is some indirect evidence from soils under sugarcane and coffee (Krebs, Tan, & Golley 1974) and oil palm (Kowal & Tinker 1959) that cropping over extended periods may result in some nutrient depletion, though the elements involved may vary with the crop and soil type. Ovington's (1962) coments on nutrient removal from forests are appropriate:

> "Whilst the average annual removal of nutrients in the forest crop is small compared with that under most agricultural systems, the long term loss from woodlands by harvesting is considerable . . . Clearly, if the soil-nutrient reserve is not supplemented in some way, a gradual depletion of the soil capital would occur as a woodland matures and is harvested . . . serious soil degradation could result within a few generations of trees."

Ovington's remarks were directed at temperate forests, but there is every reason to believe that the same issues apply to an even greater extent in the case of the tropics. In an effort to get a rough idea of the magnitude of nutrient removal from tropical forests we constructed Figure 9. This shows the total standing crop (soil, litter, roots, and above-ground vegetation) of nitrogen, phosphorus, potassium, calcium and magnesium in temperate and tropical forests. The relative size of each circle is scaled to the total standing crop, while the cross-hatched segment indicates the amount removed when boles (with bark intact) are removed. It is clear from these data that nutrient depletion from tropical forests through wood removal is potentially a serious problem and one which must be given strong consideration if increased rates of harvesting are anticipated.

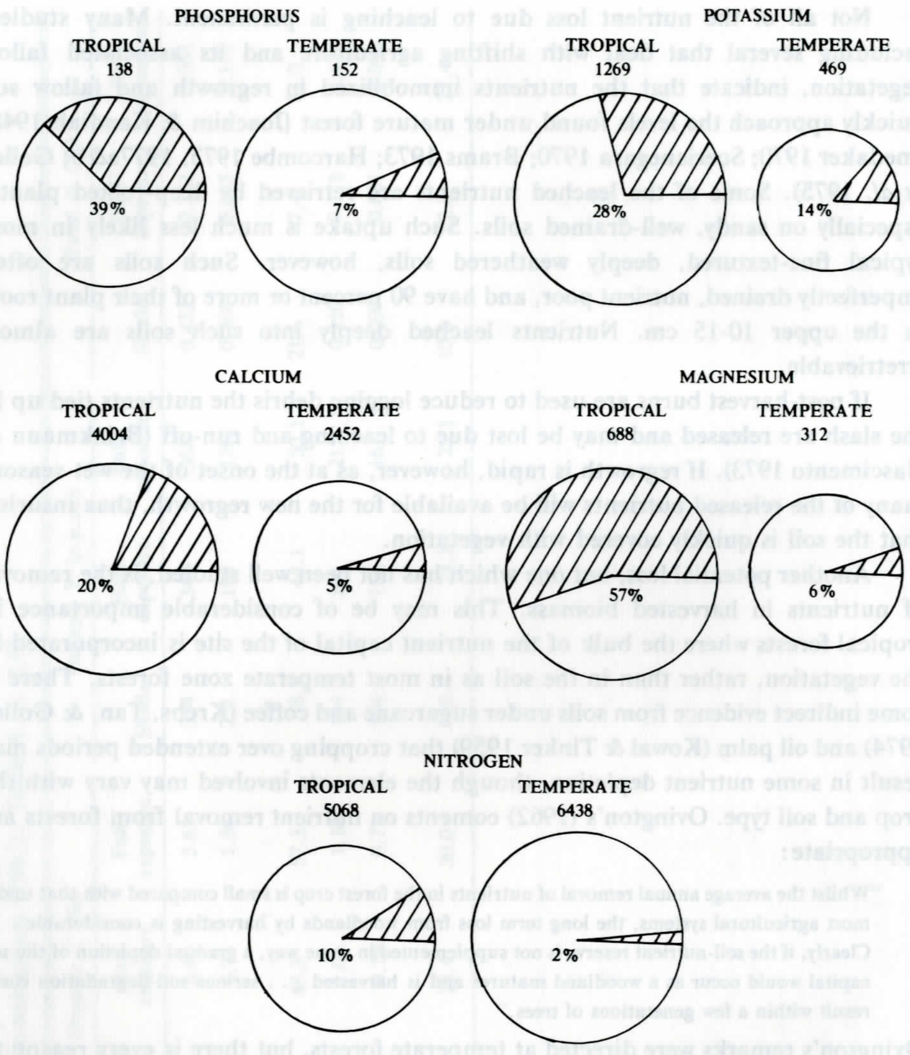

Fig. 9. Total ecosystem nutrients and the fraction lost through harvest in temperate and tropical forests. Values are Kilograms per hectare. Cross-hatching indicates the amount removed when trees are harvested (boles only), assuming that all roots, branches, and leaves remain in the forest. Temperate data are a mean of four kinds of vegetation from Ovington (1962): *Pinus sylvestris, Pseudotsuga taxifolia, Betula verrucosa*, and *Quercus robur*. Tropical data are a mean of data from Kade, Nigeria and Yangambi, Zaire (summarized in Nye & Greenland 1960) plus Puerto Rico (Odum & Pigeon 1970).

Soil Microorganisms

The least conspicuous, but perhaps the most important, potential effect of forest utilization on the soil concerns the impact on soil micro-organisms. These organisms are important in nutrient cycling and soil physical properties, and are directly involved in tree nutrition. Of special importance are the mycorrhizal fungi which are essential for the nutrition, and consequently the survival, of almost all tropical trees (Singh 1966, Went & Stark 1968, Stark & Holley 1975, Janos 1980a & b) site modifications that drastically alter the mycorrhizal fungal populations could have serious implications for regrowth and recovery.

The limited number of soil microorganism studies do indicate that some bacterial, fungal, and soil arthropod populations decrease following site disturbance (Cook 1909, Meiklejohn 1962, Blanche 1978, Lasebikan 1975). Data published by Coulter (1950) are summarized in Table 19. They indicate that the undisturbed forest has very high bacterial and fungal population levels and that these are lower under burned grass and plantations. Aspiras (data reported by Blanche 1978), however, found that a logged area in the Philippines had more bacteria, actinomycetes, and fungi than did a nearby climax forest. His data are shown in Table 20. Population densities determined by plate counts are of limited value, however, and the difficulty of accurately assessing true microorganism populations remains an unsolved problem.

Table 19. Numbers of soil microorganisms under five types of land use in peninsular Malaysia. Values are means from four plates (n=3 under Tembusu plantation) and method was designed primarily for bacterial counts. After Coulter (1950), Table II, p. 196.

Land Use	Millions per g of soil		
	Bacteria	Fungi	Actinomycetes
Unburned *Imperata*	32	.8	.2
Virgin Forest	28	1.4	0
Burned *Imperata*	13	.3	.2
Tembusu Plantation	10	1.7	0
Kapur Plantation	8	.7	.2

Some of the soil bacteria are nitrogen fixers and, as such, may be crucial components of the forest's nitrogen cycle. Nitrogen is frequently a potentially limiting factor in tropical forest growth. Dommergues (1954) reported that,

Table 20. Numbers of soil microorganisms in undisturbed and logged forests in the Philippines. Values are hundreds of thousands of organisms per g of soil. Data of R. Aspiras, after Blanche (1978), Table 3, p. 102.

	Bacteria	Actinomycetes	Fungi
Climax forest			
Undecomposed litter	2.2	0.8	2.1
Decomposing litter	0.8	0.6	5.8
Top soil	.02	0.002	11.1
Logged-over area			
Undecomposed litter	8.7	6.0	3.2
Decomposing litter	2.6	2.6	2.6
Top soil	0.3	0.1	1.8

following forest destruction, the density of nitrogen fixing bacteria was 4 to 10 times lower than that of the undisturbed forest. He also reported that the density of cellulolytic bacteria was 8 to 33 times lower than that observed before forest destruction. This, coupled with the reduction of populations of soil and litter-inhabiting arthropods, could significantly reduce the rate of litter breakdown and nutrient cycling. Meiklejohn (1962) also studied the effects of tree removal on populations of nitrifying bacteria (Table 21) and observed a decrease in population size following tree removal.

Table 21. Populations of soil nitrifying bacteria under cleared and uncleared forest and grassland in Ghana. Values are cells per gram. After Meiklejohn (1962), Table 4, p. 123.

	Forest		Grassland	
Type of Nitrifier	Trees Present	Trees Removed	Cleared	Natural
Ammonia Oxidizer	8730	6960	2320	630
Nitrite Oxidizer	490	60	10	1

Soil microorganisms in the humid tropics may be more susceptible to site exposure than those of temperate zones because temperate-zone soil microorganisms commonly have resistant stages in their life cycles which allow them to survive in a seasonally harsh environment. Tropical microorganisms, on the other hand, may not always possess such resistant stages and therefore might be drastically affected if their microenvironment is appreciably altered.

IMPACT ON WATER RESOURCES

Abundant water is one of the great natural resources of the humid tropics: most humid tropical areas receive more than two meters of rain per year and some areas receive eight to ten or more. Potential evapo-transpiration from natural forest vegetation in the tropical lowlands is about 1600 mm per year, and most of the difference between that and rainfall shows up as runoff. This runoff is crucial for irrigation in drier downstream regions, for urban and industrial consumption, and (possibly most important of all in the future) for the driving force to produce hydroelectric power in fossil-fuel-poor developing nations. Despite the great importance of the water resources of tropical nations and the great potential impact that forest utilization can have upon them, there has been very little study of the relationship between forest utilization practices and water. For example, the measurement of water (quality and quantity) flowing off of paired, calibrated watersheds, one of which receives some treatment (such as clearcutting) and the other of which serves as a control, is now a standard kind of hydro-ecological study used in temperate zones to evaluate the impact on water of various land use practices. The well known Coweeta and Hubbard Brook experiments are examples of such studies in the U.S. Hibbert (1967) summarized the results of 23 such studies, yet only one of these (see studies by Pereira and co-workers in Kenya) was tropical.

It may be possible, however, to do a judicious amount of careful projection of the abundant, detailed results from temperate zone studies into the tropics, provided that several important differences are kept in mind:

1. Rainfall input is usually much greater in tropical forests than in temperate forests.
2. The time lags due to storage in form of snow are absent from tropical forests, thus decreasing the relative turnover time.
3. Most tropical precipitation is convectional, thus occurs in the form of intense showers and results in surface flow even over soils which are not saturated.
4. Tropical soil is often deeply weathered, and therefore may act like a storage tank which buffers the rate of output.
5. Tropical vegetation is structurally complex, so variables such as interception, transpiration, and uptake from the soil are likely to be significantly different from those of temperate forests.

Two aspects of water resources are affected by forest utilization, and although they are closely interrelated, they are separated for purposes of discussion below into two sections: water yield and water quality.

Water Yield

Because the combined effects of evaporation and transpiration from a forest result in greater water return to the atmosphere than that resulting from bare-soil evaporation alone, it is generally true that removal of the forest cover results in greater total annual water yield via runoff and streamflow (see, for example, Hibbert 1967). The data upon which the above general conclusion is based are mostly from temperate forests, but the limited amount of data from the tropics suggest that it may be a valid generalization there also. Pereira *et al.* (1962), for example, found that conversion of about one third of a Kenyan watershed to tea plantation resulted in a decrease in evapotranspiration of about ten percent, when expressed as percentage of annual rainfall (see Table 22). In follow-up reports on the same study he indicated that runoff (expressed as percentage of annual rainfall) was about four to ten percent higher from watersheds that were partially converted to tea plantations than from forested watersheds, as shown in Table 23. Similarly, Kellman (1969), who worked in the Philippines, found that runoff was higher from *Imperata* grassland than from forest, and that logged-over forest yielded more runoff than agricultural fields (see Table 24). His results indicate that water yields are reduced quite quickly following the start of secondary succession.

Table 22. Water budgets for two watersheds in Kenya. Values are water depth in inches over the watershed. After Pereira, Dagg & Hosegood (1962), Table XIII, p. 39.

	Lagan			Sambret		
	1957/58	1958/59	1959/60	1957/58	1958/59	1959/60
	100%	Forest	Cover	99% Forest; 1% Clearing for Roads	77% Forest; 23% Clearing for Tea	66% Forest; 34% Clearing for Tea
Average annual rainfall	72	71	89	70	72	82
Total annual streamflow	11	11	25	13	13	27
Open water evaporation	60	59	61	60	59	61
Approximate water use	61	61	63	57	59	57
Water use as percentage annual rainfall	85	86	71	81	82	70
Average E_t/E_o Ratio	1.02	1.01	1.05	0.94	1.00	0.89

Table 23. Streamflow as percentage of annual rainfall from watersheds in forest and tea plantations in Kenya. Values in parentheses are percent of watershed cleared for tea plantation. After Pereira (1967b), Table 4, p. 446.

Year (% cleared)	Tea Plantation	Control (100% forested)	Difference
1958/59 (0)	13.4	16.5	—3.1
1959/60 (34)	23.6	16.7	+6.9
1960/61 (53)	43.8	39.4	+4.4
1961/62 (53)	42.8	36.1	+6.7
1962/63 (53)	48.9	39.1	+9.8
1963/64 (53)	45.4	35.6	+9.8

Table 24. Runoff from various cover types in the Philippines. After Kellman (1969), Tables 6 and 7, p. 48.

Cover type	Runoff (% of rain)
Primary forest	0.26
Logged-over forest	1.73
Softwood tree fallow	0.26
Imperata grassland	3.02
New abaca plantation	0.35
10 yr. old abaca plantation	0.64
New corn swidden	1.52
New rice swidden	1.09

Mueller-Dombois (1973) found that an exotic grass (*Andropogon*), which occupies some formerly forested sites in Hawaii, uses significantly less water than the native forests, thus resulting in increased runoff and potential damage from erosion. Low & Goh (1972) calculated water budgets for five watersheds in West Malaysia (Table 25) and found that the four watersheds which were forested yielded about 25 percent less runoff than the fifth watershed, which was partially logged and converted to agricultural and urban use. (See also Kenworthy 1969).

The amount of leaf area per unit ground area (i.e., leaf area index, or LAI) is generally quite high in tropical forests, with values of seven to ten commonly reported in the literature. This compares to LAI values of four to six which are frequently reported for temperate forests. The higher LAI of tropical forests may result in proportionately greater transpiration from tropical forests than from temperate forests, so the increases in water yield following forest clearing may be

Table 25. Calculated water balances for five watersheds in West Malaysia. Watershed 5 is partially deforested and in agricultural and urban land use; the other four are almost completely forested. Values are mm. After Low & Goh (1972), Table 2, p. 62.

Watershed	Rainfall	Runoff	Water loss, E_t	Storage Change	Potential Evapotranspiration, E_o	E_t/E_o
1	2156	1077 (49.9)	1079 (50.0)	—1.5 (—0.1)	1247	0.86
2	2109	1100 (52.2)	1009 (47.8)	—8.1 (—0.4)	1242	0.81
3	2162	1100 (51)	1062 (49.1)	—35.8 (—1.6)	1236	0.86
4	2482	1219 (49.1)	1263 (50.9)	—4.3 (—1.7)	1291	0.98
5	2744	1752 (63.8)	993 (36.2)	—88.9 (—3.2)	1241	0.80

proportionately higher than those following clearing of temperate forests. In some cases this additional water yield may be a welcome additional resource, but more often than not it occurs as a rushing torrent of post-storm water which frequently inundates agricultural flood plains. For example, in one area of the Atlantic lowlands of Costa Rica which has recently undergone massive conversion from forest to pasture the long-term residents report that floods are increasingly more severe and more frequent than was the case prior to the change in land use. Although such reports are undocumented by scientific data they are heard far too often to be ignored.

One aspect of water yield and its relationship to forests which is almost unique to the tropics is that situation where the presence of forest vegetation may increase the total yield from a watershed. This occurs in cloud forests, where transpiration is low (e.g., see Weaver, Byer, & Bruck 1973; Weaver 1975) and the vegetation is buffetted by moisture-laden air, frequently driven by the trade winds. In such cases the tree limbs, leaves, and epiphytes act like a three dimensional condenser which strips the water out of the air. The increased water input from this filtering action is very substantial, often accounting for half or more of the total (e.g., see Dohrenwend 1972, Weaver 1972). Many such cloud forests are dwarfed and do not contain commercial timber, but others are tall and prized by loggers. Any planned forest utilization of such cloud forests should certainly consider the potential downstream effects of decreased water yield that might result from forest cutting. These forests are usually wet throughout the year, and thus supply the continuous streams of water necessary for special uses such as small-scale hydroelectric power.

Water Quality

Two practices associated with forest utilization are undoubtedly most closely related to impact on water quality: the type of extraction technique used (tractor skidding, high-lead, etc.), and road and skid trail layout. Much logging of tropical forests is purely exploitative and it is not uncommon to see streambeds used as skid trails and dry season streambed crossings made by earth and log fills which are left after logging to be washed out by wet season rains. Such practices are clearly amenable to engineering solutions and an increase in forest utilization intensity, if done conscientiously, should not greatly increase water quality problems. A detailed study by the U.S. Environmental Protection Agency (1976) summarized the impact of forestry practices on water quality in the northwestern U.S.; many of the conclusions reached for that region might be applied to tropical areas as well. The authors of that report concluded, for example, that water quality was inversely proportional to the degree to which the forest was opened during harvesting. They found that clearcutting had the greatest impact, followed by seed tree, shelterwood, and selection cutting.

As with water yield, there have been very few field studies of the impact of forest utilization on water quality in the tropics. One of the best studies was conducted in Northern Queensland (Australia) by Gilmour (1971). He found that most of the sediment that washed off of his 17 square mile (43.5 km²) study area was derived from disturbances associated with logging, loading ramps, and roads. The sediment concentration below logging was two-to-four times greater than above logging, and in both cases increased in proportion to stream height (Fig. 10). Some of the sediment load resulting from land disturbance settles out quickly, as exemplified by Gilmour's (1971) data shown in Table 26 which indicate about fifty times more sediment immediately downstream of a loading ramp than above the ramp, yet an increase of only five-fold 50 m downstream. Gilmour (1971) also noted that:

> ". . . sediment clears rapidly once rain ceases. However, during the wet season light showers . . . frequently occur for days or even weeks at a time. Consequently, this can result in an almost continuous source of sediment-ladden water leaving the catchment."

Using a computer simulation model applied to a large watershed in the Dominican Republic, Antonini, Ewel & Ewel (1974) and Antonini, Ewel & Tupper (1975) calculated that sediment accumulation in a downstream reservoir would be almost three times more rapid if the watershed were converted to agriculture than if it were reverted to forest. Other land-use combinations (Fig. 11) resulted in intermediate rates of sediment accumulation. Unless a site is severely disturbed and seed sources are removed, succession normally proceeds rapidly in the humid lowland tropics, so the increased sediment load following harvesting should drop more quickly in the tropics than in the temperate zone.

In addition to water quality changes resulting from increased mineral sediments, organic matter inputs into streams may decrease water quality by

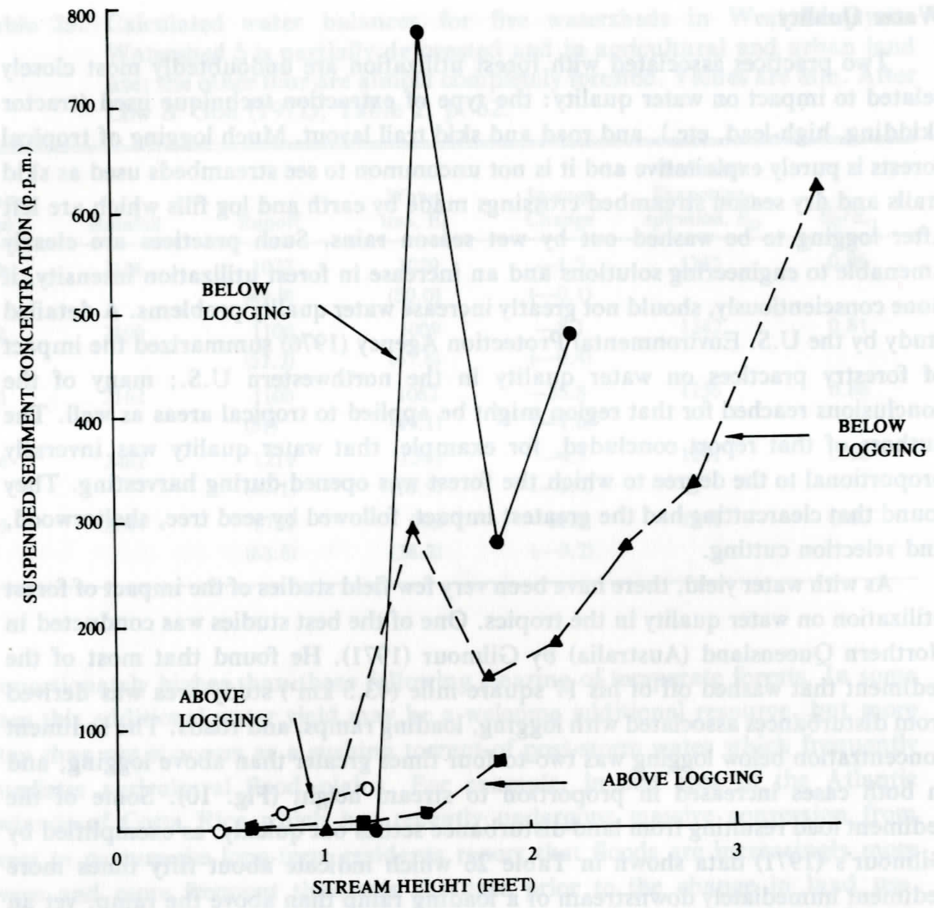

Fig. 10. Suspended sediment loads in relation to stream height above and below logging operations in Queensland, Australia. After Gilmour (1971), Fig. 3, p. 41.

increasing the oxygen demand as well as causing increased turbidity. Kellman (1969) measured organic matter losses from small plots in the Philippines and found that the loss from logged-over forest was about twenty times greater than that from primary forest. Losses from clean-cultivated crops were higher than those from forests. (Table 27)

The impact of increased intensity of tropical forest utilization on water yields and water quality is likely to be of increasing concern, especially in light of population increases and rising demands for both wood and water. Most of the potential problems, however, can be solved through the application of currently available engineering techniques concerned with road construction and harvesting.

Table 26. Sediment concentrations after rain above and below a log ramp in Queensland, Australia. After Gilmour (1971), Table I, p. 42.

Location	Sediment concentration (p.p.m.)
Upstream of ramp	48
Immediately downstream	2602
50 metres downstream	203
400 metres downstream	186

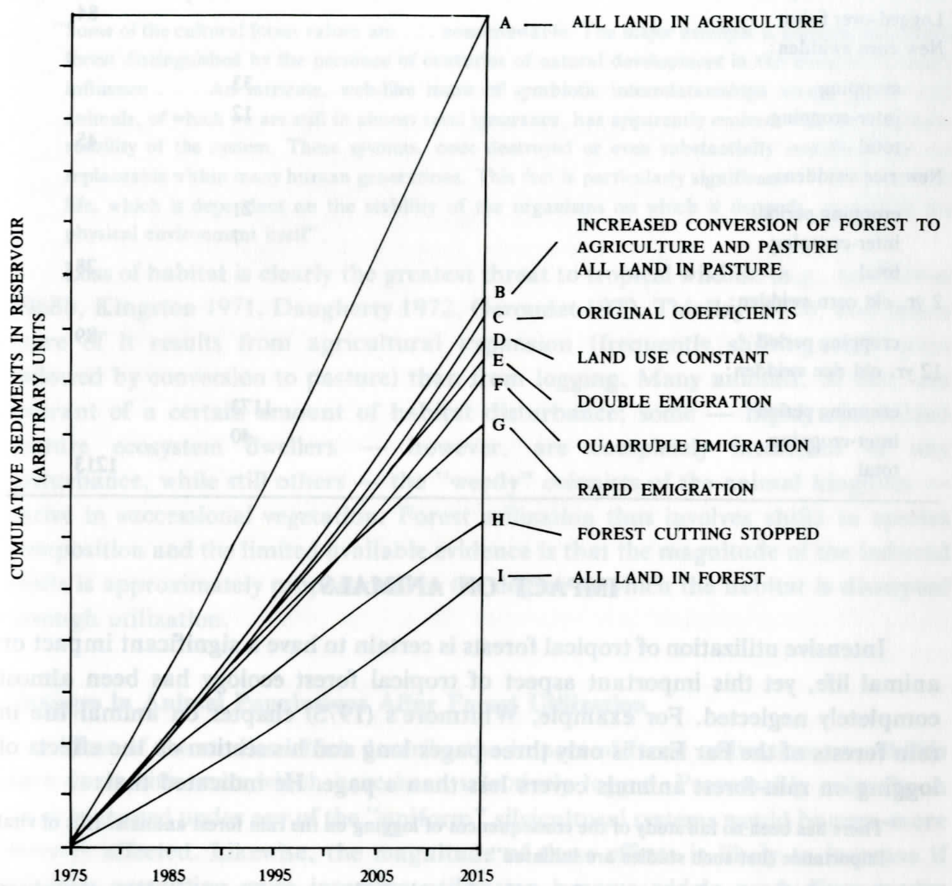

Fig. 11. Relative rates of simulated accumulation of sediments from a watershed under various kinds of land use in the Dominican Republic. After Antonini, Ewel & Ewel (1974), Fig. 3.6, p. 69.

Changes in water yield and decreases in water quality can be expected to accompany increased intensity of forest utilization, and may place restrictions on the size of forested blocks subjected to utilization at a given time.

Table 27. Organic matter losses by erosion in the Philippines. After Kellman (1969), Table 11, p. 52.

Land Use	Estimated Annual Loss (gm/m^2)	
Primary forest		5
Softwood tree fallow		7
Imperata grassland		9
New abaca plantation		11
10 yr. old abaca plantation		13
Logged-over forest		84
New corn swidden:		
cropping	33	
inter-cropping	12	
total		45
New rice swidden:		
cropping period	21	
inter-cropping	7	
total		28
2 yr. old corn swidden:		
cropping period		89
12 yr. old rice swidden:		
cropping period	1173	
inter-cropping	40	
total		1213

IMPACT ON ANIMALS

Intensive utilization of tropical forests is certain to have a significant impact on animal life, yet this important aspect of tropical forest ecology has been almost completely neglected. For example, Whitmore's (1975) chapter on animal life in rain forests of the Far East is only three pages long and his section on the effects of logging on rain-forest animals covers less than a page. He indicated that:

> "There has been no full study of the consequences of logging on the rain forest animals. It is of vital importance that such studies are initiated".

Part of the problem stems from the fact that the complex vegetation structure of humid tropical forests makes observations difficult; many species are arboreal and/or nocturnal. In addition, such studies are complicated by the great diversity of animal life found in tropical forests. To cite only a few examples: the Philippines has 620 species of rain forest birds (Rabor 1968a) and 242 species of land animals (Rabor 1968b), and 191 species of amphibians are found on Borneo (Inger 1966, cited by Whitmore 1975).

Just as the potentially useful properties of many of the plants of tropical forests are unknown, it is likely that the animals are a potentially useful resource as well. They certainly play important roles in pollination, dispersal, nutrient cycling, and checking of pest populations; they undoubtedly have a great untapped potential as biological control agents, food resources (domesticated and wild), and recreation (e.g, see Gomez-Pompa *et al.* 1972; Goodland & Irwin 1975; Tosi & Voertman 1975; Myers 1976, 1979). In addition to these direct benefits to humans there is the broad moral issue of the possible elimination of entire species through irresponsible human actions. Wadsworth (1975b) warns of the potential nonrenewability of some of the tropical forest animal resources:

> "Some of the cultural forest values are . . . nonrenewable. The major example is unmodified climax forest distinguished by the presence of centuries of natural development in the absence of man's influence . . . An intricate, web-like maze of symbiotic interrelationships among plants and animals, of which we are still in almost total ignorance, has apparently evolved with the long-term stability of the system. These systems, once destroyed or even substantially modified, are not replaceable within many human generations. This fact is particularly significant . . . to the animal life, which is dependent on the stability of the organisms on which it depends, as well as the physical environment itself".

Loss of habitat is clearly the greatest threat to tropical wildlife (e.g., see Rabor 1968b, Kingston 1971, Daugherty 1972, Geroudet 1973, Thiollay 1975), and much more of it results from agricultural expansion (frequently shifting cultivation followed by conversion to pasture) than from logging. Many animals, in fact, are tolerant of a certain amount of habitat disturbance; some — highly specialized mature ecosystem dwellers — however, are completely intolerant of any disturbance, while still others — the "weedy" colonists of the animal kingdom — thrive in successional vegetation. Forest utilization thus involves shifts in species composition and the limited available evidence is that the magnitude of the induced shifts is approximately proportional to the degree to which the habitat is disrupted through utilization.

Changes in Animal Populations After Forest Utilization

Most of the studies which describe the impact of forest utilization on wildlife have dealt with areas which have been selectively logged. Presumably animals on areas managed under any of the "uniform" silvicultural systems would be even more severely affected. Likewise, the magnitude of these effects is likely to increase if schemes permitting more intensive utilization become widely used. Even under selective cutting, about half the animals move out of the forest (e.g., Burgess 1971 cites Stevens' 1969 value of 48 percent). It is not clear what happens to the animals displaced as a result of forest cutting. Some species undoubtedly take temporary refuge in surrounding forests and reinvade their original habitat after cutting is completed, provided that the forest is not removed completely. If forest destruction covers large areas, however, the impacts are much more severe and the surrounding ecosystems probably cannot absorb immigrants other than on a very temporary basis. McClure & Othman (1965) studied bird populations in an area in West Malaysia where part of their study forest was unexpectedly destroyed; this gave them an opportunity to observe the impact of forest destruction on known populations. They concluded that:

> ". . . the destruction of the forest produces massive changes in the avifauna and . . . the remaining forest cannot and does not absorb the displaced species and individuals, first because it may not include niches favorable to them and secondly favorable niches may already be saturated. The displaced birds become wanderers to find a niche or die."

While some species suffer as a result of forest intervention, others benefit. In any case, the pre-logging population structure is inevitably modified, as documented, for example, for birds in Malaysia by Wells (1971). Struhsaker (1972) who worked with primates in Uganda found that:

> "Results . . . indicate that large-scale timber felling drastically upsets the primate species composition of the forest. The black and white colobus appear to benefit from this disturbance, being the most common monkey in felled areas and one of the least common in undisturbed forest. In contrast, the red colobus are adversely affected by timber felling, becoming uncommon in disturbed areas but being the most common monkey species in undisturbed forest. The sooty mangabey is rare in areas that have been felled on a large scale, although relatively common in adjacent and undisturbed forest. Areas in which non-commercial tree species were poisoned subsequent to large scale felling of commercial trees appear to support very few primates."

Disturbed forest and secondary vegetation probably support relatively large animal populations, even though the species composition is altered (Tables 28 & 29). Second-growth vegetation has high ***net*** productivity and secondary plant species are often prolific flower, fruit, and seed producers, many of which are important animal food sources. Harrison (1969), for example, found that mammal density was about equal in forests and in ruderal vegetation (Table 29), but that biomass and species richness were higher in the forests. He also reported (Harrison 1968 & Table 30) that commensal rats accounted for a large proportion of the species in deforested ecosystems, whereas groups such as primates and carnivores accounted for a relatively large fraction of the species in forests. Rabor (1958) also reported an increase in rats after logging in the Philippines and suggested that this might have been due, in part, to a decrease in the abundance of natural predators. Habitat and prey species population changes resulting from land clearing may be repsonsible for increases in the populations of predaceous birds such as white-tailed kites in El Salvador (Thurber 1973) and various raptors in the Ivory Coast (Thiollay 1975). Rabor (1968a) indicated that the optimum habitat for the endangered monkey-eating eagle of the Philippines consists of a mixture of mature forest and scattered clearings.

Table 28. Number of species of land mammals recorded from primary and disturbed forest in Malaysia. Primary forest observations based on 150 square miles of forest over ten years; disturbed forest observations based on 20 acres over one year. After Harrison (1968), Table I, p. 157.

Group of Mammals	Primary Forest	Disturbed Forest
Insectivora	5	1
Primates	10	4
Rodentia	34	14
Carnivora	16	6
Artiodactyla	7	5
Other mammals (F. Lemur, Pangolin, Elephant, Tapir)	4	2
Total	76	32

Table 29. Density and biomass of small mammals in various habitats in Malaysia. After Harrison (1969), Table 3, p. 177.

Vegetation Equivalent	primary forest	primary forest	secondary forest	scrub	grass
Area (ha)	17.5	12.8	4.8	10.0	6.7
Species	Numbers Present				
Tupaia glis	0	3	6	0	0
Callosciurus caniceps	0	0	1	2	0
C. notatus	10	7	8	0	0
C. nigrovittatus	1	0	0	0	0
Sundasciurus tenuis	4	0	0	0	0
Rhinosciurus laticaudatus	0	1	0	0	0
Rattus tiomanicus	0	0	16	17	12
R. argentiventer	1	0	0	2	1
R. exulans	1	0	0	6	23
R. muelleri	12	1	0	0	0
R. bowersii	1	0	0	0	0
R. whiteheadi	9	9	3	5	1
R. rajah	21	3	0	0	0
R. surifer	23	3	0	0	0
R. sabanus	2	25	0	0	0
Total	85	52	34	32	37
Density (Mammals/Hectare)	4.9	4.1	7.1	3.2	5.5
Biomass (Grams/Hectare)	840	730	810	282	324

Table 30. Numbers of species of mammals in various habitats in Malaysia. After Harrison (1968), Table III, p. 158.

	Disturbed Forest	Primary Forest	Secondary Forest	Scrub	Mixed Grassland and Scrub	*Imperata*
Forest Species: Trapped						
Primates (Treeshrew)	—	1	1	—	—	—
Rodents — Squirrels	3	2	2	1	—	—
Rodents — Rats	5	4	1	1	1	—
Forest Species — Estimated additional spp.						
Insectivores	1	1	—	—	—	—
Rodents, all	5	5	—	—	—	—
Primates	4	4	1	—	—	—
Carnivores	6	6	2	2	1	1
Artiodactyls	5	5	2	3	2	1
Other Mammals	2	2	1	1	—	—
Commensal Rats						
Trapped	2	—	1	3	3	—
Estimated	—	—	—	—	—	2
Total — Forest sp.	31	30	10	8	4	2
Commensal rats	2	0	1	3	3	2
All species.	33	30	11	11	7	4

The species composition of the fauna in a given region partially reflects the mosaic of disturbed and mature ecosystems found there. Prior to recent rapid human population growth, the faunas of most wet tropical regions were undoubtedly dominated by mature-ecosystem species. Working in a remote, recently colonized area of eastern Peru, Terborgh & Weske (1969) found that mature forest contained 141 species of birds, whereas the limited areas occupied by various kinds of modified vegetation contained only 54 species. Very few mature-forest bird species modify their behavior to adapt to second growth (Wells 1971). Mammals may be somewhat more plastic in their behavior, but most species which evolved in mature ecosystems tend to be at least partially restricted to undisturbed habitats. In the case of the 115 species of ground-dwelling Malaysian mammals, for example, 53 percent are confined to primary forest, 25 percent live in primary and tall secondary forest, 12 percent live in primary or secondary forest and can also live in cultivated areas, and 10 percent are restricted to cultivated or urban areas; most of the latter 22 percent are pests (Stevens 1968a, cited by Whitmore 1975).

Arboreal primates are an important, conspicuous group which might be greatly affected by intensive forest utilization. According to Stevens (1968a, cited by Whitmore 1975) 37 percent of the non-flying mammals in Malaysia are tree dwellers, a large fraction of which are primates. An important field study directed at assessment of the influence of logging on animal life in Kalimantan was conducted by C. Wilson and W. Wilson of the University of Washington's Regional Primate Research Center. Their study was concerned mainly with primates, but they also observed other mammals plus birds. Preliminary findings (see Tables 31-33) have been published in C. Wilson & W. Wilson (1975) and W. Wilson & C. Wilson (1978). Among their findings are the following (C. Wilson & W. Wilson 1975):

Table 31. Estimated primate density in various habitats in East Kalimantan. After C. Wilson & W. Wilson (1975), Table V, p. 259.

Habitat	km² surveyed	Number of species included in density calc.	Number of groups/km²	Number of individuals/km²
Primary lowland (ITCI)	0.54	3	11	53
Selectively logged, 8 trees/ha	0.54	3	10	39
Undisturbed and disturbed primary lowland and secondary scrub	0.37	3	7	55
Primary lowland (Kutai)	3.0	5	10	51

Table 32. Birds and squirrels noted in three habitats in East Kalimantan. Values are mean number recorded per day for 2 days (3 in primary forest). After C. Wilson & W. Wilson (1975), Table VI, p. 261.

Species	Primary	Logged	Kutai (mixed habitat)
Argus pheasant	12.7	12.0	0.5
Helmeted hornbill	6.0	3.0	1.0
Rhinoceros hornbill	6.3	6.0	0.0
Other hornbills	6.0	9.0	13.5
Common giant squirrel	5.0	3.5	6.0
Other squirrels	3.0	1.0	2.5
Total	39.0	34.5	23.5

Table 33. Habitat preferences of Sumatran primates. After W. Wilson & C. Wilson (1978), Table 3, p. 141.

Habitat	Presbytis cristata	P. melalophos	P. femoralis	P. thomasi	Macaca fascicularis	M. nemestrina	Symphalangus syndactylus	Hylobates agilis	H. lar	Pongo pygmaeus	total species per habitat
Within village	x	x			x						3
Swamp:											
Rhizophora mangrove	x				x						2
Mixed mangrove	x		x		x						3
Primary freshwater			x		x			x			3
— riverbank	x		x		x						3
— logged	x				x		x				3
Secondary forest	x	x			x						3
— riverbank	x		x		x						3
— scrub, grassland	x										1
— riverbank	x				x						2
Lowland: (0-1500 feet)											
Primary forest	x	x	x	x	x	x	x	x	x	x	10
— riverbank	x	x			x		x				4
— logged	x	x	x	x	x	x	x	x	x		9
Secondary forest	x	x	x	x	x	x	x				7
— riverbank	x		x		x	x					4
— rubber grove	x	x	x	x	x						5
— scrub, grassland	x	x			x	x					4
— riverbank	x		x		x						3
Hill: (1500-3000 feet)											
Primary forest	x	x			x	x	x	x			6
— logged		x									1
Secondary forest	x	x			x	x	x	x			6
— rubber grove		x			x						2
— scrub, grassland	x	x			x	x					4
Submontane: (3000-5000 ft)											
Primary forest		x					x	x			3
Secondary forest		x			x						2
Total (25 habitats)	20	15	10	4	22	8	8	6	2	1	

> "On the species level . . . there is great variability of response and success of adaptability among primates. Birds and squirrels seem to be the most disrupted by habitat disturbance from selective logging. While some of the other mammals are directly harmed by selective logging, others are only endangered by the hunting and slash and burn farming that can follow the opening up of the forest. Many species, then, can exist in forest that have been selectively logged at the relatively low intensity of 8 trees/ha and perhaps as high as 12 trees/ha when efforts are made to minimize the destruction of other trees during extraction."

Many of the problems encountered by arboreal primates after logging involve disruption of their aerial pathways. Many species will not descend to the ground except under emergency situations, so opening of the forest canopy excludes them from habitat which might otherwise have all of the resources necessary for their support. Extensive clearcutting, of course, eliminates all arboreal mammals, but second-growth vegetation supports various species, although different ones than those characteristic of mature forest (e.g., see Table 33). Some endangered species, such as the orangutan and the proboscis monkey of Southeast Asia, are found only in undisturbed forest.

In addition to the aerial pathways required by arboreal primates, many other animals found in tropical forests have specific requirements which are incompatible with most intensive forest management. For example, hornbills of Southeast Asia require large "overmature" trees for nesting sites (McClure 1968) and the endangered Puerto Rican parrot nests only in large, hollow specimens of a single tree species (Wadsworth 1975a). Other species are specialized with regard to their nesting and feeding habits, and intensive forest management might affect them adversely.

Besides conspicuous wildlife such as mammals and birds, forest utilization affects other groups of animals such as amphibians, reptiles, and fish. Sometimes the effects of forest utilization are not intuitively obvious (except in hindsight!) and impacts at first go unnoticed. The food chains in most tropical forest streams, for example, are detrital, being driven by the inputs of organic litter that falls and washes into the water from the forest canopy (Goodland & Irwin 1975). Removal of streamside vegetation removes this energy source and changes water temperature and turbidity. Due to such changes only 35 of 54 indigenous fish species are still found in Singapore and concern has been expressed regarding similar losses in West Malaysia (Alfred 1968).

Animal Reserve Requirements

There is no doubt that extensive areas of natural, unmanaged forest will have to be set aside if the rich tropical fauna is to be preserved. Although such preserve maintenance is not normally thought of as an absolute requirement of forest utilization, there is considerable precedent for such involvement in both public and private forestry in developed temperate zone countries. Such conservation activities would seem to be especially important in the case of multinational corporations which frequently use the developing tropical nations as a raw material source, to be processed into final products in places other than the country of origin. They should be prepared to meet their obligation to preserve a portion of the natural ecosystems that feed them. This need for forest reserves has been expressed many times and is becoming more and more widely addressed each year. Typical of the comments are those of Medway & Wells (1971), who worked in West Malaysia:

> "Among both birds and mammals, the great majority of species recorded are dependent for their survival on the continued presence of undisturbed forest. Such diverse animal communities have not evolved and cannot exist in the much less complex environments of cleared land, plantation, or secondary growth of the type that develops after the tropical forest has been felled."

One of the main problems associated with the establishment and maintenance of such preserves is the large areas of land required. The habitat requirements of many tropical birds and mammals are quite large. The orangutan, for example, requires an average of 1.5 square miles (3.8 km²) of forest per individual (Harrisson 1968). Large carnivores, including forest cats, and grazers and browsers, such as elephants, gaur, and tapirs, undoubtedly require large tracts also. Furthermore, agriculture and forest clearings act as geographic barriers to many tropical forest-dwelling animals, so the forested preserves must, to be effective, consist of large, unbroken tracts. Medway & Wells (1971) estimated the amount of land required to sustain population sizes of 500 individuals (an estimated lower limit of population size to maintain most vertebrates) of eleven species of birds and mammals in Malaysia (Table 34). They found that the area required to maintain such populations ranged from about 250 km² to 10000 km², depending on the species involved. Leck (1979) documented bird extinctions from a small (87 ha) national park in Ecuador, confirming the need for larger refuges.

Table 34 Area needed to support 5000 individuals of various species of birds and mammals in Malaysia. After Medway & Wells (1971), Table 3, p. 247.

Species	Number supported per 2 km²	Estimated area needed to support 5000 individuals (km²)
Helmeted Hornbill	1	10000
Rhinoceros Hornbill	c.1	10000
Southern Pied Hornbill	2	5000
Black Hornbill	4	2500
Bushy-crested Hornbill	5	2000
Banded Leaf Monkey	40	250
Dusky Leaf Monkey	20	500
Long-tailed Macaque	22	500
Pig-tailed Macaque	3	3333
White-handed Gibbon	6	1667
Siamang	5	2000

To assume that developing tropical nations will be willing and able to set aside, protect, and maintain extensive reserves without outside assistance is probably unrealistic. Increased intensity of forest management which could result in greater productivity from less land, coupled with social consciousness and action on the part of public and private forestry agencies, should make possible the preservation of adequate tracts of natural forest in most tropical areas, provided that such steps are taken in the very near future.

RESEARCH NEEDS

The data needed to properly assess the potential ecological impact of more intensive utilization of humid tropical forests do not exist. This gap has become increasingly evident in recent years as the rate of tropical forest harvesting and destruction continues to increase alarmingly. We have little prior experience to guide us in predicting the impact of the changes currently taking place, and the problem may be all the more acute because biological processes are often much more rapid in the wet, lowland tropics than in temperate forests. Just as this rapidity of biological processes gives reason for great concern and indicates that we must act quickly, it also acts as a blessing of sorts. Rapid biological processes such as regrowth, colonization, and organic matter and mineral cycles enable scientists to get answers in less time than might be the case in areas with a restricted growing season.

Some of the data gaps may soon be filled by individual on-going research projects as well as by the tropical programs of the International Biological Program (but IBP tropical field research never amounted to more than a very minor portion of the entire IBP program). Several international groups have met in recent years to discuss tropical ecology problems, with special emphasis on the impact of increased human activities in the humid tropics. These have included various expert panel and directorate meetings of the UNESCO Man and the Biosphere (MAB) program (e.g., see UNESCO 1972); the International Union for the Conservation of Nature (IUCN), which has held meetings in the Asian, African, and American tropics; The Institute of Ecology (TIE), which held a meeting to describe research needs in the American tropics (see Farnworth & Golley 1974); and BIOTROP, which sponsored a symposium on long-term impacts of logging (Suparto *et al.* 1978). These international meetings have succeeded in their tasks of identifying needs, data gaps, potential problems and research priorities. With the perspective of these expert evaluations now available, perhaps it is time to move ecosystem-level tropical research out of the conference room and into the field for the crucial data gathering phase.

Examples

Several research needs became evident during our literature survey. These include major areas of tropical ecology that have been completely unstudied and will require years of detailed research to resolve. Also included, however, are needs which might be satisfied by small-scale studies aimed at gathering at least some data where we now have none. Such short-term pilot studies will not provide the final answers, but will at least give some indication of how to handle potential problems. Listed below (in no particular order of priority) are ten research needs that became evident during our review of the literature. The list is not intended to be all-inclusive, but does include representatives of the kinds of studies needed. It includes both long-term needs, which will only be met by interdisciplinary research teams, as well as a few examples of areas where significant progress might be met by short-term field research. There is considerable overlap among the listed research needs, but perhaps this serves to emphasize once again the interrelatedness of all the parts — physical and biological — of complex ecosystems such as humid tropical forests.

1. The relative ecological consequences of different *sizes of forest management units,* including evaluation of effects on rate and composition of plant recolonization, animal population changes, and watershed management implications.
2. The comparative ecological impacts and net-energy costs and returns of *low intensity silviculture* of natural, multi-species regrowth *and artificial forest* regeneration. This should include evaluation of the potential impact of conversion to forests dominated by exotic tree species.
3. The implications of both loss of *genetic stock* as well as *genetic erosion* on the humid tropical ecosystems which might result from intensive management.
4. Evaluation of the population dynamics of potential *pest species,* including those which might respond to changes in forest age, structure, and species composition.
5. Total-system *nutrient budgets,* including estimates of weathering and rainfall input rates, as well as leaching, runoff, and biomass-removal loss rates.
6. Evaluation of the effects of forest management practices on *soil physical, chemical*, and *biological properties,* including impacts on soil micro-organisms involved in nitrogen cycling, soil structure, and tree nutrition (i.e., myorrhizal fungi).
7. *Land suitability classification* designed specifically to meet the needs of tropical countries. Perfection and application of a useful scheme would eliminate many of the ecological problems resulting from land competition among agriculturists, pastoralists, and foresters.
8. Determination of the effects of *repeated forest harvesting* on site quality, including nutrient stocks and rates of replenishment.
9. The relationship between forest management practices and *water quality,* including chemistry, turbidity, and temperature, *and water yield,* including impacts on the total amount, seasonal distribution, and rate of return to the initial condition.
10. Evaluation of potential *impacts on animals,* including determination of their habitat requirements, both in terms of size and quality.

Most of the kinds of research suggested above will be both time consuming and costly. To ignore the need, however, could result in permanent damage to one of the world's largest, most productive, and most complex life-support systems, one whose potential benefits to society are almost completely untapped.

A Suggested Starting Point

Research on possible ecological consequences of humid tropical forest utilization will undoubtedly move ahead on many fronts: individual research projects, scattered country-wide team efforts, synthesis through conferences and seminars, literature surveys, and site-specific studies conducted by both public and private agencies. However, if the past is any indication of the rate of expected progress, then we can expect the results to be pieced together slowly. Many studies require long periods of field research and most developing tropical nations do not have the time nor the resources to carry out the needed research. One alternative might be to sit back and let tropical ecological research proceed at the snail's pace which has characterized it in the past. Another, perhaps more attractive, alternative might be to attempt to speed things up and at least come up with some tentative results before it is too late to correct our mistakes. To delay might mean that the humid tropical forests, which may be the key renewable resource for maintaining and improving the quality of life in developing tropical countries, will be irreparably destroyed before we learn how to wisely utilize them.

Rapid progress might be made for some (but certainly not all) research needs by a four-phase procedure. First, identify a problem and gather the existing available information on that problem from the literature. Second, produce a conceptual model which places the particular problem in the context of the whole ecosystem and which shows all storages and linkages which are thought to affect the component or process of concern. Third, put values on the storages and flows in the model, using available literature, supplementary field measurements, and estimates based on knowledge of other ecosystems. Finally, simulation of such a model can lead to insight about how a system might be expected to react in response to a given management practice. It provides a means of rapidly exploring the potential impacts of actions which might otherwise require years of field monitoring. In research of this sort the development and simulation of the model provide keys and insights into determining the kinds of field data which are absolutely essential. Likewise, the field research serves to guide the development and perfection of the simulation model. Thus, the two processes, field research and modeling, go hand-in-hand; both are essential and, if properly carried out, can lead to more rapid progress than would be possible through the use of either one alone.

CONCLUSIONS

Technological advances which permit the utilization of a greater suite of species from tropical forests constitute a powerful tool for resource managers. Most importantly, such advances should greatly increase the number of ecologically sound options open to silviculturists and should permit the development of techniques which would not have been possible previously, when relatively few species could be utilized. Like many potent technological advances, however, the ability to use any tree in the forest could result in ecological disaster if abused. It must be developed only as a means of improving our ability to manage tropical forests as a renewable resource, not as a technique that would enable exploiters to mine all of the wood from the humid tropics, leaving an ecologically devastated landscape in their wake.

One management practice which certainly warrants testing in the field would be harvesting all stems of merchantable size from narrow bands, then following up with (preferably) natural and/or artificial regeneration. Most selective logging schemes leave more of the forest intact, but a great deal of loss occurs because of felling and extraction. This is even more true in the tropics than in temperate forests because of the large size of the tree crowns and the presence of lianas. If harvested strips were kept very narrow (say, 100 meters) many of the possible disadvantages of forest clearcutting would be avoided. Animals would still have access to a large forest habitat (albeit pocked with strips in different stages of regrowth), recolonization of plants from the surrounding forest would be enhanced, impacts on water yields and quality would be minimized, and soil microorganism populations would probably be quickly reestablished after logging. The major objections to harvesting in narrow strips are likely to be economic and engineering. It is evident, however, that most of the damage from current methods of harvesting is due to improper felling, skidding, and hauling. If we are serious about managing tropical forests as renewable resources then current practices will have to change anyway, and narrow clear-cut strips may be a good place to start.

Possible Benefits

There are many possible benefits that might be derived from an increase in our ability to utilize a broader range of tropical woods. A few examples are listed below.

1. ***Wood needs can be met from less land,*** leaving more land for the undisturbed preserves necessary for the survival of many plants and animals.
2. It will permit the maintenance of a forest ***mosaic***, consisting of a diverse mixture ***of high-net-productivity*** ecosystems. Just as within-ecosystem diversity is a desirable attribute in many respects, among-ecosystem diversity is a landscape feature which permits most species to survive, while prohibiting dominance by a few.
3. The prospects for successfully ***combining food production*** with ***forestry*** would be enhanced if it were possible to more fully utilize the species present. If all species were harvested it might be possible to follow up with a brief cycle of crop production prior to forest regeneration. Under most current land use schemes shifting agriculture is incompatible with forestry, and incomplete forest harvesting means that the land is unsuitable for any other than the most destructive kinds of short-term agricultural use. There is considerable precedent for such combined (agricultural and forestry) land use in the tropics with the taungya regeneration scheme, but this is most often used only as a means of artificially regenerating forest land and not as a means of permanently combining food and fiber production.
4. ***Wastage of wood will be reduced*** by permitting utilization of material damaged in logging and those species which currently are often girdled and/or poisoned because they cannot be used.
5. It will be possible to ***regenerate*** and manage ***the whole forest ecosystem,*** including most of its component species. Under current forest management practices, in which relatively few species are utilized, the forest is continually degraded. Sometimes desirable species decrease in abundance because they are selectively harvested. Other times undesirable species decrease because they are selected against in management practices such as post-harvest timber stand improvement. The ability to use all species should make it possible for foresters to perpetuate the entire forest complex, without preferentially eliminating any particular group of species except those which require vast, undisturbed tracts of mature forest for their survival and regeneration.

Potential Problems

In addition to the positive results likely to be realized by an increase in our ability to use run-of-the-woods tropical species mixes, there are several problem areas that should receive attention before such utilization becomes widely practiced. Many of the potential environmental problems were discussed in previous sections and some of these are repeated in the brief list which follows. This list is neither detailed nor all-inclusive. Rather, it suggests broad areas where problems might be anticipated and which require careful consideration before the new technology is implemented.

1. *Nutrient depletion* may result if large amounts of wood are removed. Solution of this possible problem may require special practices such as debarking at the site of felling and perhaps even forest fertilization.
2. Some *species may be lost* entirely *and* the *populations* of others might be drastically *upset* if increased utilization intensity is practiced. Population imbalances can easily lead to intolerable levels of pest buildups and impacts on species otherwise thought to be relatively unaffected by the management practices. To maintain populations of all tropical species will require a network of large tracts of undisturbed ecosystems and foresters will have to work closely with conservationists in establishing and maintaining these preserves.
3. *Water resources,* including water yield and water quality, are closely linked to land use, and watershed management practices are sure to have an effect downstream. There is no reason to believe that forest management and maintenance of water resources are incompatible (forestry is, in fact, probably the best form of land use from the point-of-view of watershed management), yet there is little precedence for such considerations in the tropics. The solutions to potential water problems are probably currently available; implementation, however, is lacking.
4. *Soil microorganisms,* which play a crucial role in the physical-chemical properties of tropical soils, are likely to be affected by intensive forest management. Their recolonization rates and the impact of their loss are unknown, but they are certain to be important in the long-term maintenance of forest site quality.
5. The *quality of the second-growth forest,* and its suitability for both economic use and as a habitat capable of maintaining the diversity of tropical life is an important unknown. In the worst possible case, the regrowth may be an unusable tangle of weedy species, in which case the increased utilization capabilities will have amounted to nothing more than a hastening of our mining of the tropical forests. There is no hard evidence that this might be the case, but it is a possibility which should be considered before increased utilization intensity is introduced on the ground.

An Epilogue

Increased intensity of tropical forest utilization is really concerned with two different resources. The first of these is the existing mature forests and all of the species found there. Many of these have highdensity wood; they reproduce in mature ecosystems and are unlikely to reappear outside of forest preserves under any sort of forest management program. Currently, many of these species are unusable and are destroyed during or after logging. Improved wood utilization technology will immediately avoid much of this waste.

The second resource of concern is the secondary forests which will be available for utilization after the primary forest has been harvested. What will the nature of this resource be? Should it be a natural species mix or should we strive for more uniform stands, perhaps with the aid of artificial regeneration? Will it be compatible with the long-term maintenance of site quality? Is it, in fact, a high quality renewable resource which can be managed for permanent yield? Tropical foresters have long debated and studied such questions, but the utilization technology required to put them to the test has not previously been readily available. Along with the potential for increasing our ability to utilize available species mixtures we should simultaneously be concerned with the nature of the forest resource that will be with us in the future.

Sometimes local socio-economic situations can upset the best-laid forest management plans, and these are often completely out of the control of land managers. The recent wars in Southeast Asia, for example, resulted in massive human migrations into previously forested areas, so this land, much of it reportedly unsuitable for premanent crop production, represents a lost renewable forest resource. Likewise, the tropical literature is crammed with example after example of the inroads of sifting cultivators into primary forest or once-logged land unsuitable for agriculture. As an example of the sort of problem more likely to be with us over large areas in the near future, Dr. J. A. Tosi of the Tropical Science Center in Costa Rica (pers. com.) describes a situation in the Atrato Valley of Colombia, one of the wettest lowland tropical environments in the world. There, a company has been building roads and logging most species from the mature forest. The first wave of regrowth was vigorous and of desirable quality, and it was the company's intention to use this as their second-cut. Local inhabitants, however, have been harvesting all the pole-sized second-growth trees for sale as fence posts and mine props outside the Atrato Valley, and the quality of the regrowth has been seriously degraded. The resulting site capture by unusable weeds is rapidly converting what might have been a usable and renewable second-growth forest into a wasteland.

An important legacy of the past fifteen years of rising ecological concern has been the hard-learned lesson that landscapes consist of well-organized systems, each consisting of interdependent parts and each linked to their neighbors. Tropical forest management must, above all, be entered into with a holistic viewpoint. The forest *is* the renewable resource, it *is* the downstream watershed, it *is* the natural preserve next door, and it *is* the socio-economic well-being of the people dependent upon it.

BIBLIOGRAPHY

Agaloos, B. C. 1963. The value of cut-over forests in the Philippines. Forestry Leaves 14: 1—6.

Alfred, E. R. 1968. Rare and endangered fresh-water fishes of Malaya and Singapore. *In:* Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 325—331.

Anderson, A. 1972. Devastation on the Amazon? Organic Gardening and Farming. Nov. 1972: 90—93.

Antonini, G. A., K. C. Ewel, and J. J. Ewel. 1974. Ecological modeling of a tropical watershed: A guide to regional planning: *In:* Spatial Aspects of Development. B. S. Hoyle (ed.). John Wiley & Sons, London, pp. 51—74.

Antonini, G. A., K. C. Ewel, and H. M. Tupper. 1975. Population and Energy: A Systems Analysis of Resource Utilization in the Dominican Republic. University of Florida, Gainesville. Center for Latin American Studies. Latin American Monographs, 2d ser., 14, 166 p.

Ashton, P. S. 1964. Ecological studies in the mixed Dipterocarp forests of Brunei State. Oxford For. Mem. 25. 75 p.

Asiddao, F. 1950. Natural versus artificial reproduction of Dipterocarp species. Phil. Jour. For. 7: 63 — 79.

Aubert de la Rüe, E. 1958. Man's influence on tropical vegetation. Proceedings of the 9th Pacific Science Congress 20: 81—94.

Auchter, R. J. 1976. Raw material supply. Future Technical Needs and Trends in the Paper Industry - II. Tappi Annual Meeting, 1976. Committee Assignment Report (CAR) No. 64. pp. 19—32.

Baur, G. N. 1968. The Ecological Basis of Rainforest Management. Blight, Government Printer, New South Wales. 499 p.

Beehler, B. 1978. Historical changes in the avifauna of the Wau Valley, Papua New Guinea. Emu 78: 61—64.

Bell, G. S. 1976. Notes on natural regeneration in Dominica, Windward Islands. Commonw. For. Rev. 55: 27—36.

Blanche, C. A. 1975. An overview of the effects and implications of the Philippine selective logging on the forest ecosystem. *In:* R. S. Suparto, *et al.* (eds.), Symposium on the long-term effects of logging in Southeast Asia. BIOTROP. Bogor, Indonesia.

Brams, E. A. 1971. Continuous cultivation of West African soils: Organic matter diminution and effects of applied lime and phosphorus. Plant and Soil 35: 401—414.

Brams, E. 1973. Soil organic matter and phosphorus relationships under tropical forests. Plant and Soil 39: 465—468.

Brinkmann, W. L. F. 1972. Weekly water-loss from spherical water-loss integrators on a clearing and below secondary growth in Central Amazonia. Acta Amazonica 2: 33—36.

Brinkmann, W. L. F., and M. N. Góes Ribeiro. 1971. Air temperatures in Central Amazonia. II. - The effects of near-surface temperatures on land-use in the Tertiary region of Central Amazonia. Acta Amazonica 1: 27—32.

Brinkmann, W. L. F., and M. N. Góes Ribeiro. 1972. Air temperatures in Central Amazonia. III. - Vertical temperature distribution on a clearcut area and in a secondary forest near Manaus (cold front conditions July 10th, 1969). Acta Amazonica 2: 25—29.

Brinkmann, W. L. F., and J. C. Nascimento. 1973. The effect of slash and burn agriculture on plant nutrients in the Tertiary region of Central Amazonia. Acta Amazonica 3: 55—61.

Brown, G. S. 1955. Timber extraction methods in N. Borneo. Malayan Forester 18: 121—132.

Brown, W. H., and D. M. Mathews. 1914. Philippine Dipterocarp forests. Philippine Journal of Science 9A: 413—561.

Budowski, G. 1956a. Regeneration systems in tropical American lowlands. Caribbean Forester 17: 76—91.

Budowski, G. 1956b. Tropical savannas, a sequence of forest felling and repeated burnings. Turrialba 6: 22—33.

Budowski, G. 1963. Forest succession in tropical lowlands. Turrialba 13: 42—44.

Budowski, G. 1965. Distribution of tropical American rain forest species in the light of successional processes. Turrialba 15: 40—42.

Budowski, G. 1968. Protection and management of natural areas in Latin American - implications for South East Asia. *In:* Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 395—400.

Budowski, G. 1970. The distinction between old secondary and climax species in tropical Central American lowland forests. Trop. Ecol. 11: 44—48.

Burgess, P. F. 1971. The effect of logging on hill Dipterocarp forests. Malayan Nat. J. 24: 231—237.

Cater, J. C. 1939. Deforestation and soil erosion in Trinidad. Tropical Agriculture 16: 230—232.

Chew, W. L. 1968. Conservation of habitats. *In:* Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 337—339.

Chudnoff, M. 1973. Development of the tropical wood resource. Office of Science and Technology. Agency for International Development. Washington, D.C. 72 p.

Chudnoff, M n.d An any-tree harvest for industrial processing in the humid tropics. Unpub. m.s. 10 p.

Clayton, W. D. 1958. Secondary vegetation and the transition to savanna near Ibadan, Nigeria. J. Ecol. 46: 217—238.

Cliff, E. P. 1973. Utilization of tropical forests (a review of the forestry literature in the Agency for International Development Reference Center). U.S. Office of Science and Technology. Agency for International Development. Washington, D.C. 26 p.

Conference on Improved Utilization of Tropical Forests, Proceedings. 1978. U.S. Department of Agriculture, Forest Service, Forest Products Laboratory. 569 pp.

Conklin, H. C. 1957. Hanunóo Agriculture. FAO Forest. Develop. Paper Number 12, 209 p.

Cook, O. F. 1909. Vegetation affected by agriculture in Central America. USDA. Bureau of Plant Industry, Bull. 145, 30 p.

Cook, O. F. 1919. Milpa agriculture, a primitive tropical system. Smithsonian Inst. Washington, Annual Report: 307—326.

Cooper, J. I., and T. W. Tinsley. 1978. Some epidemiological consequences of drastic ecosystem changes accompanying exploitation of tropical rain forest. Terre Vie 32: 221—240.

Corvanich, A. and S. Boonkird. 1978. The effect of logging on the environment in Thailand. *In:* R. S. Suparto *et al.* (eds.) Symposium on the long-term effects of logging in Southeast Asia. BIOTROP. Bogor, Indonesia.

Coulter, J. K. 1950. Organic matter in Malayan soils. A preliminary study of the organic matter content in soils under virgin jungle, forest plantations and abandoned cultivated land. Malayan Forester 13: 189—202.

Croat, T. B. 1972. The role of overpopulation and agricultural methods in the destruction of tropical ecosystems. Bioscience 22: 465—467.

Cunningham, R. K. 1963. The effect of clearing a tropical forest soil. J. Soil Science 14: 334—345.

Daugherty, H. E. 1972. The impact of man on the zoogeography of El Salvador. Biological Conservation 4: 273—278.

Davis, T. A. W., and P. W. Richards. 1933—34. The vegetation of Moraballi Creek, British Guiana. J. Ecol. 21: 350—84 Part I and 22: 106—55 Part II.

Dawkins, H. C. 1964. Productivity of tropical forests and their ultimate value to man. *In:* Proc. and Papers of IUCN 9th Tech. Meeting, Nairobi; IUCN Publ. new ser. No. 4, 1964. The Ecology of Man in the Tropical Environment. pp. 178—182.

De las Salas, G., and H. Fölster. 1976. Bioelement loss on clearing a tropical rain forest. Turrialba 26: 179—186.

Derham, P. 1970. [Nitrogen in some forests, savannas, and cultivated grounds in humid tropical Africa (Ivory Coast). Veroff. Geobot. Inst. Ruebel Zurich 45: 1—124.

Dohrenwend, R. E. 1972. The energetic role of the trade wind inversion in a tropical subalpine ecosystem. Ph.D. dissertation. SUNY College of Forestry at Syracuse University. 298 p.

Dohrenwend, R. E. 1979. Hydrologic behavior at the top of a tropical mountain. Ford Forestry Center Research Note 29, Michigan Tech. Univ., L'Anse, Michigan. 14 p.

Dommergues, Y. 1952. Influence du défrichment de forêt suivi d'incendie sur l'activité biologique du sol. Mém. de l'Institut Scientifique de Madagascar. Sér. D, 4: 273—296.

Dommergues, Y. 1953. Role de la couverture du sol dans le maintien et l'accroissement de son activite' biologique. Mém. Inst. Sci. Madagascar. D, 5: 299—313.

Dommergues, Y. 1954. Modifications de l'équilibre biologique des sols forestiers. Mém. Inst. Sci. Madagascar. D, 6: 115—148.

Donis, C. A. 1965. Shifting Agriculture (SHAG). *In:* Proceedings of the Duke University Tropical Forestry Symposium. Bulletin 18. pp. 30—46.

Echenique-Manrique, R. 1976. Is wood the only material we should obtain from tropical forest? Discussion Paper, XVI IUFRO World Congress, Oslo, Norway, June 20—July 2, 1976. Division V. Congress Group 5, Properties and Utilization of Tropical Wood.

Ewel, J. 1971. Biomass changes in early tropical succession. Turrialba 21: 110—112.

Ewel, J. 1976. Litter fall and leaf decomposition in a tropical forest succession in eastern Guatemala. J. Ecol. 64: 293—308.

Ewel, J., C. Berish, B. Brown, N. Price, and J. Raich. (In Press) Slash and burn impacts on a Costa Rican wet forest site. Ecology.

Farnworth, E. G., and F. B. Golley (eds.). 1973. Fragile Ecosystems. Evaluation of Research and Applications in the Neotropics. Springer Verlag, New York, 258 p.

Fedorov, A. A. 1966. The structure of the tropical rain forest and speciation in the humid tropics. J. Ecol. 54: 1—11.

Fosberg, F. R. 1958. On the possibility of a rational general classification of humid tropical vegetation. *In:* Proceedings of the Symposium on Humid Tropics Vegetation, Tjiawi, Indonesia. pp. 34—59.

Fox, G. D. 1972. Forestry in developing countries. Potentials, constraints, and opportunities. (Preliminary Survey). Office of Science and Technology. Agency for International Development. Washington, D.C. 74 p.

Fox, G. D. 1973. Technological opportunities for tropical forestry development. Office of Science and Technology. Agency for International Development. Washington, D.C. 31 p.

Fox, J. E. D. 1967. Selective logging in the Philippine Dipterocarp forest. Malayan Forester 30: 182 — 190.

Fox, J. E. D. 1968a. Application of ecological research on silviculture in the lowland Dipterocarp forests of Sabah. Proc. Symp. Recent Adv. Tropical Ecology. Forest Department, Sandakan, Sabah, Malaysia. pp. 710—720.

Fox, J. E. D. 1968b. Defect, damage and wastage. Malayan Forester 31: 157—164.

Fox, J. E. D. 1968c. *Didelotia idae* in the Gola Forest, Sierra Leone. Economic Botany 22: 338—346.

Fox, J. E. D. 1968d. The historical plot approach to silviculture. Sabah Society Journal 3: 182—189.

Fox, J. E. D. 1968e. Logging damage and the influence of climber cutting prior to logging in the lowland Dipterocarp forest of Sabah. Malayan Forester 31: 326—347.

Fox, J. E. D. 1968f. The soil damage factor in present day logging in Sabah. Proc. of the 3rd Malayan Soils Conference: 206—214.

Fox, J. E. D. 1969. Production in regenerating forest. *In:* Natural Resources in Malaysia and Singapore. Proceedings of the Second Symposium on Scientific and Technological Research in Malaysia and Singapore (1967). B. C. Stone (ed.), Univ. of Malaya, Kuala Lumpur. pp. 32—41.

Fox, J. E. D. 1970a. Natural regeneration of the Kambui Hills forest in Eastern Sierra Leone. Part I. Ecological status of the *Lophira/Heritiera* rain forest. Trop. Ecol. 11: 169—185.

Fox, J. E. D. 1970b. Yield plots regenerating forests. Malayan Forester 33: 7—41.

Fox, J. E. D. 1971. Second cut in lowland Dipterocarp forest. Malayan Forester 34: 167—181.

Fox, J. E. D. 1972a. Effects de l'utilization accrue de la forêt naturelle sur le succès de la régénération naturelle à Sabah. Bois For. Trop. 141: 3—27.

Fox, J. E. D. 1972b. The natural vegetation of Sabah and natural regeneration of the dipterocarp forests. Ph.D. Thesis, University of Wales. 361 p.

Fox, J. E. D. 1976. Environmental constraints on the natural regeneration of tropical moist forest. Forest Ecol. Manage. 1: 37—65.

Freas, A. D., M. Chudnoff, R. C. Koeppen, and S. B. Hutchison. 1973. Factors influencing the utilization of tropical wood species. Office of Science and Technology. Agency for International Development. Washington, D.C. 32 p.

Freise, F. W. 1934. Beobachtungen über den Verbleib von Niederschlägen im Urwald und den Einfluss von-Waldbestand auf den Wasserhaushalt der Umgebung. Forstwissentschaftliches Centralblatt 56: 231—245.

Geroudet, P. 1973. (The aye-aye of Madagascar must not become extinct.) Fauna (Oslo) 26: 24—25.

Gilmour, D. A. 1971. The effects of logging on streamflow and sedimentation in a North Queensland rainforest catchment. Commonw. For. Rev. 50: 38—48.

Golley, F. B., J. T. McGinnis, R. G. Clements, G. I. Child, and M. J. Duever (with J. Duke, J. Ewel and C. Gist). 1975. Mineral Cycling in a Tropical Moist Forest Ecosystem. University of Georgia Press, Athens. 248 p.

Gómez-Pompa, A., C. Vázquez-Yanes, and S. Guevara. 1972. The tropical rain forest: a nonrenewable resource. Science 177: 762—765.

Goodland, R. J. A., and H. S. Irwin. 1975. Amazon Jungle: Green Hell to Red Desert? Elsevier Sci. Pub. Co., Amsterdam. Reprinted from: Landscape Planning 1: 123—254.

Grant, J. S. 1957. Forests and stream flow. Malayan Forester 20: 122—125.

Greenland, D. J. and J. M. L. Kowal. 1960. Nutrient content of the moist tropical forest of Ghana. Plant and Soil 12: 154—174.

Greenland, D. J. and R. Lal. (eds.) 1977. Soil Conservation & Management in the Humid Tropics. John Wiley & Sons, N.Y. 283 p.

Greenland, D. J. and P. H. Nye. 1959. Increases in the carbon and nitrogen contents of tropical soils under natural fallows. J. Soil Sci. 10: 284—299.

Gülcur, M. Y. 1968. Renewable natural resources and their problems in the Philippines. *In:* Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 93 — 99.

Harcombe, P. A. 1973. Nutrient cycling in secondary plant succession in a humid tropical forest region (Turrialba, Costa Rica). Ph.D. Dissertation, Yale University. 131 p.

Harcombe, P. A. 1977a. The influence of fertilization on some aspects of succession in a humid tropical forest. Ecology 58: 1375 — 1383.

Harcombe, P. A. 1977b. Nutrient accumulation by vegetation during the first year of recovery of a tropical forest ecosystem. pp. 347—378 *In:* J. Cairns *et al.*, (eds.). Recovery and Restoration of Damaged Ecosystems. University of Virginia Press, Charlottesville, Va.

Harrison, J. L. 1968. The effect of forest clearance on small mammals. *In:* Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 153—158.

Harrison, J. L. 1969. The abundance and population density of mammals in Malayan lowland forests. Malayan Nat. J. 22: 174—178.

Harrisson, B. 1968. Conservation needs of the orang-utan. *In:* Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 294—295.

Hawes, R. A. and L. S. Hamilton. 1980. A method of watershed land classification and assessment for the tropics: a case study of Rio Guanare, Venezuela. Cornell International Agriculture Mimeograph 77, Cornell University, Ithaca, N.Y. 32 p.

Herrera, R., C. F. Jordan, H. Klinge, and E. Medina. 1978. Amazon ecosystems. Their structure and functioning with particular emphasis on nutrients. Interciencia 3: 223 — 232.

Hibbert, A. R. 1967. Forest treatment effects on water yield. *In:* Forest Hydrology. W. E. Sopper and H. W. Lull (eds.), Oxford, Pergamon Press. pp. 527—543.

Holdridge, L. R. 1967. Life zone Ecology. Rev. ed. Trop. Sci. Center, San José, Costa Rica. 206 p.

Holdridge, L. R. 1976. Ecological and genetical factors affecting exploration and conservation in Central America. *In:* Tropical Trees. Variation, Breeding and Conservation. J. Burley and B. T. Styles (eds.). Linnean Society Symposium Series, No. 2 pp. 199—202.

Inger, R. F. 1966. The systematics and zoogeography of the amphibia of Borneo. Fieldiana, Zool. 52: 1—402.

Janos, D. P. 1980a. Mycorrhizae influence tropical succession. Biotropica 12: (Special supplement on succession - in press).

Janos, D. P. 1980b. Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth. Ecology 61: 151—162.

Janzen, D. H. 1973. Tropical agroecosystems. Science 182: 1212—1219.

Jaiyebo, E. O., and A. W. Moore. 1963. Soil nitrogen accretion under different covers in a tropical rain-forest environment. Nature 197: 317—318.

Joachim, A. W. R., and S. Kandiah. 1948. The effect of shifting (Chena) cultivation and subsequent regeneration of vegetation on soil composition and structure. Trop. Agrict. 104: 3—11.

Jordan, C. F., R. L. Todd, and G. Escalante. 1979. Nitrogen conservation in a tropical rain forest. Oecologia 39: 123—128.

Kartawinata, K. 1975. Biological changes after logging in lowland Dipterocarp forest. *In:* R. S. Suparto, *et al.* (eds.), Symposium on the long-term effects of logging in Southeast Asia. BIOTROP. Bogor, Indonesia.

Kellman, M. C. 1969. Some environmental components of shifting cultivation in upland Mindanao. J. Trop. Geogr. 28: 40—56.

Kellman, M. C. 1970. Secondary plant succession in tropical montane Mindanao. Australian Natl. Univ., Canberra. 174 p.

Kenoyer, L. A. 1929. General and successional ecology of the lower tropical rain-forest at Barro Colorado Island, Panama. Ecology 29: 201—222.

Kenworthy, J. B. 1969. Water balance in the tropical rain forest: a preliminary study in the Ulu Gombak Forest Reserve. Malayan Nat. J. 22: 129—135.

King, K. F. S. 1975. Putting the emphasis on tropical forestry. Unasylva 27: 30—35.

Kingston, T. J. 1971. Notes on the black and white Colobus monkey in Kenya. East Afr. Wildl. J. 9: 172—175.

Kira, T., and T. Shidei. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Jap. J. Ecol. 17: 70—87.

Kowal, J. M. L., and P. B. H. Tinker. 1959. Soil changes under a plantation established from high secondary forest. J. West. African Inst. Oil Palm Res. 2: 376—389.

Krebs, J. E. 1975. A comparison of soils under agriculture and forests in San Carlos, Costa Rica. *In:* Golley, F. B., and E. Medina (eds.), Tropical Ecological Systems. Springer Verlag, New York. pp. 381—390.

Krebs, J. E., K. H. Tan, and F. B. Golley. 1974. A comparative study on chemical characteristics of tropical soils from volcanic material under forest and agriculture. Comm. Soil Sci. Plant Anal. 5: 579—596.

Lal, R. and D. J. Cummings. 1979. Clearing a tropical forest. I. Effects on soil and micro-climate. Field Crops Research 2: 91—107.

Landon, F. H. 1957. Malayan tropical rain forest. *In:* Tropical silviculture, vol. II. FAO Forestry and Forest Products Studies, No. 13. Rome. pp. 1—12.

Lasebikan, B. A. 1975. The effect of clearing on the soil arthropods of a Nigerian rain forest. Biotropica 7: 84—89.

Laudelot, H., and J. Meyer. 1954. Les cycles d'élements mineraux et de matière organique en forêt equatorial congolaise. Trans. Fifth Int. Congr. Soil Sci. 2: 267—272.

Leck, C. F. 1979. Avian extinctions in an isolated tropical wet-forest preserve, Ecuador. Auk 96: 343—352.

Leigh, C. H. 1978. Slope hydrology and denudation in the Pasoh Forest Reserve. I - Surface wash; experimental techniques and some preliminary results. Malayan Nat. J. 30: 179—197.

Lekagul, B. 1968. Threatened species of fauna of Thailand. *In:* Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 267—271.

Liew, T. C. 1974. A note on soil erosion study at Tawau Hills Forest Reserve. Malayan Nat J. 27: 20—26.

Liew, T. C., and F. O. Wong. 1973. Density, recruitment, mortality and growth of Dipterocarp seedlings in virgin and logged-over forests in Sabah. Malayan Forester 36: 3—15.

Longman, K. A., and J. Jenik. 1974. Tropical Forest and its Environment. Longman Group Limited, London. 196 p.

Low, K. S., and K. C. Goh. 1972. The water balance of five catchments in Selangor, West Malaysia. J. Trop. Geogr. 35: 60—66.

McCarthy, J. 1962. The colonization of a swamp forest clearing (with special reference to *Mitragyna stipulosa*). East Afri. Agri. J. 28: 22—28.

McClure, H. E. 1968. Some problems concerning endangered birds in South Eastern Asia. *In:* Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 307—311.

McClure, H. E., and Hussein bin Othman. 1965. Avian bionomics of Malaya 2. The effect of forest destruction upon a local population. Bird-Banding 36: 242—269.

McKenzie, E., Jr., L. T. Kurtz, and S. W. Melsted. 1977. Phosphorus fertility of some tropical soils in Sierra Leone. Soil Sci. Soc. Am. J. 41: 378—381.

Marshall, A. G. 1973. Conservation in West Malaysia: The potential for international cooperation. Biol. Conserv. 5: 133—140.

Medway, Lord, and D. R. Wells. 1971. Diversity and density of birds and mammals at Kuala Lompat, Pahang. Malayan Nat. J. 24: 238 — 247.

Meggers, B. J., E. S. Ayensu, and W. D. Duckworth (eds.). 1973. Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Inst. Press, Wash. 350 p.

Meijer, W. 1968. A botanist's view on the use of arboricides in forestry in Sabah. ***In:*** Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 164—167.

Meijer, W. 1970. Regeneration of tropical lowland forest in Sabah, Malaysia forty years after logging. Malayan Forester 33: 204—229.

Meijer, W. 1973. Devastation and regeneration of lowland Dipterocarp forests in Southeast Asia. Bioscience 23: 528—533.

Meijer, W. 1975. Indonesian Forests and Land Use Planning. Report on NSF-AID Travel Grant (May-August 1973) Program, Scientists and Engineers in Economic Development (SEED). Univ. of Kentucky Bookstore, Lexington, KY 112 p.

Meiklejohn, J. 1962. Microbiology of the nitrogen cycle in some Ghana soils. Emp. J. Expt. Agric. 30: 115—126.

Mensah, K. O. A. 1966. An analysis of logging damage in compartment 4 of Tano Suhien Forest Reserve, Ghana. Ghana J. Sci. 6: 63—69.

Misra, R., and B. Gopal (eds.). 1968. Proceedings of the Symposium on Recent Advances in Tropical Ecology. The International Society for Tropical Ecology, India. 2 vols., 773 p.

Mohr, E. C. J., F. A. Van Baren, and J. Van Schuylenborgh. 1972. Tropical Soils. 3rd ed. Mouton-Ichtiar Baru — Van Hoeve. The Hague. 481 p.

Moore, A. W., and E. O. Jaiyebo. 1963. The influence of cover on nitrate and nitrifiable nitrogen content of the soil in a tropical rain forest environment. Emp. J. Expt. Agric. 31: 189—198.

Moss, R. P. 1969. The ecological background to land-use studies in tropical Africa, with special reference to the west. ***In:*** Environment and Land Use in Africa. Thomas, M. F., and G. W. Whittington (eds.). London, Methuen. pp. 193—238.

Mueller-Dombois, D. 1973. A non-adapted vegetation interferes with water removal in a tropical rain forest area in Hawaii. Trop. Ecol. 14: 1—18.

Myers, N. 1976. An expanded approach to the problem of disappearing species. Science 193: 198—202.

Myers, N. 1979. The Sinking Ark. Pergamon Press, New York.

Myers, N. 1980. Conversion of Tropical Moist Forests. National Academy of Sciences, Washington, D.C.

Nakano, H. 1967. Effects of changes of forest conditions on water yield, peak flow and direct runoff of small watersheds in Japan. ***In:*** Forest Hydrology. W. E. Sopper and H. W. Lull (eds.), Oxford, Pergamon Pres. pp. 551—564.

National Research Council. 1980. Research Priorities in Tropical Biology. National Academy of Sciences, Washingtong, D.C.

Nicholson, D. I. 1958a. An analysis of logging damage in tropical rain forest, North Borneo. Malayan Forester 21: 235—245.

Nicholson, D. I. 1958b. Natural regeneration of logged tropical rain forest, North Borneo. Malayan Forester 21: 65—71.

Nicholson, D. I. 1960. Light requirements of seedlings of five species of Dipterocarpaceae. Malayan Forester 23: 344—356.

Nicholson, D. I. 1963. Damage from high-lead logging in Sabah. Malayan Forester 26: 294—296.

Nicholson, D. I. 1965. A review of natural regeneration in the Dipterocarp forests of Sabah. Malayan Forester 28: 4—26.

Nieuwolt, S. 1965. Evaporation and water balances in Malaya. J. Trop. Geogr. 20: 34 and 54.

Nye, P. H. 1959. Some effects of natural vegetation on the soils of West Africa and on their development under cultivation. ***In:*** Tropical Soils and Vegetation. Proc. of the Abidjan Symposium, 1959: 59—63.

Nye, P. H., and D. J. Greenland. 1960. The Soil Under Shifting Cultivation. Commonwealth Agricultural Bureaux, Farnham Royal, 156 p.

Nye, P. H., and D. J. Greenland. 1964. Changes in the soil after clearing tropical forest. Plant and Soil 21: 101—112.

Oates, J. F. 1978. The status of the South Indian black leaf-monkey (*Presbytis johnii*) in the Palni Hills. J. Bombay Nat. Hist. Soc. 75: 1—12.

Odum, H. T., and R. F. Pigeon (eds.). 1970. A Tropical Rain Forest. A Study of Irradiation and Ecology at El Verde, Puerto Rico. Division of Technical Information, U.S. Atomic Energy Commission.

Ovington, J. D. 1962. Quantitative ecology and the woodland ecosystem concept. Advances in Ecological Research 1: 103—192.

Pereira, H. C. 1967a. Afforestation and streamflow in tropical highlands (East and Central Africa). Commonw. For. Rev. 46: 323—327.

Pereira, H. C., 1967b. Effects of land-use on the water and energy budgets of tropical watersheds. ***In:*** Forest Hydrology. W. E. Sopper and H. W. Lull (eds.), Oxford, Pergamon Press, pp. 435—450.

Pereira H. C., M. Dagg, and P. H. Hosegood. 1962. The water balance of both treated and control valleys. East African Agricultural and Forestry J. 27 (special issue): 36—41.

Pernet, R. 1952. L'humus forestier et son évolution après destruction du couvert végétal. Mém. Inst. Sci. Madagascar, Sér. D, 4: 297—345.

Petriceks, J. 1955. The present state of forest exploitation in Venezuela. Emp. For. Rev. 34: 64—67.

Phillips, J. 1964. Shifting cultivation. *In:* Proc. and Papers of IUCN 9th Tech. Meeting, Nairobi; IUCN Publ. New Ser. No. 4, 1964. The Ecology of Man in the Tropical Environment. pp. 210—219.

Phillips, J. 1967. The Development of Agriculture and Forestry in the Tropics: Patterns, Problems, and Promise. Rev. ed. F. A. Praeger, Inc., New York. 221 p.

Phillips, J. F. V. 1968. The ecosystem as a basis for the investigation and development of agriculture, forestry and related industries in the tropics and subtropics. *In:* Proc. of the Symposium on Recent Advances in Tropical Ecology, Part II. R. Misra, and B. Gopal (eds.). The International Society for Tropical Ecology, India. pp. 721—739.

Poore, D. 1975. Ecological guidelines. Unasylva 27: 16—20.

Poore, D. 1976. Ecological guidelines for development in tropical rain forests. IUCN Books, Morges, Switzerland.

Popenoe, H. 1959. The influence of the shifting cultivation cycle on soil properties in Central America. Proc. of the 9th Pacific Science Congress 7: 72—77.

Popenoe, H. 1960. Some soil cation relationships in an area of shifting cultivation in the humid tropics. Transactions of the 7th Int'l Cong. of Soil Science, Madison, Wisconsin, Vol. 2. 303 — 311.

Prance, G. T., and T. S. Elias (eds.). 1977. Extinction is Forever. New York Botanical Garden, Bronx, New York.

Qureshi, A., L. S. Hamilton, D. Mueller-Dombois, W. R. H. Perera, and R. A. Carpenter. 1980. Assessing Tropical Forest Lands: Their Suitability for Sustainable Uses. East West Center, Honolulu, Hawaii.

Qureshi, I. M 1960. Regeneration of tropical evergreen rain forests. Proc. Silvicult. Conf. (India) 1956. 9: 148—150.

Rabor, D. S. 1958. Wildlife in the humid tropics picture. Proceedings of the 9th Pacific Congress 20: 95—104.

Rabor, D. S. 1968a. The present status of the monkey-eating eagle, ***Pithecophaga jefferyi*** Ogilvie-Grant, of the Phillipines. *In:* Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 312—314.

Rabor, D. S. 1968b. Threatened species of small mammals in tropical South East Asia. The problem in the Philippines. *In:* Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 272—277.

Rapera, R. B. 1978. Effects of logging on residual stands. *In:* R. S. Suparto *et al.* (eds.), Symposium on the long-term effects of logging in Southeast Asia, BIOTROP. Bogor, Indonesia.

Redhead, J. F. 1960. An analysis of logging damage in lowland rain forest, Western Nigeria. Nig. For. Inf. Bull. (n.s.) 10: 5—16.

Richards, P. W. 1952. The Tropical Rain Forest. Cambridge Univ. Press. London, 450 p.

Richards, P. W. 1955. The secondary succession in the tropical rain forest. Science Progress 43: 45—57.

Richards, P. W. 1958. The concept of the climax as applied to tropical vegetation. *In:* Study on Tropical Vegetation. Proc. of the Kandy Symposium, 1956. UNESCO. pp. 207 — 211.

Richards, P. W. 1973. The tropical rain forest. Sci. Amer. 229: 58—67.

Richardson, S. D. 1970. Gene pools in forestry. *In:* Genetic Resources in Plants. O. H. Frankel and E. Bennett (eds.). F. A. Davis, Philadelphia, pp. 353 — 365.

Rijksen, H. D. 1978. A field study of Sumatran orangutans (***Pongo pygmaeus abelii*** Lesson 1827): Ecology, behaviour, and conservation. Meded. Landbouwhogesch. Wageningen 78: 1—420.

Riquier, J. 1953. Étude d'un sol de tavy et d'un sol de forêt primaire a Périnet. Mém. Inst. Sci. Madagascar, Sér. D, 5: 75—92.

de Rosayro, R. A. 1957. The silviculture and management of tropical rain forest with special reference to Ceylon. *In:* Tropical Silviculture, Vol. II. FAO Forestry and Forest Products Studies, No. 13. Rome, pp. 77—102.

Russell, J. 1974. The effect of commercial timber extraction in regions of tropical rain forests in Dominica. World Crops (London) 26: 134—135.

Sarukhan Kermez, J. 1964. Estudio sucesional de un area talada en Tuxtepec, Oax. *In:* Contribuciones al Estudio Ecológico de las zonas Calido-Húmedas de Mexico. Publ. Esp. Inst. Nac. Invest. Forest. Mexico 3: 107—172.

Schaller, G. B. 1961. The orang-utan in Sarawak. Zoologica 46: 73—82.

Schulz, J. P. 1960. Ecological Studies on Rain Forest in Northern Suriname. Noord-Hollandsche Uitgevers Maatschappij, Amsterdam. 267 p.

Serevo, T. S. 1949. Some observations on the effects of different methods of logging on residual stand and on natural reproduction. Phil. J. For. 6: 363—381.

Seubert, C. E., P. A. Sanchez, and C. Valverde. 1977. Effects of land clearing methods on soil properties of an ultisol and crop performance in the Amazon jungle of Peru. Tropical Agriculture (Trinidad) 54: 307—321.

de Silva, G. S. 1968. Wildlife conservation in the state of Sabah. *In:* Conservation in Tropical South East Asia. IUCN Publ. New Ser. 10: 144—150.

Singh, K. G. 1966. Ectotrophic mycorrhiza in equatorial rain forests. Malayan Forester 29: 13—18.

Smith, R. F. 1970. The vegetation structure of a Puerto Rican rain forest before and after short-term gamma irradiation. *In:* A Tropical Rain Forest. H. T. Odum and R. F. Pigeon (eds.). Division of Technical Information, U.S.A.E.C. pp. D103—D140.

Snedaker, S. C. 1970. Ecological studies on tropical moist forest succession in eastern lowland Guatemala. Ph.D. Dissertation, Univ. of Fla., Gainesville. 131 p.

Soerianegara, I. 1970. Soil investigation in Mount Hondje Forest Reserve, West Java. Rimba Indonesia 15: 1 — 16.

Soerianegara, I. 1975. Assessment of logging effects with special reference to the tropical rain forest in Indonesia. *In:* R. S. Suparto *et al.* (eds.), Symposium on the long-term effects of logging in Southeast Asia. BIOTROP. Bogor, Indonesia.

Sono, P. 1975. Some observations on the effects of logging in Thailand. *In:* R. S. Suparto, *et al.* (eds.), Symposium on the long-term effects of logging in Southeast Asia. BIOTROP. Bogor, Indonesia.

Stark, N., and C. Holley. 1975. Final report on studies of nutrient cycling on white and black water areas in Amazonia. Acta Amazonica 5: 51 — 76.

van Steenis, C. G. G. J. 1958a. Basic principles of rain forest sociology. *In:* Study of Tropical Vegetation. Proc. of the Kandy Symposium, 1956. UNESCO. pp. 159—165.

van Steenis, C. G. G. J. 1958b. Rejuvenation as a factor for judging the status of vegetation types; the biological nomad theory. *In:* Study of Tropical Vegetation. Proc. of the Kandy Symposium, 1956. UNESCO. pp. 212 — 218.

van Steenis, C. G. G. J. 1958c. Tropical lowland vegetation: the characteristics of its types and their relation to climate. Proceedings of the 9th Pacific Science Congress 20: 25—37.

Stevens, W. E. 1968a. The conservation of wild life in west Malaysia. Office of the Chief Game Warden, Federal Game Department, Ministry of Lands and Mines, Seremban.

Stevens, W. E. 1968b. Habitat requirements of Malayan mammals. Malayan Nat J. 22: 3—9.

Stevens, W. E. 1969. Report to the Government of Malaysia on Game Conservation (cited by Burgess, 1971).

Struhsaker, T. T. 1972. Rain-forest conservation in Africa. Primates 13: 103—109.

Struhsaker, T. T. 1975. The Red Colobus Monkey. University of Chicago Press, Illinois, 311 p.

Suparto, R. S, *et al.* (eds.). 1978. Proceedings of the Symposium on the Long-term Effects of Logging in Southeast Asia. June 24 — 27, 1975. Darmaga, Bogor, Indonesia. BIOTROP Special Publication No. 3. 177 pp.

Sutanto, F. X. Dwi, R. Sambas Wirakusumah, and R. Permono. 1978. Regeneration and tree growth in some logged-over Dipterocarp forests in East Kalimantan. *In:* R. S. Suparto, *et al.* (eds.), Symposium on the long-term effects of logging in Southeast Asia. BIOTROP. Bogor, Indonesia.

Tagudar, E. 1968. The response of Dipterocarp seedlings when released from competing vegetation. Forestry Leaves 18: 47—53.

Thiollay, J. M. 1975. (Rapacious birds from a savannah-forest zone in the Ivory Coast: Study of a population). Alauda 43: 75—102.

Thurber, W. A. 1972. Status of the white-tailed kite in El Salvador. Condor 74: 489—491.

Tinal, Uk., and J. L. Palenewen. 1978. Mechanical logging damage after selective cutting in Dipterocarp forest at Beloro East Kalimantan. *In:* R. S. Suparto, *et al.* (eds.), Symposium on the long-term effects of logging in Southeast Asia. BIOTROP. Bogor, Indonesia.

Tosi, J. A., Jr. 1971. El recurso forestal como base potencial para el desarrollo industrial de Costa Rica. La Nación, 20—21 de Marzo, 1971.

Tosi, J. A., Jr. 1975. Some relationships of climate to economic development in the tropics. *In:* The Use of Ecological Guidelines for Development in the American Humid Tropics. International Union for Conservation of Nature and Natural Resources, Papers and Proceedings, Caracas, Venezuela, 20—22 February 1974. Session I, No. 3: 41—56. Morges, Switzerland, 1975.

Tosi, J. A., Jr. 1976. Transformación del bosque en pastizal: desarrollo o destrucción? (Comentario) Rev. Biol. Trop. 24 (Supl. 1): 139—141.

Tosi, J. A., Jr. and L. R. Holdridge. 1973. Potencial para la ordinación-téchnica del bosque natural en Costa Rica. Centro-Cientifico Tropical, Notas tecnicas y economicas. No. 1. 19 p.

Tosi, J. A., Jr., and R. F. Voertman. 1975. Making the best use of the tropics. Unasylva 27: 2 — 10.

U.S. Department of State and U.S. Agency for International Development. 1978. Proceedings of the U.S. Strategy Conference on Tropical Deforestation, Washington, D.C.

U.S. Environmental Protection Agency (USEPA). 1976. Forest harvest, residue treatment, reforestation and protection of water quality. EPA 910/9-76-020. 273 p.

U.S. Interagency Task Force on Tropical Forests. 1980. The World's Tropical Forests: A Policy, Strategy, and Program for the United States. A Report to the President. Department of State Publication 9117, International Organization and Conference Series 145. U.S. Government Printing Office, Washington, D.C. 53 p.

UNESCO. 1972. Expert panel on project No. 1: Ecological effects of increasing human activities on tropical and sub-tropical forest ecosystems in the Programme on Man and the Biosphere (MAB). UNESCO. MAB report series No. 3. 35 p.

UNESCO. 1978. Tropical Forest Ecosystems. Natural Resources Research XIV. UNESCO, Paris.

Wadsworth, F. H. 1957. Tropical rain forest. *In:* Tropical Silviculture, Vol. II, FAO, Rome. pp. 13—23.

Wadsworth, F. H. 1975a. The future of primary tropical humid forests in America. Unpub. ms. 14 p.

Wadsworth, F. H. 1975b. Natural forests in the development of the humid American tropics. *In:* The Use of Ecological Guidelines for Development in the American Humid Tropics. International Union for Conservation of Nature and Natural Resources, Papers and Proceedings, Caracas, Venezuela, 20—22 February 1974. Session III, No. 8: 129—138. Morges, Switzerland, 1975.

Walton, A. B. 1954. The regeneration of Dipterocarp forests after high lead logging. Emp. For. Rev. 33: 338—344.

Weaver, P. L. 1972. Cloud moisture interception in the Luquillo Mountains of Puerto Rico. Carib. J. Sci. 12: 129—144.

Weaver, P. L. 1975. Transpiration rates in the elfin forest of the Luquillo Mountains of Puerto Rico. Carib. J. Sci. 15: 21—30.

Weaver, P. L., M. D. Byer, and D. Bruck. 1973. Transpiration rates in the Luquillo Mountains of Puerto Rico. Biotropica 5: 123—133.

Wells, D. R. 1971. Survival of the Malaysian bird fauna. Malayan Nat. J. 24: 248—256.

Went, F. W. and N. Stark. 1968. Mycorrhizae. Bioscience 18: 1035—1039.

Whitmore, T. C. 1975. Tropical Rain Forests of the Far East. Oxford University Press, London. 282 p.

Whitmore, T. C., and Y. K. Wong. 1958. Patterns of sunfleck and shade in tropical rain forest. Malayan Forester 22: 50 — 62.

Wilson, C. C., and W. L. Wilson. 1975. The influence of selective logging on primates and some other animals in East Kalimantan. Folia Primatologica 23: 245—274.

Wilson, W. L., and C. C. Wilson. 1978. Primates in undisturbed and logged forest in Sumatra and East Kalimantan. *In:* R. S. Suparto, *et al.* (eds.), Symposium on the long-term effects of logging in Southeast Asia. BIOTROP. Bogor, Indonesia.

Wyatt-Smith, J. 1949. Regrowth in cleared areas. Malayan Forester 12: 83—86.

Wyatt-Smith, J., and E. C. Foenander. 1962. Damage to regeneration as a result of logging. Malayan Forester 25: 40—44.

Wyatt-Smith, J., and A. J. Vincent. 1962. The swing from qualitative to quantitative assessment of individual tree crown parameters in the Malayan Forest Service. Malayan Forester 25: 276—291.