STUDIES OF SITE-FOREST RELATIONSHIPS IN THE MIXED DIPTEROCARP FOREST OF SARAWAK

IAN C. BAILLIE

Ph.D [illegible]

STUDIES OF SITE-FOREST RELATIONSHIPS IN THE MIXED DIPTEROCARP FOREST OF SARAWAK

by

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DECLARATION

I hereby declare that the work presented in this thesis has been performed by myself, except where specific acknowledgements are made. All quotations are distinguished by quotation marks and all sources of information are acknowledged by reference to the authors. The work has not been included in any previous application for a degree.

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SUMMARY

This study is a continuation of investigations into the relationships between site conditions and the local variation in the floristics, physiognomy and hollow decay of the Mixed Dipterocarp Forest of Sarawak.

Chapter 1 describes the objectives and execution of the project, in the context of forestry research in Sarawak.

Chapter 2 describes the Mixed Dipterocarp Forest, in relation to the other main forest types of Sarawak. It describes the environment of the MDF, particularly the main soil type, the Red Yellow Podzolic soils.

Chapter 3 reviews previous work on the site-forest relationships in the MDF of Brunei and Sarawak. There is also a review of some of the relevant work in lowland rainforests in other parts of the humid tropics.

Chapter 4 describes the collection of data. Previously established plots with pre-existing forest data were used. In 1969-70 site conditions were characterised on 291 plots, grouped into 45 clusters, that had been established during the Forest Industries Development Project MDF inventory. Site characterisation in the field was not intensive, but numerous soil samples were submitted for laboratory analysis. During 1971-72 site data were collected from 39 MDF ecological plots, previously established by the Botany section. Field characterisation was more intensive and fewer soil samples were analysed in the laboratory.

Chapter 5 describes the statistical analyses of the data. Site data were simplified and clarified by factor analysis. With the data from the FIDP plots, the effects of site conditions on the distribution of individual species, the total forest basal area, the basal areas of individual species, the total forest stemrot severity, and the severity of stemrot in individual species were examined. Intergeneric and interspecific differences in butt-rot frequency were examined. With the MDF ecological plot data, the effects of site conditions on the distribution of floristically defined forest types were examined by discriminant analysis.

Chapter 6 contains the results and discussions concerned with site effects on local floristic and physiogonomic variation in the MDF. The factor

analyses are described and discussed. There appear to be significant site effects on the distribution of some individual species but less on their basal areas and on the basal area of the forest as a whole. The distribution of the floristically defined forest types is associated with differences in site conditions. Site characteristics related to underlying geology appear to be the most important as floristic determinants, although locally variable topographic characteristics become more important if the sampling range is restricted.

Chapter 7 contains the results and discussions concerned with site effects on the variation in hollow decay. There are market intergeneric and interspecific differences in the frequency of buttrot. There are considerable site effects on the severity of stemrot within individual species. Site conditions appear to have less effect on the severity of stemrot in the forest as a whole.

Chapter 8 discusses the implications of the results. The multidimensional complexity of site-forest relationships in the MDF is stressed. It is suggested that the limits of local soil and forest floristic variation are determined by the nature of the soil parent material. Within these limits the forest and site interact considerably, although both also have substantial independent variation.

The silvicultural implications are discussed. While complete reliance on natural regeneration continues, no major changes are indicated in the results. If assisted regeneration is ever considered, the results are of practical importance, as they indicate that considerable benefits could result from attention to species-site compatability.

The implications of the results for forest inventory, soil survey and intersectorial land allocation are discussed. The value of interdisciplinary information exchange is stressed, but no major procedural changes are indicated.

The general conclusion is that considerable practical experimentation on the effects of site conditions and on the possibility of site management is required, particularly in post-exploitation forests.

UNITS AND ABBREVIATIONS

UNITS

Metric units were used in the field as far as possible. However, both sets of plots used in this project were established in Imperial units. Where Imperial units are used in the text, the metric equivalents are given in parentheses at the first appearance.

ABBREVIATIONS

The abbreviations used in the text, tables and figures are listed alphabetically.

AFO	Assistant Forest Officer.
ARC	Agriculture Research Centre, Semongok.
BA, ba	Basal area.
BMD	Biomedical Statistical Programs, UCLA, Los Angeles.
BS%	Base saturation percentage.
BSI	British Standards Institute.
Bt	Bukit (= hill, Malay/Iban).
CBR	California Bearing Ratio.
CEC	Cation exchange capacity.
COLE	Coefficient of linear expansion.
DAB, dab	Diameter above buttress.
DBH, dbh	Diameter at breast height.
DCA	Department of Civil Aviation, Kuching.
DID	Drainage and Irrigation Department.
DIVINF	Divisive Information Analysis.
DRC	Development and Resources Corporation, New York.
DRH, drh	Diameter at reference height.
EDTA	Disodium Ethylenediaminetetra-acetate.
FAO	Food and Agriculture Organisation of the United Nations, Rome.
FG	Forest Guard.
FIDP	Forest Industries Development Project, Malaysia.
FR	Forest Reserve.
FRI	Forest Research Institute, Kepong, West Malaysia.
FS	Find sand.
GAB, gab	Girth above buttress.

GBH, gbh	Girth at breast height.
HMSO	Her Majesty's Stationery Office, London.
LRD	Land Resources Division, ODM, London.
MDF	Mixed Dipterocarp Forest.
ME%, me%	Milliequivalents per 100 g of fine earch.
MMS	Malaysian Meteorological Service, Kuala Lumpur.
ns	Not significant.
ODM	Ministry of Overseas Development, London.
p	Probability level (scaled from 0 to 1.00).
PF	Protected Forest.
Phytar	Phytogeographical area.
ppm	Parts per million.
PSF	Peat Swamp Forest.
R	Multiple regression coefficient.
r	Bivariate correlation coefficient.
RM	Red Meranti (section of genus *Shorea*).
RYP	Red Yellow Podzolic soil.
SB	Selangan batu (section of genus *Shorea*).
sd	Standard deviation.
Seadist	Shortest distance to coast.
sg	Specific gravity.
TSV	Total stem volume.
UCLA	University of California, Los Angeles.
UNDP	United Nations Development Programme, New York.
UNESCO	United Nations Educational, Scientific and Cultural Organisation, Paris.
USAEA	United States Atomic Energy Authority.
USDA	United States Department of Agriculture, Washington D.C.
VFS	Very fine sand.
WM	White meranti (section of genus *Shorea*).
YM	Yellow meranti (" " ").

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CHAPTER I

ORIGINS OF THE STUDY

1.1 Forestry and Forest Research in Sarawak

Sarawak is the largest and least densely populated state in the Federation of Malaysia. It covers about 124,400 km^2 on the north-west coast of Borneo, ranging in latitude from 0°50'N to 5°00'N and in longitude from 109°30'E to 115°40'E (see Figure 1.1). Its heterogeneous population totalled just under one million in the 1970 census. The largest population group are the Dayaks, using the term in the broad Indonesian sense to include all the longhouse-dwelling, non-Muslim, shifting cultivators of upland rice in the interior. The other major groups are the Chinese, mostly engaged in trade, and the mainly coastal Malays and Melanaus, who practise a mixed economy of swamp rice cultivation, fishing and petty trading and who are predominantly Muslim (Harrisson, 1959 and 1970).

Industrialisation is so far slight and the only major mineral resources are the coastal and offshore oil and natural gas fields in the North. The economy is still predominantly agro-forestal. Agriculture is almost entirely by small-holders, in contrast to the other states of Malaysia, where large commercial plantations are extensive and important. The predominance of smallholder agriculture is the result of conscious and consistent policies of the pre-1946 Brooke regime, and is being perpetuated by current agricultural development programmes, with their emphasis on planned smallholder settlement schemes.

The most extensive agricultural system is the shifting cultivation of upland rice, on a subsistence basis. Little or no surplus is produced for the urban sector and the state generally has to import part of its rice requirements. Rubber *(Hevea brasiliensis)* and black pepper *(Piper nigrum)* are the main cash crops, although oil palm *(Elaeis guineensis)* is increasing in importance. The government actively encourages the change from subsistence to cash cropping. However, land pressures are not generally very intense, except in some peri-coastal areas, and in parts of West Sarawak, so that progress is slow. Development away from subsistence agriculture is also hampered by the importance of the various phases of the upland rice cultivation cycle in the social and religious life and structure of the Dayak communities (e.g. Freeman, 1955).

Figure 1.1 LOCATION

Timber and other forest products are major items in the state's economy, particularly its external trade. In the first half of 1971 timber and wood manufactures accounted for 30% of Sarawak's total exports. Their real importance is actually greater than this, as the export total is inflated by the practice of importing crude oil from Brunei, and re-exporting it, with or without further processing. If the total export figures are adjusted by taking the net, rather than gross, oil exports, then timber and wood manufactures represent 48% of the total (Department of Statistics, 1972). Although agricultural, industrial and mineral production are increasing, forestry is expected to continue as a major employer and export revenue earner for the forseeable future (Senada, 1977).

Systematic logging on a large scale began in 1948 (Smythies, 1951). It was originally restricted to the Peat Swamp Forests. The main timber extracted was ramin *(Gonostylus bancanus)* and, in sawn form, this is still one of Sarawak's most valuable timbers. Exploitation of the upland forests began in the 1960s. With the progressive depletion of the immediate reserves of the Peat Swamp Forests, the upland forests have become increasingly important. In 1967, 66% of all forest products came from the Peat Swamp Forests. By 1971 the proportion had fallen to 55%, and this trend is thought to have continued (Department of Statistics, 1968-72).

The Forest Department is responsible for the overall management of the state's forest resources. The long term objectives were defined in the 1954 Forest Policy. The two main aims are to ensure an adequate supply of timber and forest products for the state's domestic requirements in perpetuity, and to protect soil and water resources. Given the large areas of forest and the small population, mere fulfilment of these aims leaves the forest potential considerably underutilised. The Forest Department is therefore further empowered to regulate the exploitation of forests so as to encourage the development of a permanent, export-oriented forest industry. The Department also ensures the full exploitation of the forest resources of any land that is to be cleared and alienated for agriculture or other non-forestry purposes (Smythies, 1963).

The extraction and marketing of the timber are carried out by licenced private enterprises, under the control of the Forest Department (Walker, 1968). Ownership of the land remains vested in the state, and the licencees' rights cease once the exploitation phase is complete. The silvicultural management of the logged forests is undertaken directly by the Forest Department. In order to ensure a return on management expenditure incurred in the regeneration phase, it is necessary for the Forest Department to have security of tenure. This has been achieved by the creation of Forest Reserves and Protected Forests. These are legally designated to remain under forest for ever, and comprise the state's Permanent Forest Estate, which covered about 31% of the state in 1972.

The post-exploitation silvicultural management of permanent forests is aimed at the growth of a valuable timber crop in the following rotation, as rapidly and economically as possible. The current routine silvicultural practices rely entirely on natural regeneration. Plantation forestry is still at the experimental stage (Lee, 1972 (a)).

Development of successful silvicultural systems based on natural regeneration requires a considerable knowledge and understanding of the floristics, structure and dynamics of the forest, supplemented by silvicultural experimental results. When the Forest Department established a small Research Section, it was natural that the early work concentrated mainly on the ecology (Anderson, 1961 (a), 1964 (a) and 1973) and silviculture (Clarke, 1964 and 1968; Palmer, 1971; Lee, 1972 (b)) of the then economically predominant Peat Swamp Forests.

Systematic investigations in the non-swamp forests began in the late 1950s. Brunig (e.g. 1965, 1969 (a) and 1974) concentrated on the ecology and dynamics of the Kerangas (heath) forests. Although of great intrinsic interest, these are limited in area and economic potential. Ecological work in the more important Mixed Dipterocarp Forests (MDF hereafter) began in the small non-Malaysian enclave state of Brunei (see Figure 1.1) and continued in the 1960s in Sarawak (Ashton, 1964 (a), and 1973). Systematic silvicultural experimentation began in the late 1960s (Palmer, 1971; Lee, 1972 (c); Lau, 1972).

The parts of Ashton's extensive findings relevant to this project are reviewed in Chapter 3. In brief, he found that edaphic conditions appear to have considerable influence on the floristic and structural variation within the MDF. Consistent objective floristic classification of the MDF appears to be possible, and the subdivisions so formed reflect site conditions to a considerable degree. These findings are contrary to experience in the similar Lowland

Dipterocarp Forests of West Malaysia, as discussed in more detail in Chapter 3. There, biological and chance factors appear to be the main determinants of the floristic composition and physiognomy of these forests. Ashton's findings are therefore of considerable ecological interest and importance.

1.2 Objectives and Execution of Present Project

As well as their intrinsic scientific interest, Ashton's results have several potentially useful practical implications. The most important is the possibility of refining silvicultural procedures in the MDF so as to favour the early growth and competitive status of species known to be well suited to local site conditions. This kind of refinement will only be possible in forests with abundant and diverse regeneration. Otherwise, silviculture will necessarily have to concentrate on such regeneration as is present, irrespective of its known or suspected suitability to the site.

Another possibility is to increase the precision of pre-exploitation forest inventories in the MDF by allowing for variation in rock type, topography and soil type in the sampling design and in the extrapolation of results.

A third possible benefit could be the use of forest characteristics as indicators of soil conditions. This could be an aid to soil and land capability surveys, particularly if site conditions can be related to structural characteristics of the forest canopy that are distinguishable on remote sensing imagery (Webb et al., 1971; Ashton and Brunig, 1974; Moss, 1975).

The existence of marked soil-forest associations may not only be a potential aid in the execution of soil surveys but could also be useful in their interpretation and application. At present in Sarawak, as in most other places, forestry is allocated land not required for urban, industrial or agricultural uses (Baharuddin and Mustafa, 1968; Panton, 1970; Hepburn, 1974; Huntings, 1974 (a)). Because returns on investment in forestry are generally poor and delayed, and because forestry employs only a limited number of permanent workers, these priorities are usually unexceptionable. However, there may be some marginal cases in which knowledge of an area's forestry potential, if predictable from site conditions, might be of use for the most rational allocation of land.

Mainly because of these practical possibilities, continued investigation into soil-forest relationships in the MDF was included in the work of the Forest Soil Survey in the 1966-70 Forest Research Development Plan (Forest Department, 1966). In this plan, Project SL2 was entitled:

"The investigation of soils under Mixed Dipterocarp Forest"

and the objective was:

"to investigate the soils under Mixed Dipterocarp Forest and to determine whether soil variations may be correlated with vegetation."

From the section on work planned, it is clear that the possible refinement of MDF silviculture is of major interest.

Subsequent discussions with colleagues in the Forest Department, with members of the FAO team of experts assigned to the Forest Industries Development Project (FIDP), and with scientists outside Sarawak enlarged the scope of the investigation to include the other potential applications mentioned above.

Another major addition was the inclusion of the study of relationships between site conditions and hollow decay in the MDF. This type of defect is widespread in the MDF and greatly detracts from the volume and quality of the timber extracted. It also adds considerably to the difficulties, danger and cost of logging in the MDF. As yet there have been no systematic biological studies of the pathogens involved, their vectors or their modes of action. However, in North Sarawak, loggers have reported that they find such decay to be most serious on sandy soils, particularly on ridge crests and upper slopes. In view of this, and of the economic and practical importance of hollow decay, and as a soils investigation in the MDF was to be undertaken anyway, examination of site effects on the occurrence and severity of decay was included in the project.

The revised general objectives of the project can therefore be summarised as:

The continued investigation of general relationships between site conditions and the variation in floristic composition, stand structure, hollow decay characteristics and, hence, the economic potential of the Mixed Dipterocarp Forest in Sarawak, with particular reference to:

(a) The possible refinement of silvicultural practices according to site conditions.

(b) The possible increase in precision of forest inventory by allowing for variations in site conditions.

(c) The possible use of forest characteristics as an aid in soil and land capability surveys.

(d) The possibility of including site potential for forestry in land use planning, particularly in cases where forest alienation or reservation is involved.

It is clear that these are general objectives, aimed at information gathering and hypothesis generation, rather than hypothesis testing. This seems appropriate to the present state of knowledge of the subject (see Chapter 3), and it also fits better with some of the practical constraints on data collection outlined in Chapter 4.

Fieldwork for the project began in mid-1969 and was initially planned for two field seasons; it was later extended by almost two more seasons. As well as this project, the small Forest Soil Survey section had some departmental soil survey commitments, but from 1970 onwards these were relatively undemanding. The field programme was prematurely terminated in 1972, but by then, sufficient data had been collected to justify proceeding with their statistical treatment. This could not commence immediately because of the backlog of analytical work on the large number of soil samples that had been sent to the laboratory. The backlog was substantially cleared by mid-1974, and it was arranged that the writer spend a year at the University of Aberdeen, working full time on the completion of the project. The year ran from October 1975 to September 1976, and was financed by the U.K. Ministry of Overseas Development, London, as Research Scheme R.3018. In the event, the statistical work took the whole twelve months, and writing up was not completed until 1978.

CHAPTER 2

THE MIXED DIPTEROCARP FOREST OF SARAWAK AND ITS ENVIRONMENT

.1 The Forest

.1.1 Forest Types of Sarawak

Except for insignificant areas on beaches, river banks, sand bars and rocky cliffs, evergreen forest is the natural vegetation of the whole of Sarawak. Virgin forest probably still covers more than half of the state, although logging and clearing for planned and spontaneous agricultural development are currently making considerable inroads. The most extensive areas of undisturbed forest are in the relatively inaccessible interior of Central and North Sarawak. The most extensive clearing and disturbance of the forests is in the coastal and pericoastal areas, and in the relatively densely populated parts of West Sarawak.

A recent comprehensive classification of the state's forest types is summarised in Table 2.1 (Brunig, 1969 (b)). It is basically similar to earlier classifications (e.g. Browne, 1955), although more detailed. In Table 2.1 it can be seen that the floristically and structurally complex Mixed Dipterocarp Forest (MDF) is the most extensive type. It is found on most reasonably well-drained soils below about 1,000 m. altitude. Although apparently tolerant and adaptable, the MDF is not ubiquitous, and does not occur in some of the more severely restrictive environments. The environmental constraints may be edaphic, such as deficiencies, excesses or imbalances of soil moisture or nutrients, or they may be climatic, as in the case of the higher mountains. Specialised, highly adapted forests are found in these restrictive environments. The forests are generally ecologically simpler than the MDF, being floristically poorer, of less complex structure, and/or of lower stature and biomass.

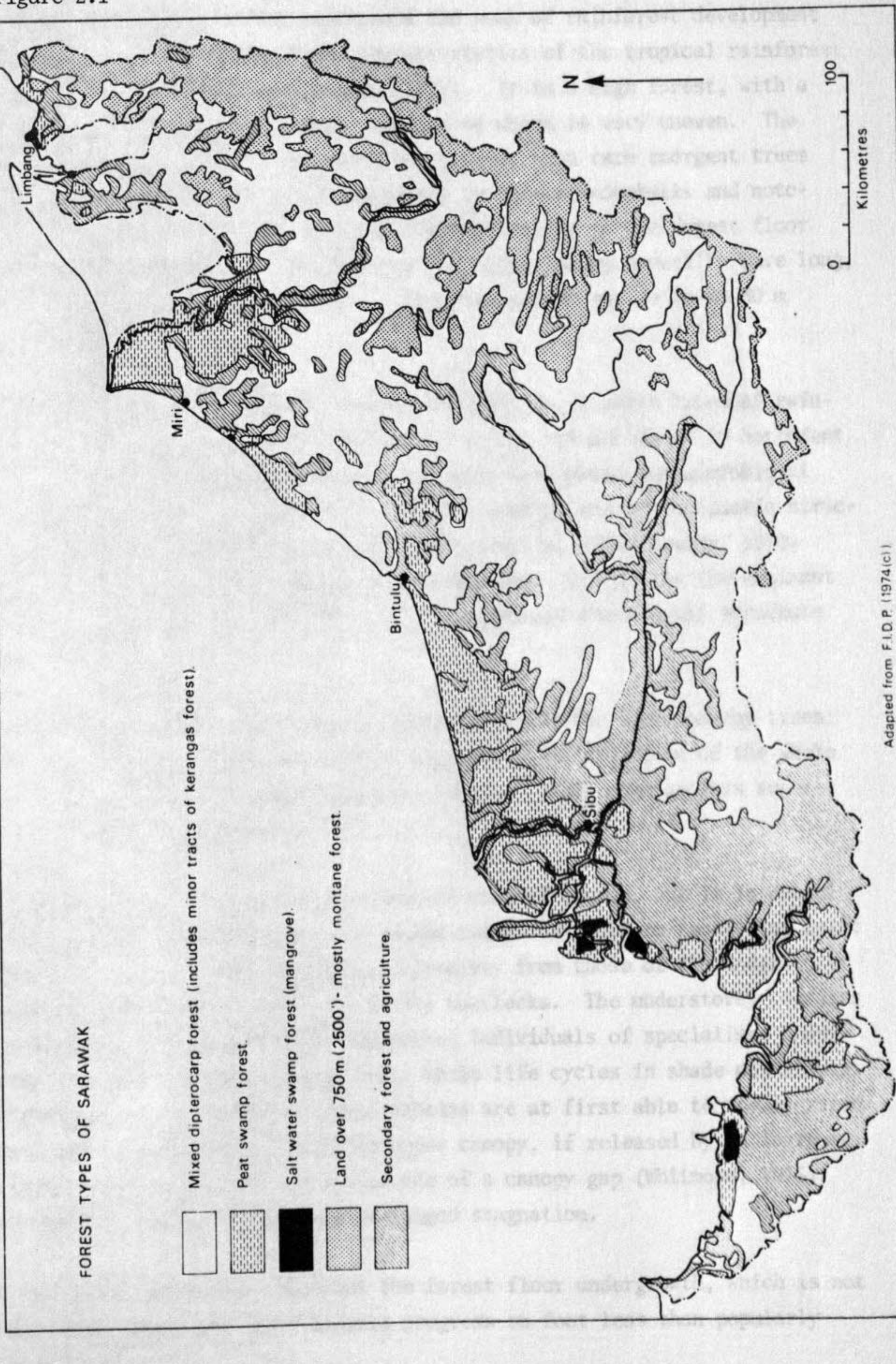
With such broadly defined types, the boundaries between them may be quite diffuse, particularly between the MDF and the Kerangas Forest, and between the MDF and Montane Forest. The main characteristics of the forest types are briefly summarised in Table 2.1, and their generalised distribution is shown in Figure 2.1.

TABLE 2.1 Forest types of Sarawak (summarised from Brunig 1969(b))

Forest Type	Floristic Composition	Physiogonomic Structure	Environment	Approximate Area* Km²	% of State	References
Lowland Forests						
Mixed Dipterocarp Forest	Very rich. Larger size classes dominated by Dipterocarp family but not by any single species.	Very uneven, dense, multilayered canopy. Low light and undergrowth at ground level.	Most well and imperfectly drained soils below 1000 - 1200 m, except for podzols and related soils on very siliceous parent materials, and limestone	70 400	57	See Section 2.2 and Chapter 3.
Specialised lowland forests of restrictive edaphic environments						
Beach Forest	Generally simple. May be pure *Casuarina equisetifolia* in places	Scrub or low forest. Also areas of scattered trees.	Recent marine sands and lower slopes of rocky cliffs	200	<1	Brunig, 1961 Ashton, 1971
Mangrove Forest	Pure stands or simple mixtures of mangrove species	Simple structured forest that may reach 25 m	Recent deposits with shallow saline or brackish ground water	1 700	1	Chai, 1974, 1975 and 1976.
Peat Swamp Forest	Varies from floristically rich mixed swamp forest to stands in which all canopy trees belong to one species, *Shorea albida*	Varies from uneven, tall, dense canopy through smooth, very tall, sparse canopy of *Shorea albida* to low stunted forest in centre of some swamps.	Oligotrophic peats of plateaux and alluvium not subject to flooding. Main vegetation of extensive coastal plain	14 700	12	Anderson, 1961(a). 1964(a), and 1973; Leo and Lee, 1971.
Kerangas Forest	Poorer than MDF. Patches where single tree species may be dominant or even form pure canopy stands. Dipterocarps generally of minor importance	Dense even canopy with high albedo. Canopy lower and simpler than MDF. More light at ground level and more undergrowth than MDF	Podzols and related soils developed on very siliceous parent materials, mostly Quaternary marine terraces on sandstone dipslopes	3 700	3	Brunig 1961, 1965, 1969(a) and 1974.
Riverain Forest	Fairly rich, contains commercially important *Shorea macrophylla* (engkabang) and *Eusideroxylon zwageri* (belian)	Irregular but distinctly storied canopy	Recent alluvial deposits along river courses subject to flooding of varying frequency.	500	<1	Browne, 1955; Brunig, 1969(b)
Limestone Forest	Rich, very distinctive flora. Dipterocarps of minor importance	Tall, uneven canopy	Limestone soils, which include acid mors as well as calcareous soils.	<500	<1	Anderson, 1965
Forests of higher altitudes						
Montane Forest	Generally poorer than MDF. Oaks, Chestnuts, Laurels, Conifers and Ericaceae common. *Vatica* spp are only common Dipterocarps.	Low canopy of twisted, stunted trees, festooned with moss at higher altitudes	Altitudes above 1000 - 1200 m	<1000	<1	Browne, 1955
Non-forest and young secondary Forest	Pure stands or simple mixtures of macrophyllous trees, shrubs and grasses (particularly *Imperata cylindrica*). Also cleared agricultural and urban areas	Varies from moderately low, even canopied forest to open grassland.	Areas of high human population densities	32 200	26	Anderson, 1960; Dunsmore and Anderson, 1970
			Total	124 400	100	

* Areas rounded from Palmer's (1971) revision of 1966 planimetric estimates (Lands and Survey Dept. 1966).
Non-forest has probably increased significantly since then, mainly at expense of MDF.

Figure 2.1



Adapted from F.I.D.P. (1974(c))

1.2 The Mixed Dipterocarp Forest

The Mixed Dipterocarp Forest represents the peak of rainforest development in Sarawak, and shows most of the characteristics of the tropical rainforest as classically described by Richards (1952). It is a high forest, with a deep, dense leaf canopy, the upper surface of which is very uneven. The canopy reaches to 35-55 metres above the ground, with rare emergent trees exceeding 60 metres. The trees are mostly evergreen mesophylls and notophylls, and their dense shade reduces light intensity at the forest floor to 1-5% of full daylight. The trees of the upper canopy generally have long, straight and relatively slim boles. The crown points may be up to 30 m above the ground.

The trees are the dominant life form in the MDF, as in other tropical rainforests. The other life forms such as the herbs, the mechanically dependent autotrophic plants, the heterophytes, and also the animal and microbicial communities are all dependent on the complex spatial and microclimatic structure provided by the trees (Richards, 1952; Cintron, 1970; Cowley, 1970; Hutton and Rasmussen, 1970; Murphy, 1973; Whitmore, 1975). As the dominant group of autotrophic plants, the trees also dominate the trophic structure of the forest.

It has been shown that, for some forests, data from the upper canopy trees alone are sufficient for satisfactory floristic classification of the whole forest, with data from the subordinate synusiae being more or less superfluous (Williams and Webb, 1969).

The canopy of the MDF does not show marked stratification, but it is useful to consider the upper canopy trees, whose crowns are able to receive at least some direct solar or sky radiation, separately from those of the understorey which are in perpetual shade, except for sunflecks. The understorey consists of a mixture of young stock and the mature individuals of specialised understorey species, which go through their whole life cycles in shade conditions. The young stock of the upper canopy species are at first able to resume rapid growth and to be recruited into the upper canopy, if released by an increase in light, such as follows the appearance of a canopy gap (Whitmore, 1975). This capacity declines with very prolonged stagnation.

The low light intensities restrict the forest floor undergrowth, which is not usually very dense and which hampers progress on foot less than popularly imagined. There are a number of shrubs and forbs but the vegetation is often sparse or dominated by tree and palm seedlings and saplings.

The root systems of tropical rainforests have been less intensively studied than the above ground structures. In some of the literature there is a tendency to exaggerate the shallowness of rooting in these forests. There is undoubtedly a concentration of fine roots in the upper horizons (Huttel, 1973; Klinge, 1973 (a)) and much of the trees' uptake of mineral nutrients appears to take place at, or very close to, the soil surface (Jordan, 1970 (a); Kline and Mercado, 1970; Stark, 1971).

However, a considerable number of coarse and medium diameter roots can extend to, and beyond, a depth of one metre. The forest probably exploits the subsoil for moisture and mechanical support, even if nutrient uptake there is very limited. The vertical and lateral patterns of root distribution appear to be quite plastic within species, as well as showing interspecific differences. They can vary widely with site conditions (Foerster, 1971; Huttel, 1973; Kerfoot, 1963; Freezaillah and Sandrasegaran, 1969; Longman and Jenik, 1974). Poor subsoil drainage and aeration in particular seem to restrict rooting depths.

Observations in the Sarawak MDF suggest that a common root system morphology in large trees on well-drained sites is one without a central taproot, but with thick vertical sinkers off the main horizontal laterals. These sinkers are often located at 2-10 metres from the bole and often penetrate to below one metre. A few have been seen at depths of more than three metres, penetrating well into incompletely weathered shale. The horizontal laterals are generally shallow, often within 30 cm of the soil surface. They may stretch up to 30 metres from the stem, so that a tree's rooting diameter may be at least as great as its crown diameter. Similar kinds of root structure have been noted in lowland rainforests in Colombia (Foerster, 1971).

Floristically, the tropical rainforest is the richest of all major plant formations, and the Sarawak MDF is no exception. The Sarawak checklist currently contains over 2,700 tree species, and the true total may be nearly 3,000. The MDF is the richest and most extensive forest type in the state and contains over 2,000 tree species.

The great floristic richness ranges from regional down to very local scales. In the Brunei MDF, Ashton (1964 (a)) found as many as 130 tree species attaining diameters (at breast height, 1.3 m) of at least 10 cm on a single hectare. Similar levels of local floristic richness occur in the Sarawak MDF (Ashton, 1973). Although high, these are not exceptional levels of floristic diversity and are exceeded in other tropical rainforests (e.g. Poore, 1968).

If the size criteria for inclusion are reduced, the number of species enumerated on small areas can be considerably increased. In a Central Amazonian rainforest, an area of 0.2 ha was found to contain almost 2,000 individual plants of height 1.5 m or greater, belonging to over 500 species (Fittkau and Klinge, 1973). At an even smaller scale, a 50 m^2 plot in the same forest contained 76 individual plants belonging to at least 52 species (Klinge, 1973 (b)). It is thought that similar orders of localised floristic diversity obtain in the Sarawak MDF.

A corollary of the combination of high local floristic diversity and the large sizes of individual mature trees is that the population densities of large trees of all species are low, although seedlings and saplings of a single species may be locally and temporarily profuse. Even the more abundant species may have less than 10 large trees per hectare and the rarer species may be represented by only a single individual in several hectares. Thus a characteristic of the MDF, and of many other tropical rainforests, is the absence of single species dominance in the larger tree synusiae. However, although no single species dominates the MDF, this forest type derives its name from the dominance of the larger size classes and the upper canopy by members of the numerous *Dipterocarpaceae* family (Ashton, 1964 (b) and 1968).

A characteristic of the dipterocarps in these forests is their irregular and gregarious flowering and fruiting. Periods of 2-9 years may pass with no, or only insignificant, flowering and fruit production. Then the majority of mature trees, not only of one but of nearly all the species of diptocarps in an area, will flower in a single season (Cockburn, 1975). The possible adaptive advantages of this mechanism through herbivore satiation have been discussed by Janzen (1970). As dipterocarp seeds do not remain viable on the forest floor for long, the irregular fruiting means that there is no constant soil-borne reservoir of propagules available. The growing seedlings and saplings therefore represent a site's total regeneration potential, except immediately after a fruiting. The protection and encouragement of this regeneration is the basis of successful dipterocarp silviculture (Wyatt-Smith, 1961 (a); Nicholson, 1965; Fox, 1971).

The irregularly-produced fruits of the dipterocarps are mostly heavy and unpalatable (McClure, 1966; Medway, 1972) and seed dispersal is generally poor (Burgess, 1972; Liew and Wong, 1973). This leads to loosely clumped distributions of progeny around parent trees (Singh, 1974; Poore, 1968; Richards, 1973). These groves are not generally dense enough to even approach single species canopy dominance. The extent to which this clumping tendency is manifest decreases as dispersal ranges increase and the groves become more diffuse. It also depends to some extent on the abundance of the species. For the most abundant species, the groves may tend to coalesce at their fringes and become indistinguishable (Fox, 1971).

A feature of tropical rainforests, including the MDF, is the close spatial proximity and apparent ecological similarity of closely related and morphologically similar taxa. The actual degree of overlap in ecological ranges is debatable, and forms part of the subject of the present study.

The high incidence of hollow decay in the mature trees of the MDF has already been noted, and is discussed further in Chapters 3 and 7.

.2 The Environment of the Mixed Dipterocarp Forest

.2.1 Climate

The climate of Sarawak is characterised by high, even temperatures and heavy, relatively aseasonal rainfall. In global classifications the state's climate is of the equatorial perhumid type. Even in the more detailed classification that was devised to cover only the climatic range of Indonesia, all Sarawak meteorological stations qualify for the most humid, aseasonal category (Schmidt and Ferguson, 1951; Mohr et al., 1972).

Mean air temperatures are in the range of 26-29^{o}C. in the lowlands. Monthly means vary less than 2^{o}C. In the open, the diurnal range is about 5-8^{o}C., being higher in periods of clear, dry weather. Under high forest, the diurnal range is about 2-3^{o}C. at ground level but increases to about 5-8^{o}C. at the top of the canopy (Baillie, 1970 (a)).

The mean annual rainfall varies from about 2,500 mm to over 5,000 mm. The approximate isohyets are shown in Figure 2.2(a). Compared with many other tropical areas, the rainfall is evenly distributed through the year. However, detailed examination of the rainfall records shows that there are definite seasonal tendencies in some areas. The seasonality depends on the local balance between the equinoctial and monsoonal elements of the climate (Beckinsale, 1957). The equinoctial pattern tends to give localised, high intensity convectional rainstorms of short duration. These are relatively evenly distributed through the year, although they may show slight post-equinoctial peaks (I.M. Scott, pers.comm., 1972). They tend to be less frequent in coastal areas (Andriesse, 1972).

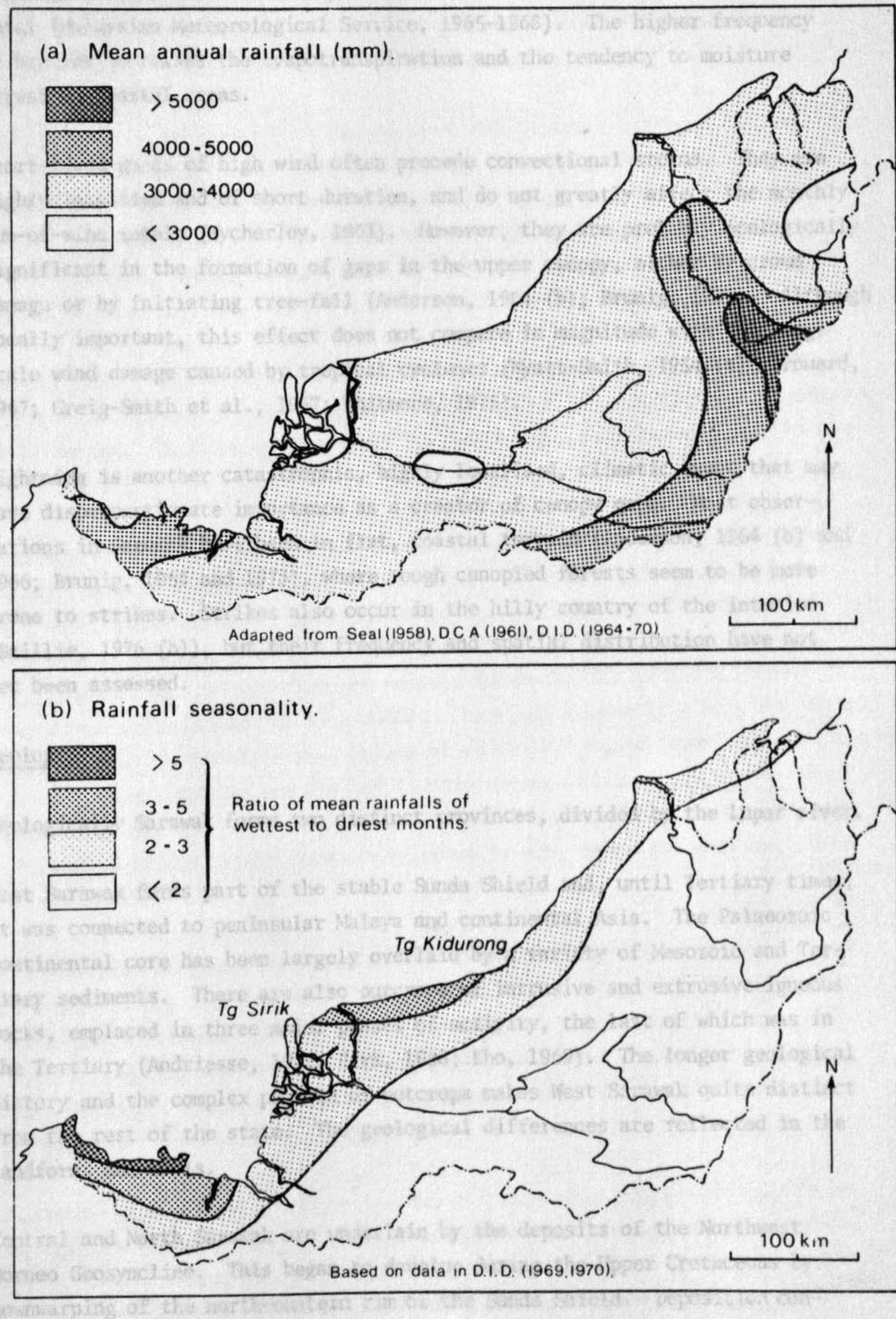
The monsoonal pattern gives a seasonal distribution of rainfall. The on-shore Northeast monsoon around the end of the year brings heavy and persistent rainfall, particularly to north-facing coasts. The effect is not quite so strong on north-west and west-facing coasts, especially in North Sarawak. The effect of this monsoon (the 'landas') decreases inland, although it still remains quite noticeable in the interior. The mid-year Southwest monsoon is fairly dry, as the highlands of Indonesia cast a slight rain shadow.

The important contribution from the monsoonal element gives a seasonal rainfall distribution in coastal areas, particularly on the north-facing coasts of West Sarawak, and the Tanjong Sirik-Tanjong Kidurong stretch of Central Sarawak. In the interior of the state, the dominance of the equinoctial element gives a rainfall that is evenly distributed through the year. Figure 2.2(b) shows the approximate isopleths of rainfall seasonality.

Open water evaporation and evapotranspiration varies little through the year, or between the four Sarawak meteorological stations that have had Class A Evaporation Pans for substantial periods. The monthly mean is about 150 mm, with daily values fluctuating from 0 to 10 mm. The high evaporation rates mean that fairly intense moisture deficits will occur towards the end of periods of sustained dry weather. Because of the relative constancy of evaporation, the occurrence of moisture deficit is largely determined by variations in the rainfall. Examination of continuous meteorological records has shown that periods of moisture stress on vegetation occur more frequently in areas with seasonal rainfall distributions, and may be quite frequent in coastal areas, even on deep soils. They appear to be rare events in the interior (Brunig, 1969 (c) and 1971; Baillie, 1976 (a)).

Overall run-of-wind is low, and flat calm accounts for more than 50% of all readings at inland stations. Land and sea breezes reduce the proportion of flat calms to about 20% at coastal stations, but even there wind velocity

Figure 2.2 RAINFALL IN SARAWAK



readings in excess of 5 metres per second account for less than 5% of the total (Malaysian Meteorological Service, 1965-1968). The higher frequency of breezes increases the evapotranspiration and the tendency to moisture stress in coastal areas.

Short-lived gusts of high wind often precede convectional storms. They are highly localised and of short duration, and do not greatly affect the monthly run-of-wind totals (Wycherley, 1963). However, they are probably ecologically significant in the formation of gaps in the upper canopy, either by crown damage or by initiating tree-fall (Anderson, 1964 (b); Brunig, 1973). Although locally important, this effect does not compare in magnitude with the large scale wind damage caused by tropical cyclones (Wyatt-Smith, 1954 (a); Brouard, 1967; Greig-Smith et al., 1967; Whitmore, 1975).

Lightning is another catastrophic, highly localised, climatic event that may have disproportionate importance as a creator of canopy gaps. Most observations in Sarawak have been in flat, coastal terrain (Anderson, 1964 (b) and 1966; Brunig, 1964 and 1973), where rough canopied forests seem to be more prone to strikes. Strikes also occur in the hilly country of the interior (Baillie, 1976 (b)), but their frequency and spatial distribution have not yet been assessed.

.2.2 Geology

Geologically Sarawak forms two distinct provinces, divided by the Lupar river.

West Sarawak forms part of the stable Sunda Shield and, until Tertiary times, it was connected to peninsular Malaya and continental Asia. The Palaeozoic continental core has been largely overlaid by a variety of Mesozoic and Tertiary sediments. There are also outcrops of intrusive and extrusive igneous rocks, emplaced in three major phases of activity, the last of which was in the Tertiary (Andriesse, 1972; Kirk, 1968; Kho, 1969). The longer geological history and the complex pattern of outcrops makes West Sarawak quite distinct from the rest of the state. The geological differences are reflected in the landforms and soils.

Central and North Sarawak are underlain by the deposits of the Northwest Borneo Geosyncline. This began to develop during the Upper Cretaceous by downwarping of the north-eastern rim of the Sunda Shield. Deposition continued spasmodically throughout the Tertiary, with the arcuate axis of deposition moving gradually towards the North and North east. After uplift and erosion, the earlier deposits in the South and South west probably contributed much of the material for the later deposits to the North.

The detailed interpretation of the geosynclinal deposits has been the subject of considerable discussion (e.g. Haile, 1963; Brondijk, 1963; Geiger, 1963). There have even been doubts about the use of a strongly sedimentary-oriented geosynclinal model at all. It has been suggested that many of the structures are volcanically controlled, and that the deposits have been volcanically reworked (McManus and Tate, 1976; R.B. Tate, pers.comm., 1977).

Despite these reservations, Haile's (1968 (a)) sedimentary model, based on the concepts of Aubouin (1965), is preferred because of its simplicity and emphasis on lithology. It forms the basis of the following geological resumé, and of Table 2.2 and Figure 2.3.

The deposits of the Upper Cretaceous and Early Tertiary (Paleogene) are mainly pelagic, and argillaceous rocks predominate. Prolonged phases of shallow water conditions appear to have intervened periodically, giving rise to massive beds of fine-grained greywacke sandstones. Although subordinate throughout the stratigraphic column, they may account for up to 35% of the thickness of some formations (Leichti et al., 1960). There was evidently a long hiatus in deposition in the Mid-Tertiary, during which the Paleogene deposits were intensely folded and faulted and subject to mild metamorphism. Many of the argillaceous rocks are now phyllitic. Angles of dip in these deposits, collectively referred to as the Rajang Group, are generally very steep and many are close to vertical.

Unconformable Neogene deposition commenced in marine conditions, giving a predominance of argillaceous rocks in the Baram Group. Intercalated fine-grained sandstones are common and may be locally dominant. Later deposition was in isolated lagoonal and deltaic basins. This led to the predominantly arenaceous sediments of the Brunei Group. Although sandstones predominate, they are generally fine- or very fine-grained.

The whole geosynclinal area was tectonically unstable throughout the Tertiary. The Neogene deposits are deformed, although not as intensely as those of the Rajang Group. There have also been intermittent bursts of unequivocal igneous activity, giving rise to outcrops of basic and acid igneous rocks. These outcrops are not very extensive.

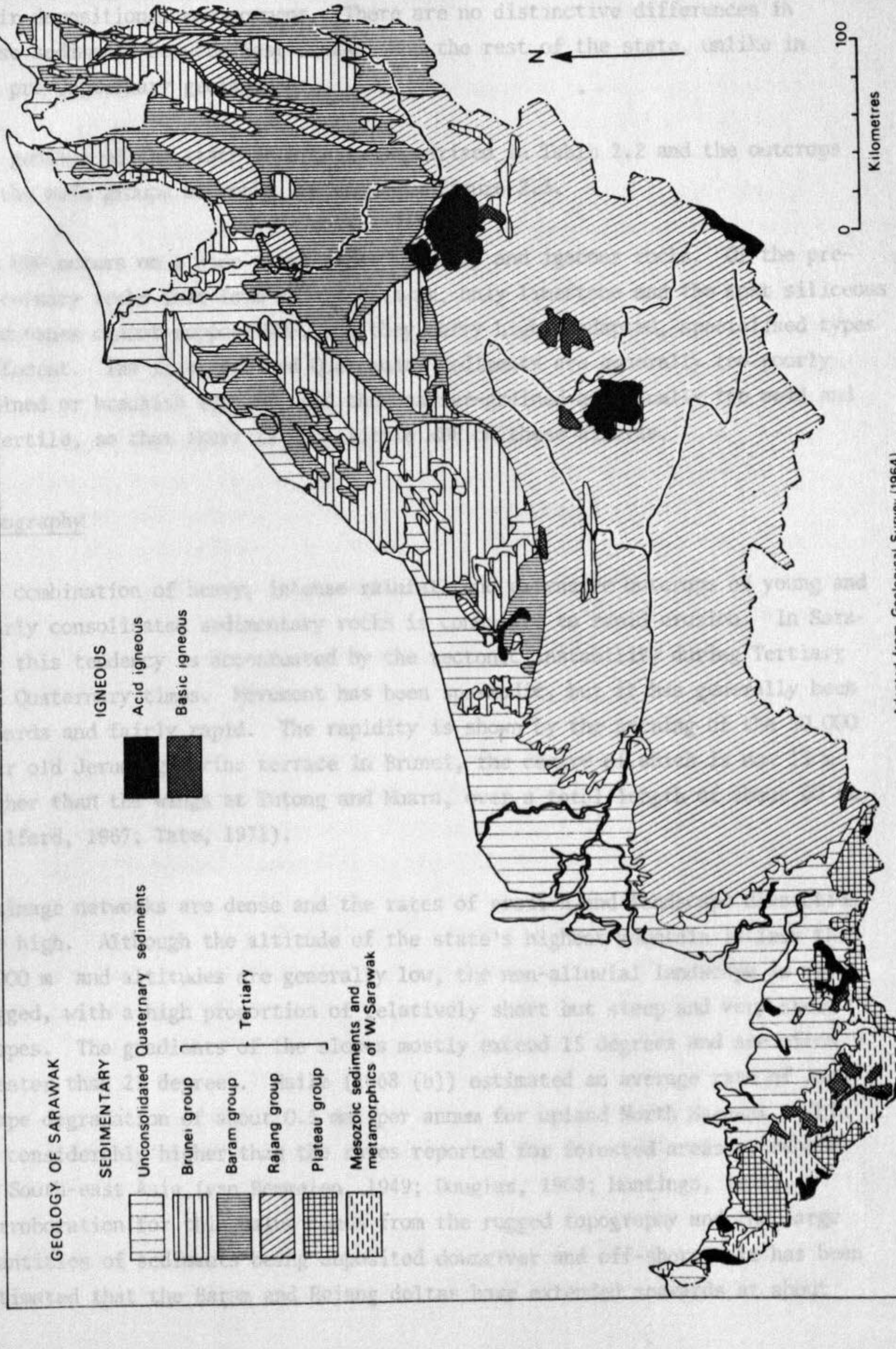
TABLE 2.2 Geology and Topography in Sarawak

Sedimentary		Formation and Lithology	Characteristic Landforms	Natural vegetation[†]
Group	Age			
Quaternary		Shallow water, fluvial and marine. Textures vary from clay to sand	Alluvial landforms	Mangrove, Peat Swamp, Riverain and Kerangas Forests
Brunei	Neogene (Miocene-Pliocene)	Isolated shallow water basins. Predominantly arenaceous. Moderate dips.	Prominent cuestas with marked dip and scarp structures	MDF and Kerangas Forest
Baram	Neogene (Eocene-Miocene)	Shallow marine. Shales predominant with some marls and sandstone. Moderate dips	Low dissected terrain with some minor cuestas	MDF and occasional Kerangas Forest
Rajang	Paleogene (Upper Cretaceous-Lower Miocene)	Mostly pelagic but some shallow marine. Predominantly argillaceous but sandstones locally important. Steep dips.	Strike-aligned steep-sided, narrow-topped ridges.	MDF
Plateau (West Sarawak only)	Tertiary (Upper Cretaceous -Miocene)	Isolated shallow water basins. Predominantly arenaceous. Moderate dips.	Prominent cuestas with marked dip and scarp structures	MDF and Kerangas Forest
Mesozoic (West Sarawak only)		Very varied. Includes shales, marls, sandstones.	Very varied	MDF and occasional Kerangas Forest
Mesozoic - Pliocene		Limestone	Turmkarst	Limestone Forest*
Igneous				
Palaeozoic - Quaternary		Intrusive and extrusive. Basalts, granites, granodiorites, dacites, rhyolites.	Varied	MDF

* Group names after Haile (1963 and 1968(a))

† All geological groups, except Quaternary, alluvium carry small areas of Montane Forest.

Figure 2.3



Adapted from Geological Survey (1964)

In coastal areas and along the lower reaches of the main rivers, there are extensive Quaternary deposits. They vary greatly in texture, according to their depositional environment. There are no distinctive differences in these sediments between West Sarawak and the rest of the state, unlike in the pre-Quaternary geology.

The geology of the state is briefly summarised in Table 2.2 and the outcrops of the main groups of rocks are shown in Figure 2.3.

The MDF occurs on a wide range of sedimentary and igneous rocks. Of the pre-Quaternary rocks that form upland Sarawak, only limestone and the most siliceous sandstones cannot support MDF, and they carry highly adapted, specialised types of forest. The finer-grained Quaternary sediments are generally too poorly drained or brackish for MDF, and the coarser-grained are usually too acid and infertile, so that there is very little MDF on these alluvia.

2.2.3 Topography

The combination of heavy, intense rainfall and extensive outcrops of young and poorly consolidated sedimentary rocks is conducive to rapid erosion. In Sarawak this tendency is accentuated by the tectonic instability during Tertiary and Quaternary times. Movement has been spasmodic, but it has generally been upwards and fairly rapid. The rapidity is shown by the arching of the 50,000 year old Jerudong marine terrace in Brunei, the centre of which is now 15 m higher than the wings at Tutong and Muara, over a total length of about 60 km (Wilford, 1967; Tate, 1971).

Drainage networks are dense and the rates of erosion and landscape dissection are high. Although the altitude of the state's highest mountain is less than 3,000 m and altitudes are generally low, the non-alluvial landscape is very rugged, with a high proportion of relatively short but steep and very steep slopes. The gradients of the slopes mostly exceed 15 degrees and are often greater than 25 degrees. Haile (1968 (b)) estimated an average rate of landscape degradation of about 0.5 mm. per annum for upland North Sarawak. This is considerably higher than the rates reported for forested areas elsewhere in South-east Asia (van Bemmelen, 1949; Douglas, 1968; Huntings, 1971). Corroboration for this value comes from the rugged topography and the large quantities of sediments being deposited downriver and off-shore. It has been estimated that the Baram and Rejang deltas have extended seawards at about

5-10 m per year for the past 6,000 years (Haile et al., 1963; Anderson, 1964 (a); Lallane de Haut, 1965; Tate, 1971).

In upland areas the main erosion processes are slopewash, soil creep, treefall and landslips. Piping is also locally important, but seems to be confined to the gentler slopes, with maximum gradients of about 25 degrees (Loeffler, 1974; Baillie, 1975). The relative contributions from these processes to the total erosion rate fluctuate widely in space and time, and no comprehensive estimates of their relative importance in Sarawak have yet been attempted.

Judging from the frequent occurrence of microterracing, formed by the accumulation of wash detritus behind surface roots on steep slopes, slopewash appears to be active and important in the Sarawak MDF. However, it is thought that only run-off is an active agent. The thin litter layers seem to provide sufficient protection against splash erosion, and well-developed stone or branch-capped soil columns are rare under undisturbed forest. Andriesse (1972) regarded slopewash processes as relatively unimportant in the forested areas of West Sarawak. This is corroborated by findings in Indonesia (van Bemmelen, 1949) and West Malaysia (Morgan, 1974). In contrast, workers in Papua and New Guinea found slopewash to be an important erosion process (Ruxton, 1967; Loeffler, 1977).

Soil creep is thought to be important in upland Sarawak. The boundary between the apparently mobile material in the solum and the *in situ* weathering parent material beneath is often marked by a stone layer of variable thickness. In a pit dug and remeasured according to the method developed by Young (1963), on a 10 degree slope in West Malaysia, the rate of creep at a depth of 7 cm was about 5 mm per annum (Eyles and Ho, 1970). The rate decreased rapidly with depth, and did not show the second maximum, attributed to subsoil shearing, that is found in soils in the wetter parts of Puerto Rico (Lewis, 1976). Similar pits have been established in the pericoastal hills of Central Sarawak, but no results are as yet available (I.M. Scott, pers.comm., 1974). It is anticipated that rates in Sarawak will generally be higher than in West Malaysia because of the steeper slopes and the greater abundance of 2:1 lattice clay minerals (Lewis, 1976).

Treefall is ecologically very important, and it also appears to be a major topogenic process. Shallow depressions and low, irregular hummocks, formed by the roughly lenticular bodies of soil torn up by toppling trees, are a common sight in some MDF areas. Assuming that the average Sarawak MDF tree-fall displaces a lens of soil 5 m in diameter and 70 cm maximum thickness at the centre, and that half of the displaced soil falls back into the excavation, and that soil disturbance by treefall has a mean return time of 2,000 years, it can be estimated that treefall is equivalent to a mean erosion rate of 0.1 mm per annum. Treefall is often initiated by wind pressure on the crown (Denny and Goodlett, 1956). In Sarawak it is often associated with the localised and brief gusts of strong wind that precede convectional rainstorms.

Shallow landslips are quite common in the Sarawak MDF on certain rock types, particularly some of the intricately intercalated shale, siltstone and fine sandstone sediments of the Brunei group (Wall, 1966). There are probably long periods of relative stability interrupted by short periods of fairly intensive and widespread landslip activity. A similar pattern has been described for gully formation in West Malaysia (Morgan, 1974). Sarawak landslip activity is associated with periods of very heavy rainfall, such as the exceptional Northeast Monsoon storms of early 1963 (Jeeps and Gates, 1963). It has been suggested that, in some forests on steep slopes, the high, localised loading imposed on the regolith by the mass of a large individual tree may override the binding effects of its root system, so that a mature forest cover may increase the landslip hazard (Dryness, 1967). This may be an important consideration in the MDF, and is discussed further in Chapter 7.

In attempts to interpret the present physiography of Sarawak, there have been considerable discussions on the identification of erosion surface remnants dating from a possible Pleistocene peneplanation cycle (Leichti et al., 1960) or cycles (Kirk, 1957; Wilford, 1967; Wall, 1967). The main evidence for such cycles is the high degree of summit concordance over large areas, particularly in Central Sarawak. However, the actual unequivocal erosion surface remnants are few, small and difficult to interpret.

Because the non-alluvial landscape of Sarawak consists almost entirely of steep, active slopes, identification of earlier erosion surfaces is less helpful and important than in some other tropical areas, such as parts of Africa (e.g. King, 1967). In West Sarawak the interaction of current erosion processes with underlying rock types was found to be much more useful in interpreting the present landscape (Andriesse, 1972).

This conclusion also seems to be applicable in other parts of the state, and the landscapes of Central and North Sarawak also show marked lithological control. In Central Sarawak the near-vertical beds of the Rajang Group give rise to a distinct ridge and vale topography. The stratigraphically subordinate greywacke beds are more competent than the predominant shales, and remain as positive relief features, forming the spines of symmetrical, steeply-flanked and narrow-topped ridges. These often persist for many kilometres along the line of the geological strike. In the lower, pericoastal areas these ridges have been eroded to form more rounded, hilly landscapes. These hills also show considerable strike-alignment (Scott, 1965).

On the Neogene sediments in North Sarawak the arenaceous rocks form positive relief features. However, as the angles of the dip, though variable, are generally quite low, the sandstone beds tend to form cuestas rather than symmetrical ridges. The most marked scarp- and dip-slopes are found on the outcrops of the Brunei Group, which have very thick sandstone beds. A similar type of landscape is produced by the lithogically similar Plateau Group of Tertiary sediments in West Sarawak. In North Sarawak, some of the sandstone beds in the Baram Group sediments are also massive enough to form marked cuestas, but, in general, the predominantly argillaceous rocks of this group give a low, very dissected terrain, similar to that of the Mesozoic shales of West Sarawak. Dissection of the cuesta landforms is extremely active.

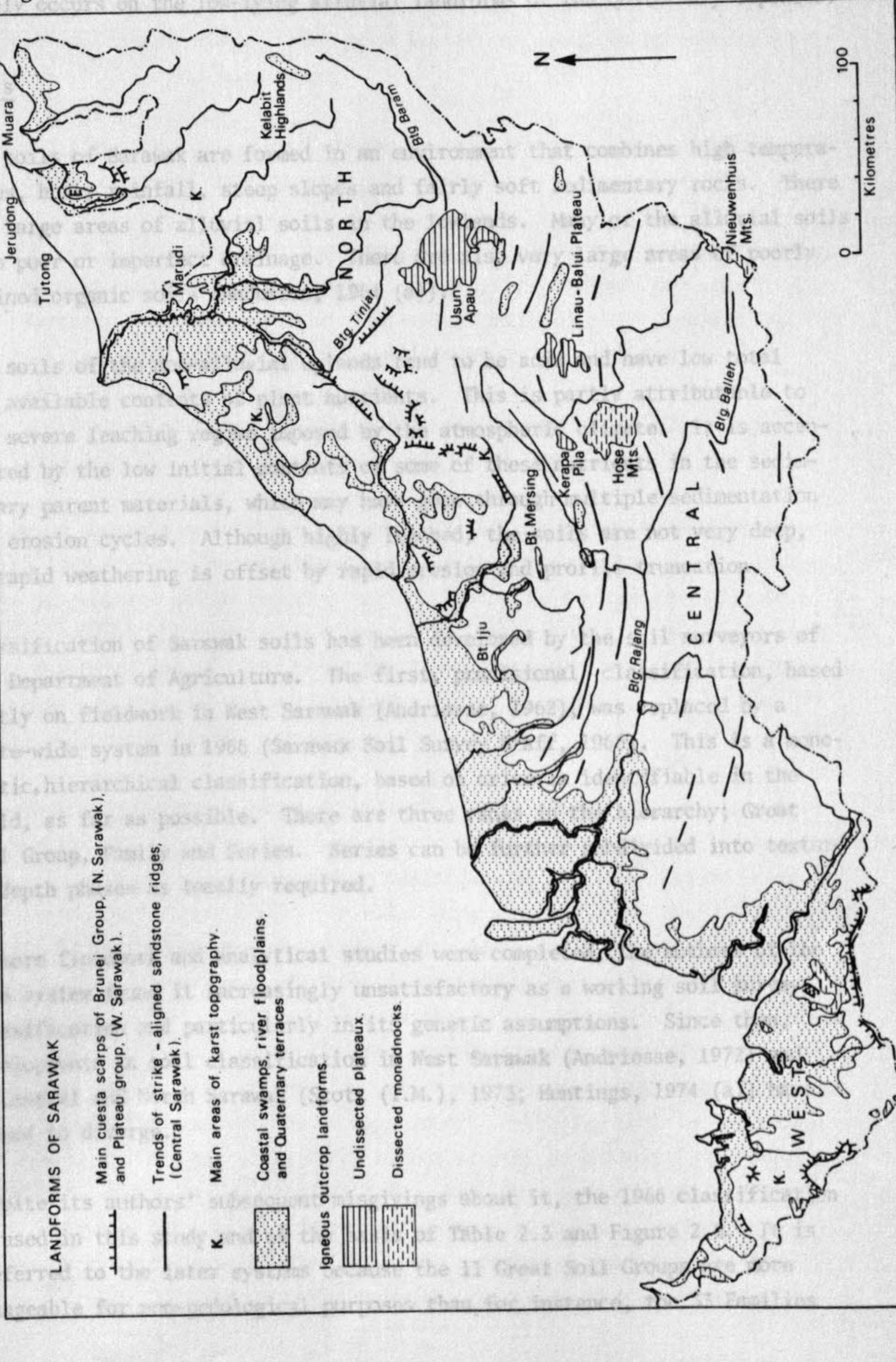
Throughout the state, the limited outcrops of limestone give a distinctive Turmkarst topography with prominent steep-sided and spectacularly pinnacled hill masses, which rise almost sheer out of flat solution platforms (Wilford and Wall, 1965).

The topography of the outcrops of igneous rocks is very varied, depending on the age, structure and situation of the rock. Some of the Quaternary extrusives of the interior of Central Sarawak form fairly undissected plateaux, whereas the older rocks tend to give more dissected monadnock landforms (Kirk, 1968).

The association of geology and landforms is summarised in Table 2.2, and the generalised distribution of the major landscape types is shown in Figure 2.4.

As can be seen in Table 2.2, MDF is the natural vegetative cover of all the upland landforms of Sarawak except for areas above about 1,000 m the karst

Figure 2.4


LANDFORMS OF SARAWAK
Main cuesta scarps of Brunei Group, (N. Sarawak), and Plateau group, (W. Sarawak).
Trends of strike - aligned sandstone ridges, (Central Sarawak).
K. Main areas of karst topography.
Coastal swamps, river floodplains, and Quaternary terraces
Igneous outcrop landforms.
Undissected plateaux.
Dissected monadnocks.
N
0 100
Kilometres
Muara
Jerudong
Tutong
Marudi
Kelabit Highlands
NORTH
Btg Baram
Btg Tinjar
Usun Apau
Linau-Balui Plateau
Nieuwenhuis Mts.
Btg Balleh
Hose Mts.
Kerapa Pila
Bt. Mersing
Bt. Iju
Btg Rajang
CENTRAL
WEST
K.

areas, and some areas on the dipslopes of very siliceous sandstones. MDF rarely occurs on the low-lying alluvial landforms of the Quaternary deposits.

2.4 Soils

The soils of Sarawak are formed in an environment that combines high temperatures, heavy rainfall, steep slopes and fairly soft sedimentary rocks. There are large areas of alluvial soils in the lowlands. Many of the alluvial soils have poor or imperfect drainage. There are also very large areas of poorly drained organic soils (Anderson, 1964 (a)).

The soils of the non-alluvial uplands tend to be acid and have low total and available contents of plant nutrients. This is partly attributable to the severe leaching regime imposed by the atmospheric climate. It is accentuated by the low initial contents of some of these nutrients in the sedimentary parent materials, which may have gone through multiple sedimentation and erosion cycles. Although highly leached, the soils are not very deep, as rapid weathering is offset by rapid erosion and profile truncation.

Classification of Sarawak soils has been developed by the soil surveyors of the Department of Agriculture. The first, provisional classification, based mostly on fieldwork in West Sarawak (Andriesse, 1962), was replaced by a state-wide system in 1966 (Sarawak Soil Survey Staff, 1966). This is a monothetic,hierarchical classification, based on criteria identifiable in the field, as far as possible. There are three ranks in the hierarchy; Great Soil Group, Family and Series. Series can be further subdivided into texture or depth phases,as locally required.

As more fieldwork and analytical studies were completed, the authors of the 1966 system found it increasingly unsatisfactory as a working soil survey classification and particularly in its genetic assumptions. Since then, developments in soil classification in West Sarawak (Andriesse, 1972) and in Central and North Sarawak (Scott (I.M.), 1973; Huntings, 1974 (a)) have tended to diverge.

Despite its authors' subsequent misgivings about it, the 1966 classification is used in this study and is the basis of Table 2.3 and Figure 2.5. It is preferred to the later systems because the 11 Great Soil Groups are more manageable for non-pedological purposes than,for instance, the 33 Families of the 1973 Central and North Sarawak classification. It also has the advantage of being applicable, however imperfectly, to the whole state, and not just in certain parts. Finally, it has become familiar inside and outside Sarawak (e.g. Huntings, 1969).

Table 2.3 summarises the Great Soil Groups, and Figure 2.5 shows the approximate distribution of the more extensive groups.

From Table 2.3 it can be seen that the MDF grows mainly on the very extensive Red Yellow Podzolic and associated Skeletal soils, developed from the predominant Tertiary sedimentary rocks. The less extensive Lateritic soils are also entirely under MDF, except for small areas at high altitude.

Other soils which have small areas of MDF, or intergrades to MDF, are the Grey White Podzolic soils, Brown Forest soils and Podzols.

Shallow or moderate solum depth, predominant reddish yellow or yellow colours, and the lack of sharp horizon boundaries are the main morphological features of the Sarawak Red Yellow Podzolic soils. Litter layers are generally thin, reaching maximum thicknesses of about 5-8 cm on some of the coarse textured soils, but often patchily absent in the finer textured families. The litter decomposes rapidly, and the soil organic matter is incorporated into the profile by intense faunal action.

The organically darkened, brown or yellowish brown mineral topsoil is generally shallow, and gives way to a brownish or reddish yellow subsoil within 15 cm. In some profiles developed on sandstones of low iron content, pale upper subsoil layers may qualify as albic horizons, but these are not common. Subsoil colours become gradually redder with depth, although this tendency may be weak. The reddening is often accompanied by multicoloured mottling of variable intensity. This mottling is thought to be partly due to incomplete weathering of the parent material, but very localised hydromorphism may also contribute, particularly in the fine textured soils overlying shales (Foelster, 1973). The mottles and patches of more intact weathering rock increase with depth, until softer weathering rock, either *in situ* or colluvial, predominates, generally at depths of one metre or less. Rock-free sola of more than two metres depth are very rare, and are mostly found in the more permeable and stable coarse textured soils developed from sandstones, particularly on ridge crests. A common feature of the underlying weathering rock are the thin

TABLE 2.3 Soils of Sarawak

Great Soil Group (1)	General characteristics		Parent Material	Land form	Natural Vegetation (2)	Approximate Area (3) (as % of state)
	Morphological	Analytical				
Skeletal Soils	Shallow, poorly horizonated soils lithic (hardrock) or paralithic (soft rock) within 25 cm of surface of mineral soil. Texture and colour varies with parent material.	Very variable according to parent material, but generally less weathered than corresponding deeper soil	All main rock types, but sedimentaries predominant	Mainly steep slopes	Mainly MDF, but also Kerangas, Riverain, Limestone and Montane Forests	30-45(4)
Brown Forest Soils	Yellowish brown-brown non-skeletal soils. Texture variable but no apparent increase in clay with depth.	C.E.C. and base status moderate, increasing to high in subsoil	Marls or calcareous shales Sandy lenses in limestone.	Low dissected shale terrain or karst	MDF. Possibly pockets of Limestone Forest	Neglig-ible
Lateritic Soils	Reddish brown fine textured non-skeletal soils. No apparent increase in clay with depth. Stable fine crumb or blocky structure, friable; porous, permeable subsoil	Clay minerals predominantly kaolinitic and goethite. Base status and reserve phosphorus relatively high.	Basic-intermediate igneous and metamorphic rocks	Generally moderate-steep slopes on prominent hills	Mainly MDF. Also some Montane Forests	
Red Yellow Podzolic Soils	Non-skeletal soils. Brownish or yellowish upper horizons becoming redder in subsoil. Textures variable. Increase in clay with depth cometimes apparent. Dense blocky subsoil structures, some with shiny ped coatings	Clay minerals dominantly illite-vermiculite with some kaolinite on shales, but kaolinite dominant in coarse textured soils from sandstone. Base status and reserve phosphorus generally low	Mainly sedimentary rocks	Hill slopes. Also patches on high river terraces	MDF. Also some Montane and MDF-Kerangas intergrade Forests	30-50(4)
Grey White Podzolic Soils	Similar to Red Yellow Podzolic soils except that matrix colours are paler	Similar to Red Yellow Podzolics except for lower free sesquioxides	Sedimentary rocks and old marine alluvia	Low hilly terrain and dissected marine terraces.	Kerangas and Kerangas-MDF Intergrade Forests	1
Podzols	Thick mor litter layer. Bleached white or light grey eluvial horizon abruptly over black or dark brown humus pan within 120 cm of mineral soil surface. Usually light textured.	Very poor in all nutrients Low clay content may include secondary quartz	Quartose marine alluvia and siliceous sandstones	Marine terrace tops and gently graded cuesta dip-slopes	Mainly Kerangas Forest. Occasional Kerangas-MDF Intergrade Forests.	1
Gley soils	Non-skeletal soils with wet, grey matrix in top metre.	Not extensively sampled	Mostly fluvial alluvia. Also crystalline rocks	Mostly flood plains or low terraces. Also plateaux tops.	Riverain Forest. Montane Forest	3
Saline Gley Soils	Similar to Gley Soils but with Saline or brackish groundwater	High salt content. Often with pyrites, which oxidise on drainage giving very low pH	Marine and Estuarine alluvia	Tidal flats	Mangrove Forest	2
Peat Soils	Wet wood-derived peat. Ranges in depth from 25 cm to 25 m.	Oligotrophic. Very low ash and nutrient contents	Generally over alluvia. Also pockets on sedimentary rocks.	Basin swamps behind beaches or levees. Also pockets on plateaux	Peat Swamp Forest	12
Recent Alluvial Soils	Non-gleyed, non skeletal poorly developed soils on recent deposits. Textures variable	Relatively high base status	Recently deposited alluvia	Levees and beaches	Riverain and Beach Forests	1

Notes: (1) Great Soil Groups after Sarawak Soil Survey Staff (1966) except for omission of doubtful Ground Water Laterite Group.

(2) Forest types after Brunig (1969 (b)).

(3) Areas to 1% (Baillie, 1970(b)) from soil map of Sarawak (Sarawak Soil Survey Staff, 1968(a)).

(4) 1968 Soil Map has compound mapping unit of shallow Red Yellow Podzolic and associated Skeletal soils, covering 63% of state.

Figure 2.5


SOILS OF SARAWAK
Lowland soils (Peat, Podzols, Grey White Podzolic, Gley and Recent Alluvial soils).
Deeper Red Yellow Podzolic soils (with minor Grey White Podzolic soils).
Lateritic soils and associated Skeletal soils.
Skeletal soils and shallower Red Yellow Podzolic soils
Limbang
Miri
Bintulu
Sibu
Simanggang
Kuching
N
0
100
Kilometres
Adapted from Sarawak Soil Survey, 1968 (a)

TABLE 2.4 Physical and chemical characteristics of Sarawak MDF soils

Great soil Group	Red		Yellow		Podzolic		Lateritic	
Family (1)	Arip series		Nyalau		Merit		Tarat	
Profile Number (2)	FG4A		F3AU		F3Q		FC11A	
Parent material	Rhyolite		Greywacke		Shale		Basalt	
Horizon (3)	Topsoil	Subsoil	Topsoil	Subsoil	Topsoil	Subsoil	Topsoil	Subsoil
Sample depth (cm)(4)	0-3/5	50-60	0-5	30-40	0-10	45-55	0-10	30-40
Clay (<2 μm) %	44.8	39.4	14.9	15.6	36.7	33.7	50.1	58.2
Silt (2-50 μm) %	29.5	27.8	7.6	12.6	42.6	46.6	19.6	23.0
Sand (>50 μm) %	25.7	32.8	77.5	71.8	20.7	19.7	30.3	18.8
Total porosity %	68.1	63.8	(50-65) (5)	(40-50)(5)	(55-65)(5)	(50-60)(5)	69.7	67.2
Organic C %	8.5	0.3	2.5	0.2	2.1	0.3	4.2	1.3
Total N %	0.49	0.07	0.26	0.03	0.26	0.12	0.44	0.19
C:N ratio	17.3	4.9	9.6	6.7	8.0	2.5	9.6	6.8
pH (water)	4.3	4.6	3.8	4.2	3.8	4.7	4.7	5.0
Exchangeable Ca me %	(0.8)(6)	(0.3) (6)	Tr	Tr	0.7	0.1	(0.6) (7)	(0.1)(7)
" Mg "	(0.4)	(Tr)	0.2	0.1	1.0	0.5	(1.6)	(0.7)
" K "	(0.2)	(0.1)	0.2	Tr	0.5	0.1	(0.4)	(0.1)
" Na "	(0.2)	(Tr)	Tr	Tr	0.1	0.1	(0.3)	(0.1)
TEBme %	(1.6)	(0.5)	0.4	0.1	2.3	0.8	(2.8)	(0.9)
CECme %	(17.4)	(5.5)	10.9	6.9	14.4	13.1	(14.8)	(10.5)
Base saturation %	(9.3)	(7.0)	3.7	1.4	16.0	6.1	(19.3)	(8.8)
'Available' P ppm	(7) (6)	(2) (6)	(6) (8)	(1) (8)	(6)(8)	(3) (8)	(4) (7)	(<1) (7)
'Reserve' P "	83	16	170	50	400	270	1290	940
" Ca "	210	200	100	90	320	170	2340	1180
" Mg "	520	790	310	470	3120	4780	5430	4390
" K "	825	1185	2170	3480	6710	6860	6170	5870
Fe + Al oxides %	(15-35)(9)	(20-45)(9)	2.8	5.0	13.6	13.6	(39.4)(7)	(50.3)(7)

Notes to Table 2.4

(1) Family names according to 1966 classification (Sarawak Soil Survey Staff, 1966), except for Arip series (Scott, 1973).

(2) Analyses refer to profiles described and sampled in the course of this project.

(3) The horizons summarised are the upper mineral A1 horizon (topsoil) and the subsoil horizon with the best developed blocky structure, ped coatings and reddish colours (subsoil).

(4) For profile numbers FG4A and FC11A, the samples analysed were bulked composites from 5 profile pits (see 4.3.2). The mean subsoil sampling depths are given in this table.

(5) Profiles F3AU and F3Q are located on FIDP plots, and have no bulk density or porosity data. The ranges given are from similar soils on MDF ecological plots.

(6) Profile FG4A has no exchangeable cation data. The exchangeable cations and available P data shown are from a similar profile (B353-9) described and sampled by Scott (1970).

(7) Profile FC11A has no exchangeable cations data. The exchangeable cations and available P data are from the Tarat family profile prepared for the field excursion of the 1968 Malaysian Soils Conference (Sarawak Soil Survey Staff, 1968 (b)). The 1968 profile may have an andesitic component in the parent material. Data from an unequivocally basalt-derived profile are given in Andriesse (1975), but the methods of analysis are not identical to those used in the other profiles in this table.

(8) There are no data for availables for these profiles. The figures given are from similar soils prepared for the field excursion of the 1968 Malaysian soils Conference (Sarawak Soil Survey Staff, 1968 (b)).

(9) No data on Fe and Al oxides in rhyolitic soils in Sarawak are yet available. Limits for these oxides in the Abok family in West Sarawak (Sarawak Soil Survey Staff, 1966 and 1968 (b); Andriesse, 1975) are given.

material. There are considerable contents of moderately well crystallised kaolinite throughout the profile. There may be a little crystalline goethite but only very slight, if any, traces of gibbsite (Dumbleton, 1965; Jenkins, 1974; Andriesse, 1975). There may be considerable quantities of amorphous secondary oxides and hydroxides, including silica.

In the coarse textured soils, derived from sandstones, well crystallised kaolinite is the dominant clay mineral. There are some 2:1 lattice minerals, mainly illites, but these are less important than in the fine textured soils. There are considerable contents of goethite and there may be slight traces of gibbsite (Jenkins, 1974; Andriesse, 1975).

As can be seen in Table 2.4, the Red Yellow Podzolic soils are very acid, with pH (water) values of less than 4.0 in many topsoils. Soil pH values generally increase with depth but are often less than 5.0 throughout the solum. The coarse textured soils tend to be more acid than those of finer texture. The low pH values reflect the very low base status. The exchangeable bases in many subsoils total less than 1 milliequivalent per 100 g of fine earth, especially in the coarse textured families. Because of the 2:1 lattice clay minerals present, cation exchange capacities are moderate, sometimes exceeding 15 milliequivalents per 100 g of fine earth. This means that base saturation percentages are extremely low, often less than 10%. It appears that aluminium dominates the exchange complex (Andriesse, 1975).

As can be seen in Table 2.4, organic matter contents in the mineral horizons of the Red Yellow Podzolic are low to moderate. Mineralisation is rapid and C:N ratios are generally below 12. Total nitrogen levels in the topsoils are mostly in the 0.3 - 0.5% range. Available phosphorus levels, as determined by extractants such as very dilute acids or weakly acidic buffered salt solutions, are usually extremely low. Even reserve phosphorus (extractable by ignition with concentrated hydrochloric acid - see Appendix I) may be less than 100 ppm in some of the coarser textured subsoils. Trace element levels tend to be deficient, as has been specifically determined in the case of boron (A.R.C., 1968). However, elements characteristic of highly leached soils may be present in toxic quantities. Manganese toxicity has been suspected in black pepper *(Piper nigrum L.)* (Sim, 1972), and aluminium toxicity has been noted in the same crop (de Waard and Sutton, 1960).

As expected, this combination of chemical characteristics indicates very low chemical fertility, and these soils generally give marked responses to inorganic fertilisers (e.g. Raj, 1968). The main exception is the lack of any potassium response on the fine textured soils (Bailey, 1967; Dunsmore, 1970). Exchangeable potassium levels are often less than 0.5 milliequivalents per 100 g of fine earth. Reserve potassium levels are high, and may exceed 5,000 ppm This potassium is probably held as interlayers by the 2:1 lattice clay minerals. Although not extracted by the neutral ammonium acetate leaching, it appears to be eventually available to crops (Beckett, 1964; Talibudeen, 1974). It may also act to increase the stability of these minerals against weathering (de Alwis and Pluth, 1976).

In general the chemical fertility of the fine textured soils is higher than that of the coarser textured families, but the latter tend to have better physical characteristics, particularly porosity, aeration and solum depth (Huntings, 1974 (a)).

The Lateritic soils are not extensive, being restricted to the outcrops of basic crystalline rocks. Although not deep by general humid tropical standards, their profiles are generally deeper than those of the Red Yellow Podzolic soils. Textures are generally fine and, in the field, there is generally no apparent increase in clay content with depth. The increase in clay content shown by the granulometric analyses summarised in Table 2.4 is atypical. Moreover, interpretation of conventional granulometric analyses in these soils is problematical, due to the high contents of free iron and aluminium oxides and the consequent difficulties of complete clay disperison (Andriesse, 1975).

Colours are generally brown or reddish brown throughout the profile, although there is one olive brown series of very limited extent. Structures are crumb or fine blocky, with no, or only weakly developed, ped coatings. Bulk densities are low and total porosities are higher than in the Red Yellow Podzolic soils, particularly in subsoil horizons. The subsoils have a friable consistence (Baver, 1972).

Poorly crystallised kaolinites are the dominant clay minerals, with subordinate but substantial contents of goethite and persistent traces of gibbsite (Andriesse, 1975). There are no 2:1 lattice clay minerals, so that coefficients of linear expansion (COLE) are generally lower than in Red Yellow Podzolic soils of comparable texture.

As can be seen in Table 2.4, the Lateritic soils, although very leached, are slightly more fertile than the Red Yellow Podzolic soils. Soil pH values range from 4.5 to 6.0. The sum of the exchangeable bases can be as high as 20 milliequivalents per 100 g of fine earth in the topsoils, and over 4 in the subsoils. CEC values vary greatly according to the external pH. In buffered neutral or alkaline conditions, values of up to 40 milliequivalents per 100 g of fine earth may be recorded. However, at field pH, the values are much lower, and indicate that the true base saturation percentage values are considerably higher than shown in Table 2.4, with subsoil values sometimes reaching 60% (Andriesse, 1975).

Although not apparent in marked organic darkening of the soil colours, organic matter contents are generally slightly higher than those of the Red Yellow Podzolic soils. The C:N ratios are generally below 12, and mineralisation appears to be rapid. Although available phosphorus values are very low, reserve phosphorus levels are much higher than in the Red Yellow Podzolic soils, and may exceed 1,000 ppm, even in the subsoils.

The high subsoil porosities and good aeration conditions, and the moderate chemical fertility make these amongst the most productive and flexible agricultural soils in Sarawak. They are able to support a wide range of crops, including demanding species such as cocoa and coffee.

The morphological characteristics of the Red Yellow Podzolic and Lateritic soils vary considerably and over short distances. The chemical properties are also thought to vary rapidly. The most variable properties are likely to be those most affected by forest processes. These include organic matter and exchangeable cation properties. Properties that are related more directly to the soil parent material such as texture, reserve nutrients and free iron and aluminium oxides are thought to be less variable.

The nature and sequence of processes in the pedogenesis of a group of Red Yellow Podzolic and Lateritic profiles in West Sarawak have been studied in considerable detail by Andriesse (1975). This has helped to clarify the apparently anomalous combination of properties of these soils, particularly in the Red Yellow Podzolics. Some features, such as the absence of weatherable primary minerals, the low pH values and the extremely low exchangeable base status are indicative of intense leaching and advanced weathering, either in the current cycle of pedogenesis, or previous to the sedimentary deposition of the parent material. Other features such as the persistence of the 2:1 lattice clay minerals and the generally shallow sola, conventionally indicate less mature stages of soil development.

Andriesse concluded that the first stage in soil development is the rapid breakdown and desilication of the primary minerals, leading to an initial relative accumulation of iron and aluminium. These are incorporated into secondary clay minerals or remain in various free oxide and hydroxide forms. These secondary products are then themselves subject to rapid weathering, and the iron and aluminium are partially leached, giving rise to a minor but consistent relative accumulation of silica, either in amorphous form or as secondary chalcedony. The final stage is furthest advanced in the more highly weathered surface hrozons. It is possible that the mobilised aluminium may be redeposited in the subsoil, due to small but critical increases in soil pH. The leached iron does not appear to be redeposited within the solum, and Andriesse suggests that it is the source of the iron oxide and hydroxide deposits often found along joints, bedding planes and old root channels in the subjacent weathering rock. Lateral leaching into the surface drainage system may also account for some of the iron removed, as throughflow is thought to be important in these soils (Morgan, 1973; Baillie, 1975).

This sequence of podzolic leaching of iron and aluminium, after initial lateritic weathering and desilication, differs from the model proposed for pedogenesis in upland Sabah, where prolonged and intense lateritic weathering after initial argilleluviation is thought to lead to soils dominated by kaolinites and iron and aluminium oxides and hydroxides (LRD, 1975). The breakdown of clay minerals in surface horizons proposed by Andriesse accounts for the subsoil increases in clay content, where they occur, without invoking lessivage. Micromorphological evidence has shown this movement of intact clay particles to be generally insignificant in Sarawak soils.

Although leaching is intense and weathering very rapid, continual erosion and profile truncation prevents the sequence outlined by Andriesse reaching its final stages, the Podzols, except in deep and permeable soils on stable sites, and derived from parent materials initially low in weatherable minerals. In most of upland Sarawak the less mature Red Yellow Podzolic soils are the norm, and the Podzols only form on quartzose alluvia or on stable, gently graded siliceous sandstone cuesta dip slopes (Andriesse, 1969 (a) and (b), 1970).

The postulated immaturity of most of the Red Yellow Podzolic soils partly accounts for the persistence of the 2:1 lattice clay minerals. However, the exchangeable base status of these soils is much lower than expected for soils with high contents of these minerals. This apparent disequilibrium is not unique to Sarawak and significant contents of these minerals have been noted in shale-derived soils on stable sites in other humid tropical weathering regimes, such as in Natal (Le Roux, 1973), Amazonia (Sombroek, 1966; RADAM, 1974) and Vietnam (Litsitsnya, 1968). It may be that the stability of the micaceous clay minerals is only relative, and that their accumulation is due to the even more rapid weathering of the other parent material minerals (Makumbi and Jackson, 1977). Other mechanisms that may contribute to the stability of these minerals include coating by secondary iron and aluminium oxides (Eswaran and Yeow, 1976) and the contraction of the lattice structure by interlayer, non-exchangeable potassium (de Alwis and Pluth, 1976). The high levels of exchangeable aluminium may also play a part.

The Sarawak Red Yellow Podzolic soils bear only a superficial resemblance to the soils of that name as originally described in the south-eastern United States (Simonson, 1949; Thorp and Smith, 1949; McCaleb, 1959). These are soils in which intact clay translocation is one of the most important pedogenic processes. The lack of evidence for this process in the Sarawak soils was one of the main causes for the dissatisfaction with the 1966 Sarawak soil classification by its creators. However, it is of interest that a similar situation has arisen elsewhere, and soils similar to the Sarawak Red Yellow Podzolics still bear that name in Amazonia (RADAM, 1974) and Thailand (Pisoot, 1974).

The apparently anomalous combination of soil properties noted in the discussion on pedogenesis makes it difficult to satisfactorily assign the Sarawak Red Yellow Podzolic soils to the higher categories of the most widely applied global soil classifications, i.e. the USDA (Soil Survey Staff, 1975) and the FAO (Dudal, 1968; FAO-UNESCO, 1974) systems.

The coarser-textured soils, dominated by kaolinitic clay minerals, can probably be assigned to the Oxisols (USDA) or Ferrasols (FAO), although the contents of 2:1 lattice clay minerals and the CEC values may be rather high. The finer textured soils have too high contents of 2:1 lattice clay minerals to qualify for this group. The lack of granulometrically or micromorphologically confirmed argillic horizons means that they cannot be assigned to the Ultisols (USDA) or Acrisols (FAO), the group which contain the original Red Yellow Podzolic soils of the United States. By default, therefore, the Sarawak Red Yellow Podzolic soils are generally classified with the weakly developed soils, i.e. the Inceptisols (USDA) or Cambisols (FAO). However, the absence of weatherable primary minerals and the very low base status are at variance with the general concept of this group (Andriesse, 1972 and 1975; I.M. Scott, 1973; Huntings, 1974 (a)).

Anomalies of this kind are inevitable in the widespread application of monothetic hierarchical classifications, based on profile properties (Webster, 1968). They can be avoided in polythetic systems, and in the horizon property-based system of FitzPatrick (1971).

The range of soil textures and depths means that the Sarawak Red Yellow Podzolic soils encompass a wide range of edaphic potential. However, the textural and depth variants generally occur in extremely intricate distributions, so that, even at semi-detailed level, it is often necessary for soil surveyors to map compound units of families and/or series. With such mapping, it is difficult to estimate the relative extents of the component families, but point sampling indicates that the medium and fine textured soils are of about equal importance, and considerably more extensive than the coarse textured soils. The relative lack of very coarse textured soils is mainly due to the greywacke nature of many of the sandstones, which yield significant clay contents on weathering (Huntings, 1974 (a)).

A common distribution pattern in the ridge and vale topography of Central Sarawak is for deep, coarse or medium textured sandstone-derived soils to occur along the ridge crests. The steep flank slopes generally have shallower and less developed soils. These are fine textured where the underlying shales predominate, but may be medium textured where there is substantual colluvial admixture of sandstone material from upslope. Depths vary greatly and over short distances, but tend to be less on the steeper slopes. A similar pattern, with deeper soils on ridge crests, has been found on shale outcrops of Southern Thailand (Huntings, 1974 (b); Virgo and Holmes, 1977).

In North Sarawak, the pattern is less clear. On the gently graded dipslopes there is a complex of Podzols, Skeletal and deep coarse or medium textured Red Yellow Podzolic soils (e.g. Brunig, 1974 (a)). On the scarp slopes and on the active slopes of the valleys dissecting the dipslopes, soils are generally shallower and of finer texture.

CHAPTER 3

LITERATURE REVIEW

Site-Forest Relationships in the Sarawak Mixed Dipterocarp Forest and Similar Forests

.1 Introduction

Since the pioneer phytogeographical studies of Schimper (1903), there has been general agreement that the main subdivisions of the tropical rainforest formation are determined by climatic seasonality and altitude. Details of criteria, nomenclature and boundary placement may vary, sometimes quite considerably, but the same basic classification pattern is apparent throughout the literature. The climatic gradient runs from the evergreen forests of the humid, aseasonal tropics, to the forest-savannah ecotone in subhumid or semi-arid, very seasonal climates (Richards, 1952 and 1961; Walter, 1971; Holdridge et al., 1971; Whitmore, 1975; Lawton, 1976). There is similar broad agreement on the existence of a marked altitudinal gradation from lowland to montane forests.

Except for the Montane Forest, all the Sarawak forest types in Table 2.1 are variants of the evergreen forests of aseasonal tropical lowlands. In this climatic regime there may be periods of moisture deficiency (see section 2.2.1) but these are irregular and relatively short and mild. Variations in elements of the climate such as temperature or moisture are ecologically less important than at higher altitudes and latitudes. The most extensive forests in this group are floristically very rich and structurally and ecologically complex, and generally exhibit the characteristics already described for the MDF (see section 2.1.2), except that they are not necessarily dominated by the dipterocarps, or any other single family. These forests are able to develop in most of the edaphic environments available and may be regarded as the 'climatic climax' vegetation. There are, however, some edaphic environments that are too severe for these forests. These restrictive sites carry specialised, highly adapted forests, which are generally lower, poorer and simpler than the climatic climax forests. Throughout the humid tropics similar kinds of edaphic limitation give rise to structurally and ecophysiologically similar forests. For instance, the Kerangas forest of Sarawak is similar in structure, but not floristic composition, to heath forests in tropical podzols in Africa and the neotropics (Lemée, 1961; D.R.C., 1967; Richards, 1961). The forests of these and other restrictive environments may be regarded as 'edaphic climax' forests. The important role of site conditions in determining their distribution is not generally in doubt.

There is much less agreement on the importance of edaphic influences on the floristic composition and the distribution of individual species within the 'climatic climax' forests, such as the MDF. From the description of the MDF (see section 2.1.2) it is clear that, for a tree to eventually reach the upper canopy, it is necessary for there to have been a parent fruiting in close proximity, for conditions to be favourable to successful germination, seedling and sapling survival, and finally for an opportune gap to appear in the overhead canopy to permit sapling recruitment. Some of these processes are infrequent and irregular and others have high attrition rates, so that the final recruitment of any individual tree represents the end result of a concatenation of chance events. For some workers, chance considerations alone are sufficient to account for the condition of the forest at any time and place. They regard the environment as fairly uniform and nearly optimal. They do not think that the environment plays a significant part in interspecific competition. They attribute the current floristic diversity of the forests to a relatively uninterrupted evolutionary history, extending back to the Tertiary. During this time, genetic drift and non-adaptive speciation has been possible because of the assumed non-demanding nature of the environment (e.g. Fedorov, 1966). A consequence of this assumed lack of significant site-species interaction is that the floristic composition of any part of the forest can vary at random through the whole range of the forest. The forest is seen as a slowly but continually changing kaleidoscopic continuum. Floristic subdivisions would therefore probably be unstable over long periods, and their instantaneous spatial distribution would not relate to site conditions.

Other workers have found that there appears to be consistent associations of species in some forests and that these associated groups show a degree of fidelity to restricted ranges of site conditions. For these workers, chance considerations alone are inadequate to account for the observed distributions. At one or more stages in the sequence from fruit production by the parent tree to eventual recruitment into the upper canopy, the edaphic environment appears to exercise a differential effect in interspecific competition. This enables site compatible species to have a higher probability, though not the certainty, of survival and maturity. The edaphic environment is not seen as near-optimal, but as a definite constraint on plant growth. The floristic diversity of the forest is seen as the result of a long and relatively uninterrupted evolutionary history. In this case, however, the evolution is thought to have been highly adaptive, leading to a multiplicity of species, each competitively successful in adapting to its own restricted niche. The coexistence of large numbers of such species in small areas seems to indicate a high degree of exploitation of the resources of the environment by the total forest ecosystem (Ashton, 1969).

It is improbable that all species are equally edaphically selective and there may be many that are quite indiscriminate. If these predominate in an area, forest-site interactions will not be readily apparent, and the forest will appear very much as the result of the combination of chance events and reproductive pressures. A similar situation will occur where edaphic conditions are almost uniform or vary only gradually with distance. Chance factors and reproductive pressures will again appear to be all-important. In such habitats, other agents of natural selection may, of course, be highly effective.

In the following sections, some of the literature relevant to the importance of the edaphic role is reviewed. The sections deal separately with the Sarawak and Brunei MDF, other dipterocarp-dominated evergreen forests in Malaysia, and finally with other evergreen forests of aseasonal, tropical lowlands.

3.1.2 Previous Research in the MDF of Brunei and Sarawak

Brunei is included with Sarawak in this section because much of the later work in Sarawak stems directly from Ashton's pioneer studies in Brunei. The MDF of the Brunei enclaves is contiguous with, and indistinguishable from, that of the surrounding areas of North Sarawak (see Figure 1.1).

From observations made during his taxonomic studies of the dipterocarps of Brunei (Ashton, 1964 (b)), Ashton gained the general impression that many dipterocarps, including some of commercial importance, had restricted edaphic ranges, and that the floristic and structural variation within the MDF was as much related to topography, geology and soil type as it was to altitude. In order to test this impression objectively, he established 100 one acre (0.4 ha) plots. Fifty of these were on deep, coarse and medium textured sandstone-derived Red Yellow Podzolic soils on low, rolling, pericoastal terrain at Andalau. The other fifty were in rugged terrain at Kuala Belalong in the Ulu Temburong, with fine textured Lithosols or shallow and medium depth Red Yellow Podzolic soils derived from shales. Using the computationally simple Bray and Curtis (1957) technique, he objectively ordinated the plots of the two sites, using the basal areas of all species present. The first two floristic axes extracted by the ordination strongly reflected clines in soil and topographic conditions (Ashton, 1963 and 1964 (a)), thus objectively confirming his initial impressions. He later revisited the plots and collected more detailed site data. The floristic data were reworked using more recent and complex classification and ordination techniques. The initial findings of strong edaphic effects on the distribution of species were confirmed (Austin et al., 1972). At Andulau the highest stature forests occur on the deeper soils, generally on the more gently graded slopes, but the highest levels of floristic diversity were found on the slopes. Taking the Kuala Belalong data in isolation, it was found that both stature and floristic diversity were highest on the deeper soils of the lower broad ridge and spur crests.

Because of the potential practical importance of these findings, a major project in Ashton's Sarawak programme in 1963-6 was the verification and extension of these Brunei studies.

A major part of the present project involved revisiting and pedologically recharacterising Ashton's Sarawak plots and therefore details of his field and statistical methods are described in Chapters 4 and 5. He collected a great deal of forest and site data, the full analysis of which will still take a considerable time. However, he has reported his preliminary findings at some length (Ashton, 1973). In brief, he found that, even when extending the range of observations to a much greater variety of rock and soil types than those sampled in Brunei, edaphic factors are major influences on variation within the MDF. The forests range in structure and floristics from dense, relatively low statureforests, with few stems in the larger size classes, on acid parent materials such as rhyolite and siliceous sandstone, through the floristically very rich, structurally complex, high volume forests on intermediate parent materials such as dacite, greywacke, and mixed sandstones and shales, to the very high volume, but floristically less diverse, forests found on the most eutrophic parent materials, such as slightly calcareous shales and basalts. These forests are characterised by a high number of stems in the larger size classes.

As well as influencing forest structure and overall floristic diversity, edaphic conditions also related to the distribution of many individual species. As in Brunei, many of the dipterocarps showed more or less restricted edaphic ranges.

In addition to the detailed static forest and site data collection, Ashton initiated dynamic growth studies, by establishing permanent plots. These enable the monitoring of girth increments, tree mortality, and recruitment by periodic remeasurement. The results from the first 5 years period showed that the most rapid increments in timber volume were on the soils of intermediate texture and fertility. Volume increments on the coarse textured infertile soils were about the same as those on fine textured, fertile Lateritic soils derived from basalt. However, in the sandy soils growth was very much concentrated in the smaller, sub-commercial, size classes, and mortality amongst these was high. On the fertile soils, the growth was mostly in the larger stems. Stand density and the volume increment in the smaller size classes appeared to be suppressed by the very dense shading of the deep, thick upper canopy.

Because of the covariance of many site and soil properties along the generalised soil fertility gradient described, it is difficult to isolate which are the critical edaphic factors. It seems clear that chemical fertility is important, as well as soil physical conditions, and Ashton suggested that phosphorus may be the single most important nutrient. Phosphorus appeared to be critical at reserve levels below about 150 ppm. Above this, phosphorus appeared to decline in importance and other nutrients or possibly some non-chemical factors may be more influential. In contrast to the Brunei findings, local topography is unimportant over the whole range of forest sampled. If, however, restricted segments of the forest spectrum are examined, topography does appear to be a major factor. This is probably the situation obtaining in the Brunei plots, which were located on a restricted range of sedimentary rock types.

Ashton and his co-workers have not concentrated solely on the role of edaphic factors in these forests. Biological processes, evolutionary history and Quaternary changes in the environment have also been considered (Ashton, 1969, 1972 (a), (b) and (c), 1976; Kaur et al., 1978). Nontheless, Ashton remains a leading proponent of the importance of edaphic factors in tropical rainforests.

As the analyses of the data from the Sarawak plots are still in progress, comment on the present stage of the project is largely irrelevant. However, two points seem worth making. The first is that, so far, the existence of the soil-forest relationships has generally been inferred qualitatively from inspection of various graphical representations of arrays and relationships. Only when there are quantitative estimates of the relative importance of edaphic factors can the practical implications of the findings be evaluated. The second point is that with the distribution of plots and sites adopted (described in Chapter 4), it is difficult to separate the contribution of edaphic factors from effects of spatial proximity.

In a forest dominated by species like the dipterocarps, with poor seed dispersal, plots close together have higher probabilities of floristic similarity than plots that are widely separated, other factors remaining constant. If the edaphically similar plots in a set are also spatially close, then floristic similarity may be partly or wholly due to edaphic similarity, but there is the possibility that spatial proximity is also a contributing factor Whitmore (1975) seems satisfied that proximity does not confound Ashton's Brunei results, and that these do show real edaphic effects. Similar conclusions seem justified for the Sarawak results, as discussed in Chapter 6. The possibility of such confounding is a major problem in the interpretation of data from clumped plots in these forests. It recurs frequently in the discussions in Chapters 6 and 7.

Apart from Ashton's work, there have been no other major systematic plant ecological studies in the MDF of Sarawak and Brunei. Other plant ecologists have studied the role of edaphic factors in determining the distribution of the main Sarawak forest types (e.g. Richards, 1936 and 1963; Ashton, 1971; Janzen, 1974; Whitmore, 1975; Brunig, 1965 and 1974) and have therefore been mainly concerned with the outer limits of the MDF range. The environmental limits of the MDF have been mentioned in the course of systematic studies of other main forest types (for references, see Table 2.1). In these various studies, soil moisture status is often regarded as being at least equal in rank to soil chemical fertility as a discriminant between the main forest types.

Soil surveyors in Sarawak generally find floristic and structural variation within the MDF of only limited assistance in the delineation of soil mapping units. In contrast, the boundaries between the main forest types are found to be very good indicators of major changes in soil conditions (e.g. Dames, 1962; Andriesse, 1972; Wall, 1966; Scott, 1972; Baillie, 1972). A possible application within the MDF has been noted in North Sarawak where marked differences in the photogrammetric image of the MDF canopy have been found to relate to changes in the exchangeable base status of the soils, caused by bands of calcareous shales in the underlying rocks. Even this case is slightly marginal, as the distinctively low stature forest on the most calcareous of the shales appears to be transitional to Limestone Forest. Similarly, the soils are possibly best classified as intergrades between Red Yellow Podzolic and Brown Forest soils (C.P. Lim, pers.comm., 1971; Huntings, 1974 (a)).

The files of the Forest Department contain many early comments on soils and forest in the MDF, made by forest officers on tour. However, they are often brief and couched in qualitative terms, referring to the forest briefly as being 'good' or 'mediocre', etc., with perhaps some indications of the main timber groups present in quantity. Their interest in soils was not generally related to site effects on the forests. They were usually more concerned with the land's agricultural potential and desirability, and hence the risk of it being lost to forestry, either officially through excision or by unofficial encroachments of shifting cultivation (e.g. Carroll, 1934).

The Forest Department's forest inventory organisation, the Working Plans Section, now routinely collects soils information. This information is scant and interpreted in subjective and qualitative terms. However, although not systematic and comprehensive, these data have tended to confirm Ashton's findings on the edaphic factors.

In the reports of the recent large scale Forest Industries Development Project (FIDP) forest inventory, there are indications that site conditions were found to be of some importance. However, as the present project involved work on FIDP plots and with FIDP forest data, the main FIDP reports made only brief mention of the topic (FIDP, 1974 (c)).

3.1.3 Site-Forest Relationships in Low Altitude Dipterocarp Forests elsewhere in Malaysia

Although aseasonal low altitude dipterocarp forests are extensive outside Malaysia, particularly in Kalimantan, there is relatively little modern literature available on them. Within Malaysia, the forests most akin to the Sarawak MDF are in parts of South west Sabah (Fox, 1971). The once-extensive Lowland Dipterocarp Forest of peninsular West Malaysia also share many species and characteristics with the Sarawak MDF (Wyatt-Smith, 1961 (b)).

The climate of the southern part of West Malaysia is similar to that of most of Sarawak, although not quite as wet. In the north of the peninsula, however, the climate is more distinctly seasonal than any in Sarawak (Dale, 1959 and 1960). The peninsula has been tectonically fairly stable during Neogene and Quaternary times, and the topography at low altitudes is considerably less rugged than in Sarawak. Because of the gentler slopes and generally lower erosion rates (Douglas, 1970), the non-alluvial soils tend to be deeper and probably older than their Sarawak equivalents. Nonetheless, despite their presumed longer history of leaching, analytical data and agronomic experience suggest that they are, in general, equal or superior in fertility to most Sarawak Red Yellow Podzolic soils (Coulter, 1972). This is thought to be due to the generally higher initial base contents of West Malaysian sedentary soil parent materials. Crystalline rocks are more extensive in the peninsula than in Sarawak. Although many are of acid-intermediate composition, they give soils of higher chemical fertility than the polycyclic geosynclinal sediments of Sarawak (Law and Selvadurai, 1968).

In addition to being deeper, more stable and slightly more fertile, the lowland soils of West Malaysia appear to be less variable than non-alluvial soils in Sarawak.

In the absence of the confounding effects of steep topography and rapid soil variation, the forests show a clearer altitudinal zonation than does the Sarawak MDF. There are two distinct zones in West Malaysia within the altitudinal range of the Sarawak MDF, i.e. Lowland Dipterocarp Forest (0-300 m.) and Hill Dipterocarp Forest (300-800 m.), (Symington, 1943; Ashton, 1964 (a); Whitmore, 1975). Although altitude is important, it is of interest that the distribution of *Shorea curtisii*, one of the most conspicuous components of the Hill Dipterocarp Forest, is more influenced by topographic position and local soil moisture relations than by altitude and associated temperature changes (Burgess, 1972).

Within the Lowland Dipterocarp Forest, earlier workers generally concluded that edaphic factors have little discernible or significant effect on the local floristic composition. This appeared to be largely determined by the combination of chance factors and reproductive pressure (Symington, 1943). These general conclusions have been supported by the results of some of the later and more detailed ecological studies. Poore (1968) concluded from his comprehensive analysis of a large area of lowland forest on sedimentary rocks in Pahang that the distribution of the less common species may be influenced by site conditions, particularly drainage, but commoner species are not thus affected. The current distribution of these species may be attributed to the combination of gap frequency, reproductive pressure, localised phytogeographic migration, and chance factors. Lee (1967) concluded that soil conditions were relatively unimportant in the present distribution of mature kapur *(Dryobalanops aromatica)* trees and did not appear to substantially affect the vigour of kapur in its mature stages. In an early examination of 10 one acre (0.4 ha) plots in the Pasoh Forest Reserve in Negri Sembilan, it was concluded that edaphic conditions were of less importance than spatial proximity and chance factors in the distribution of individual species and in the floristic ordination of the plots (Wong and Whitmore, 1970).

These studies tend to be concerned with forests in gently graded landscapes, with relatively gradual soil changes. As noted above, edaphic effects are generally likely to be less apparent in such cases. These studies also had fairly limited environmental data, so that their conclusions have to be somewhat tentative.

Not all of the West Malaysian studies have concluded that edaphic factors are unimportant. In a summary of Malayan forest types, Wyatt-Smith (1961 (b)) indicated a tentative association between some of the floristic divisions of the Lowland Dipterocarp Forest and certain rock and soil types. An examination of the stature and commercial potential of the forest in the Bukit Lagang F.R., Selangor, showed considerable variation with topography and soil drainage status (Wyatt-Smith, 1960).

As already noted, Lee's (1967) general conclusion was that site conditions did not greatly affect the distribution and vigour of individual kapur *(Dryobalanops aromatica)* trees. However, some of his intermediate results do indicate statistically significant differences between the forests on the main soil series of his study sites. The bulk of the kapur-dominated forests occur on soils derived from sedimentary rocks of Triassic age. There are some groves of kapur forest on granite-derived soils but they are not extensive. Apart from parent material, soil depth appeared to be the most important soil characteristic. The kapur component of the forest appeared to be unaffected, but the non-kapur flora is much richer on the deeper soils. Lee suggests that the difference may be due to variation in site stability. On stable sites, indicated by deeper soils, the forest is able to develop relatively undisturbed some of the forest types do have wide edaphic ranges, although others, such as the Selangan Batu forests, appear to be edaphically quite restricted. He also noted that the distribution of many individual dipterocarp species appears to be controlled by site restrictions. However, soil-forest associations in these forests are apparently not strong enough for them to be of much assistance to soil surveyors (Thomas, 1968; LRD, 1975).

3.1.4 Site-Forest Relationships in other Evergreen Forests in Tropical Lowlands

Evergreen forests of aseasonal tropical lowlands outside Western Malesia do not show dipterocarp dominance, or indeed any widespread family dominance. However, there are floristic and structural affinities between some of them and the MDF, making findings on their soil-forest relationships of general relevance to the present project. Unfortunately, most comment on soils concerns the edaphic differences between the major 'edaphic climax' forest types, rather than within the 'climatic climax' forest.

Some detailed and statistically advanced investigations into soil-forest relationships in tropical rainforests have been conducted in North eastern Australia. Because the rainforest in this area is close to its climatic and latitudinal limits, the general applicability of results obtained there is questionable. Another complicating feature in some of these studies is the long distances between the study sites, so that there are possibilities of edaphic effects being confounded by climatic or regional phytogeographic trends. In general, it appears that soil parent material and chemical fertility are of major importance in determining the distribution of the major forest formations (Stocker, 1969; Webb, 1963). Phosphorus seems to be a particularly important nutrient (Beadle 1953 and 1966), although the major cationic nutrients are also important (Webb, 1963 and 1969). On a regional scale, soil physical factors seem to be less important, provided that the drainage is neither excessive nor very poor (Tracey, 1969). In a detailed study of regrowth in an artificial clearing in an otherwise intact area of subtropical forest in Queensland, both species' site preferences and probabilistic events were shown to be important in determining the distributions of individual plants and species, in space and time, up to 12 years after regrowth commenced (Webb et al., 1972).

The rainforest regions of West Africa have more seasonal rainfall distributions and more pronounced dry seasons than Sarawak. Moreover, the main climatic gradient of decreasing humidity inland is fairly steep, so that comparisons between widely separated forest areas tend to be dominated by the effects of climatic differences. Even when specifically concerned with soils, studies often refer to situations where soils and forests are each varying with a major climatic gradient rather than convarying with one another (e.g. Nye and Greenland, 1960; Ahn, 1961 and 1970; Swaine and Hall, 1976). Several authors have noted that the highest stature and timber volume forests are found at intermediate points along the humidity gradient. The relative stunting of forests in the highest rainfall areas has been attributed to poor soil aeration (Ahn, 1961 and 1970; Longman and Jenik, 1973). Low base status has also been invoked by Swaine and Hall (1976) but these authors did not examine subsoil morphological conditions and the possibility of poor drainage. The total annual rainfalls involved (< 2,500 mm) are not excessive by tropical rainforest standards, nor are the soils exceptionally leached and base deficient. This phenomenon of critically poor drainage is thought to be peculiar to Africa on a large scale. This is probably because of the extensive areas of stable and gently sloping topography, compared with the more broken tropical rainforest landscapes of Indo-Malesia and, to a lesser extent, the Neotropics.

Lemée (1961) reviewed earlier findings on soil-forest relationships within the evergreen forest of the lowlands, with particular reference to francophone Africa. Much of the material reviewed was concerned with the site differences between the major 'edaphic climax' forest types. Within the 'climatic climax' forest of the non-alluvial lowlands, soil drainage and extremes of soil fertility were generally found to be the most important of the edaphic determinants of forest composition.

The separation of the climatic and edaphic factors of the forest environment by principal component analysis was partially successful for a wide range of forest stands in Southern Nigeria. Much of the forest variation was attributable to climate or to climatically induced soil changes. However, within one of the major soil/climate units, soil parent material was also important (Hall, 1977). Similarly, there appears to be some floristic differentiation according to rock and soil type within the mainly climatic subdivisions of the closed canopy forests of Ghana (Swaine and Hall, 1976).

Detailed studies in small areas reduce the confounding by climatic variation. Unfortunately, the most detailed study of natural vegetation in anglophone

West Africa, at the Olokemeji Forest Reserve in Nigeria, is not relevant to this project because it has a markedly seasonal climate and is close to the deciduous forest-savannah ecotone (Hopkins, 1962 and 1970). Studies in the more aseasonal climatic zones have generally tended to discount site factors as major forest influences (e.g. Jones, 1955-6; Fox, 1970). However, it is clear from the detailed descriptions that topography and soil drainage were of considerable importance in the Okomu Forest Reserve near Benin, Nigeria. Marked structural and floristic changes were noted along the catena from the undissected plateau surface, down the connecting slopes, to the dissecting drainage system (Jones, 1955-6).

Moraballi Creek, Guyana, was the site of the classic pioneering study by Davis and Richards (1933-4) that first attracted attention to the influence of site conditions on local variation in an evergreen tropical rainforest. They recognised five distinct and consistent forest types along a catena running from the stunted Wallaba forest, characteristic of the leached white sands of the upper slopes and plateaux, down to the Mora forests of the poorly drained, silty soils of the valleys. Of the five types, the Wallaba, Mora, and possibly also the Greenheart forests found on the reddish brown, very coarse, sandy soils of the upper slopes, appear to be 'edaphic climax' forests. However, the mid and lower slope communities, the Mixed Forest and the Morabukea forests, are apparently edaphically determined variants of the 'climatic climax' forest.

Most other studies of soil-forest relationships in the neotropics have been concerned with the edaphic determinants of the boundaries between the major 'edaphic climax' and 'climatic climax' forests (e.g. Williams et al., 1972; Stark, 1971). However, in a detailed study of some forests in Surinam, Schulz (1960) examined the edaphic factors related to the distribution of individual species in the mesophytic forest. Many species seemed to occur in a pattern unrelated to soil conditions. Others seemed to be more or less restricted to certain ranges of soil depth, soil texture or, possibly, soil calcium and magnesium levels. The possible pitfalls in the investigation of soil-forest relationships in these extremely complex communities are illustrated by Schulz's findings for the species *Qualea rosea*. In one area it seemed to be confined to deep loose sands, whereas in a highland area some distance away it was found to be most abundant on medium and fine textured soils. This difference may be due to an interaction with altitude and climate or to ecotypic variation within the species.

In the Rio Jari area of Para state, Brasilian Amazonia, the writer saw marked edaphic restrictions on the occurrence and abundance of some of the most common upper canopy species of the native forest. The Brazil nut tree, *(Bertholletia excelsa)* is much more frequent on fine textured and slightly more fertile soils derived from shales, diabase or argillaceous alluvium. In contrast Maçaranduba *(Manilkara huberi)* is characteristic of deep, coarse textured soils derived from Tertiary fluviatile sands. These and other site preferences are marked enough for the species to be used as indicators of site conditions by working foresters and, to a lesser extent, by soil surveyors (e.g. Sombroek, 1966).

Two other major studies in the neotropical rainforests may be mentioned. First, the U.S. Atomic Energy Authority project at El Verde, in the Luquillo Experimental Forest, Puerto Rico, has provided much detailed information on the functioning of the rainforest at one site. The exchange and flows of material and energy through the ecosystem were studied in particular detail. However, relatively few comparisons were made with forests in other areas, so that the general validity of the findings is not easy to determine (Odum and Pigeon, 1970). The comparative studies that were carried out were not usually concerned with local variation, except in relation to altitude (Wadsworth, 1970). The sites compared were often in different climates (Tschirley et al., 1970) or even on different islands (Soriano-Ressey et al., 1970). Moreover, the relevance of the El Verde studies to the Sarawak MDF is reduced by the fact that the Tabonuco *(Dacryodes excelsa)* forest at the main study site appears to be floristically rather poor (Briscoe and Wadsworth, 1970; Little, 1970). It may have been subject to human disturbance (Odum, 1970 (a)). Furthermore, it appears to show adaptation to frequent hurricanes (Odum, 1970 (b)). Recurrent wind damage of this type obliterates the effects of slow-acting and relatively muted edaphic effects (Greig-Smith et al., 1967). In addition, the forest of the main study site is designated as Lower Montane Forest (e.g. Jordan, 1970 (b)), although it is at an altitude of less than 500 m. This illustrates the depression and compression of altitudinal climatic and ecological zones in island or coastal sites.

The second major study is the Life Zone Project, reported by Holdridge et al. (1971). This is generally less informative, and specifically less relevant to the present Sarawak studies than some of the El Verde results. Because of the Life Zone Project's emphasis on climate as a determinant of forest characteristics, the study sites were so distributed that separation of climatic and edaphic influences is very difficult. In the event, it does not even appear to have been attempted, despite the collection of a considerable amount of potentially valuable site data.

3.1.5 Resumé of Previous Work on Site-Forest Relationships in Tropical Rainforests

From the foregoing, brief review of some of the voluminous literature available, it is clear that there is a considerable range of opinions on the importance of edaphic inlfuences on variation in the 'climatic climax' evergreen forests of the tropical lowlands. Some of the apparent contradictions are explicable if the environmental milieu and working methods and assumptions of the individual studies are examined.

The condition of the forest at any point in time and space is the result of the interaction of physical and biological processes, current and historical. If the variation in one aspect of the milieu is more pronounced than in the others, that factor will apparently predominate as the major determinant of forest variation. Thus forests which have been subject to catastrophic disturbance, such as by wind (e.g. Wyatt-Smith, 1954 1(a); Greig-Smith et al., 1967) or by human activity (e.g. Jones, 1955-6), are unlikely to show marked edaphic influence. Even in relatively undisturbed forests, biological and chance factors will appear to predominate if site conditions are homogeneous.

In the studies where edaphic factors have been found to be important, there may be differences over relative influence of various aspects of the site conditions. Some of these discrepancies can also be resolved by examination of the relative variability of the different factors. This is shown by Ashton's Sarawak results (Ashton, 1973). For each set of plots on a restricted range of soil parent material, he found that local topography, and the associated soil changes, are major forest determinants. When sampling a wider range of forest, soil and rock types, he found that soil parent material and associated differences in chemical fertility were more important, and that the differential role of topography is diminished.

Such considerations of sampling scale mean that generalisations about the relative importance of edaphic factors are of restricted validity. They apply only for specified ranges of site and forest conditions.

Some of the differences between various studies may be partly due to the scantiness of environmental data, in contrast to the intensity of characterisation of the forest. Schulz's (1960) study in Surinam and Ashton's (1964 (a) and 1973) work in Borneo are notable exceptions.

Finally, in addition to the conflicting field evidence, there also appear to be conceptual reservations about the validity of multiple niches in very diverse plant communities. These are discussed further in Chapter 8.

3.2 Relationships between Hollow Decay and Site Conditions

3.2.1 Introduction

No systematic biological studies of the Sarawak MDF timber rot organisms, their life cycles or mechanisms of operation have yet been carried out. Unlike the other parts of the present project, the investigation of relationships between stem rot and site conditions is not a logical sequel to earlier studies. It was added to the scope of the present project because of the great economic importance of these timber rots, and in order to gain full benefit of the concurrence of the timber decay studies of the FIDP and of the present forest-site studies.

Although little is yet known about the decay organisms, the FIDP programme in the MDF included an extensive examination of the extent, severity and the practical and economic consequences of the timber rots. The FIDP study was not concerned with the site relationships of the rots. However, it was observed that the problem appeared to be slightly more severe in Central Sarawak than in the North (FIDP, 1974 (c)). The problems of the collection, analysis and interpretation of the FIDP data are discussed in detail by Panzer (1975).

Field observations showed that termites are closely associated with the rot fungi in the MDF. However, it is not known whether termite damage precedes and facilitates fungal infection, or *vice versa,* or whether the relationship is more complex. Infection of dipterocarp trees in Sabah by the black stain fungus *Botrydiploida theobromae* is through holes made by the beetles of the shothole-borer type (Thapa, 1968 and 1971). Termite activity and fungal decay of timber have been related in the dipterocarp forests of West Malaysia (Unger, 1974). Some of the fungi in these forests have also been identified but their roles in the rot process are not yet known (Hilton, 1974).

The involvement of termites illustrates the complexity of the overall rot process. Site conditions and hollow decay can interact in a variety of ways. There may be a direct site-pathogen relationship, particularly if the pathogen passes part of its life cycle as a soil inhabitant. Another possibility is that site conditions affect the relative frequencies of susceptible and durable host trees. Even if site conditions do not affect the floristic composition of the forest, they may influence the intraspecific variation in susceptibility/resistance of the potential host trees. There is also the possibility of site interaction with one or more of the disease vectors, such as termites. Finally, site conditions may influence the frequency of infection opportunity, if this depends on mechanical rupture of the host tree's epidermis, such as might be caused by stone abrasion of the roots, or wind damage to the crown.

In the absence of previous work in the Sarawak MDF, and because of the apparent paucity of studies or observations in other evergreen forests of tropical lowlands, the literature search on site-stem rot relationships was extended to forests, natural and planted, in higher latitudes. Because of floristic, structural and ecological differences between these forests and the MDF, the relevance of some of the findings to Sarawak may be tenuous. However, they do give an insight into the progress made in this general field, and do suggest possible interpretations of Sarawak data.

The review is in two sections. The first deals with a few of the recent studies that have investigated or commented upon direct relationships between site conditions and timber decay. The second section deals with relationships between site conditions and the properties of timber that are thought to be related to its durability to rot infection.

3.2.2 Direct Site-Hollow Decay Relationships

It has been suggested that, in the West Malaysian Lowland Dipterocarp Forest, susceptibility to the brittle heart type of decay is negatively related to timber specific gravity, and that the decay is less common in unfavourable growth sites, such as swamps or poorly drained lower slopes. In the better growth sites, timber is laid down more rapidly and less densely, and is less resistant to the decay (Wyatt-Smith, 1958).

Ofong (1974) observed that cankers in *Maesopsis eminii* in Uganda are more common on trees that are growing on shallow and apparently erodible soils.

This may be a case where root abrasion and increased infection opportunity is a major mechanism of the site-rot interaction.

In many studies in subtropical and temperate forests, soil drainage and moisture are the most important site factors affecting timber rot. This is shown by the dieback caused by *Phytophthora cinnamomi* in the Jarrah *(Eucalyptus marginata)* forests of Australia. Infection tends to be more serious in the moister soils on lower slopes, apparently because of the high moisture requirements of the fungus during its soil-borne, non-pathogenic phase (Batini, 1973; Shea, 1975; Weste and Ruppin, 1975).

In a comprehensive review of the effect of soil moisture status on plant root diseases, Cook and Papendick (1972) concluded that the relationships could be extremely complex, but that infection hazard generally tends to be higher in poorly drained and fine textured soils, as in the case of Jarrah dieback.

However, exceptions to this trend include the infection of loblolly pine *(Pinus taeda)* by the buttrot *Fomes annosus* in the south-eastern United States. The frequency of infection in stands was positively correlated with soil sand contents (Alexander et al., 1975). For given infection frequencies, tree mortality appears to be higher on well drained and coarse textured soils (Kuhlmann, 1973). Similar trends were found in the severity of heart rot infection in black spruce in Ontario (Basham, 1973). Heart rot infection of trembling aspen has more complex site relationships. The probability of this infection is least in medium textured and well drained soils. It increases in coarse textured soils of excessive drainage and in poorly drained sites (Basham, 1958).

Soil fertility has also been related to the incidence and severity of timber stemrots. In some studies it appears that slow-growing trees on infertile sites lay down timber of higher density and greater rot resistance than trees on more fertile soils. Examples where high soil fertility has been positively associated with high stemrot levels include the studies of Wyatt-Smith (1958), Etheridge (1958), Hollis et al. (1975), and Marks et al. (1973). However, there are other reported cases, in which nutrient stress appears to increase stemrot levels (e.g. Newhook and Podger, 1972; Garbaye and Pinon, 1973; Sutherland et al., 1973; Pobegailo, 1975). There have also been studies in which soil fertility appeared to be unimportant (e.g. Pechmann et al., 1973; Rehfuess et al., 1973; McCrackern, 1974).

3.2.3 Relationships between Site Conditions and Timber Durability and Associated Properties

The timber property that is most closely related to resistance to fungal decay is the nature and quantity of the polyphenolic secondary metabolites (Scheffer and Cowley, 1966; Bakshi and Singh, 1970; Shigo and Hillis, 1973). The deposition of these compounds is a major characteristic of the change from living sapwood to inert heartwood. Generally, the younger, outer heartwood has higher concentrations than the pith. The fungistatic potency of these compounds has been demonstrated *in vitro* and inferred *in vivo* in many studies. One of the pioneering studies was by Buckley (1931) in West Malaysia, using dipterocarp timbers.

The chemical structures of these compounds seems to be characteristic of the plants in which they occur. Many compounds are named after the genus or species from which they have been isolated. The dipterocarps have been phytochemically studied in some detail, and compounds such as dipterocarpol, dryobalanol, and shoreic acid have been isolated from their leaves, resins or timbers (e.g. Ponsinet et al., 1968; Bisset et al., 1971). Although the basic structures are invariable and genetically controlled, there may be some increase in the degree of condensation of the compounds and a consequent decrease in fungistatic potency inwards from the outer heartwood to the pith (Hillis, 1968).

Some compounds of this type also have inhibitory effects on termites and other insects (Bultmann and Southwell, 1976). The effect has been shown to be indirect in some cases, and it is the termites' symbiotic protozoa, rather than the termites themselves, that are suppressed (Carter et al., 1975; Beal, 1976).

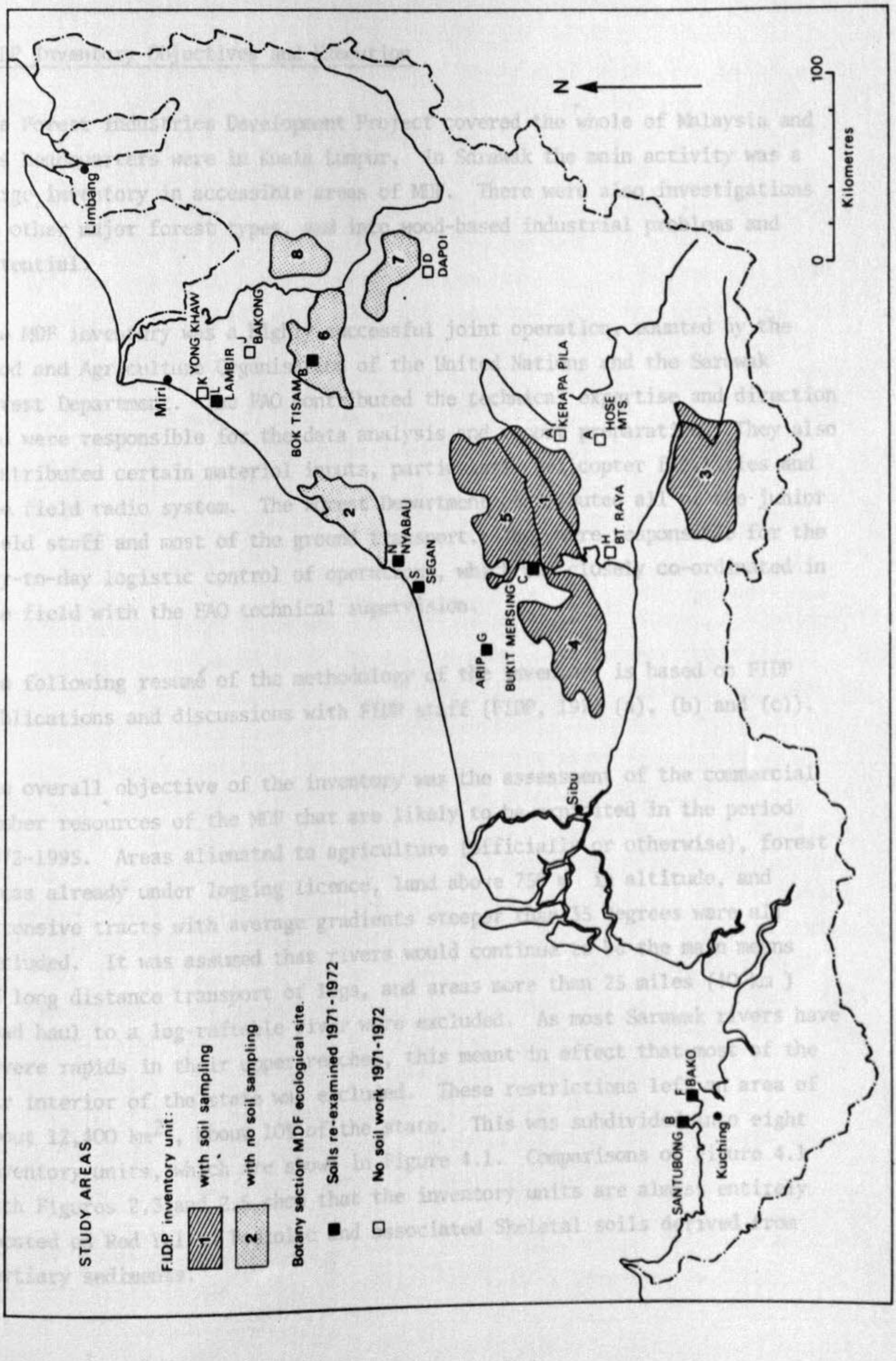
The effect of the edaphic environment on intraspecific variation of the concentration of these compounds, and hence the tree's resistance to fungal and termite attack, is complex. As their precursors are photosynthesised carbohydrates not utilised for other plant functions, any factor that alters the relative rates of photosynthesis, new cell formation, and respiration, can affect the formation of these compounds.

There is some evidence from work on temperate tree species that levels of polyphenolics increase in trees on sites of low fertility (e.g. McMillin, 1970; Nelson et al., 1969; Forrest, 1975). The apparent negative relationship between mineral nutrition status and wood polyphenol content is not always confirmed. Ito and co-workers (1974) found that polyphenol synthesis in *Cryptomeria japonica* appeared to be inhibited by mineral nutrient deficiencies. In a study that measured the contents of the extractives in sapwoods only, the levels of polyphenolic compounds were found to be unaffected by intensive inorganic fertilisation of temperate conifers, even though timber growth rates were greatly increased (Klem, 1972).

Tension and compression wood tends to have lower contents of polyphenolic extractives and to be more susceptible to insect and fungal attack than normal stem timber (Dadswell and Hillis, 1962; Hillis, 1962; Shigo and Hillis, 1973). As more wood of this type is laid down when the tree is under mechanical stress, such as can be caused by persistent wind pressure or by tree lean on steep slopes (Phipps, 1974), this may be a way in which topography can affect decay levels (Boone and Chadnoff, 1972).

Silica crystals are known to occur in many MDF timbers, particularly those of the keruing group *(Dipterocarpus spp.)* (Balan Menon, 1965; Burgess, 1965; Murthy, 1965). It has been suggested that high silica levels are associated with high contents of polyphenolic extractives (Scurfield et al., 1974) and hence possibly with enhanced rot resistance. It is of interest in this connection that the keruings have the lowest levels of buttrot incidence of the major groups of medium density dipterocarp timbers (see Chapter 7). However, graveyard tests do not always confirm that the keruings are noticeably more durable than the other common dipterocarp timbers (e.g. Jackson, 1957). Siliceous timbers are known to be more resistant to marine borers of the *Teredo* type, although timber density and polyphenolic extractive contents are equally important (Southwell and Bultmann, 1971; Ong and Lee, 1972). However, high contents of silica crystals did not seem to significantly increase resistance to terrestrial termite attack (Bultmann and Southwell, 1976).

Figure 4.1


STUDY AREAS
F.I.D.P. inventory unit:
with soil sampling
with no soil sampling
Botany section MDF ecological site.
Soils re-examined 1971-1972
No soil work 1971-1972
Kilometres
0
100
N
Limbang
Miri
K YONG KHAW
L LAMBIR
J BAKONG
B BOK TISAM
D DAPOI
KERAPA PILA
A HOSE MTS.
H BT. RAYA
N NYABAU
S SEGAN
C BUKIT MERSING
G ARIP
Sibu
F BAKO
B SANTUBONG
Kuching
1
2
3
4
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8

4.2 Forest Industries Development Project Plots

4.2.1 FIDP Inventory Objectives and Execution

The Forest Industries Development Project covered the whole of Malaysia and its headquarters were in Kuala Lumpur. In Sarawak the main activity was a large inventory in accessible areas of MDF. There were also investigations in other major forest types, and into wood-based industrial problems and potential.

The MDF inventory was a highly successful joint operation, mounted by the Food and Agriculture Organisation of the United Nations and the Sarawak Forest Department. The FAO contributed the technical expertise and direction and were responsible for the data analysis and report preparation. They also contributed certain material inputs, particularly helicopter facilities and the field radio system. The Forest Department contributed all of the junior field staff and most of the ground transport. They were responsible for the day-to-day logistic control of operations, which was closely co-ordinated in the field with the FAO technical supervision.

The following resumé of the methodology of the inventory is based on FIDP publications and discussions with FIDP staff (FIDP, 1974 (a), (b) and (c)).

The overall objective of the inventory was the assessment of the commercial timber resources of the MDF that are likely to be exploited in the period 1972-1995. Areas alienated to agriculture (officially or otherwise), forest areas already under logging licence, land above 750 m in altitude, and extensive tracts with average gradients steeper than 35 degrees were all excluded. It was assumed that rivers would continue to be the main means of long distance transport of logs, and areas more than 25 miles (40 km) road haul to a log-raftable river were excluded. As most Sarawak rivers have severe rapids in their upper reaches, this meant in effect that most of the far interior of the state was excluded. These restrictions left an area of about 12,400 km^2 , about 10% of the state. This was subdivided into eight inventory units, which are shown in Figure 4.1. Comparisons of Figure 4.1 with Figures 2.3 and 2.5 show that the inventory units are almost entirely located on Red Yellow Podzolic and associated Skeletal soils derived from Tertiary sediments.

The sampling points within the units were distributed as randomly as possible, and stratified only to give an even spatial density. To achieve this, the aerial photographic coverage of the unit was first planimetrically measured, and then overlaid with a regular square grid of points, each equivalent to 100 acres (40 hectares) on the ground. The points were numbered serially. The density of sampling points for the unit was calculated from predictions of likely precision, based on experience in other tropical rainforests, and on grounds of logistic feasibility. This density was converted into a round figure of the number of 100 acres per sampling point (say n). A figure between 1 and n was chosen at random (say k) and the 100 acre overlay point with the serial number k marked the location of the first sampling point. The locations of subsequent sampling points were marked by the overlay points with the serial numbers k + n, k + 2n, etc. This gave an evenly distributed sampling pattern that was completely unbiased with respect to forest or site conditions. The density of sampling points was about one per 18 km^2 of forested area. It varied slightly if small areas of non-MDF forest were included in the unit. Eventually over 500 sampling points were established in the eight inventory units.

At each sampling point there was a cluster of nine plots. Nine-plot clusters were originally estimated to be the optimal compromise between the statistically desirable maximum dispersion of the plots and the logistic and cost advantages of a highly clustered plot distribution. Subsequent analysis of the field results confirmed that nine was about the right figure. The nine plots were laid out in a strictly followed 3 x 3 square layout, as illustrated in Figure 4.2(a), with 4 chains (88 yards or approximately 80 metres) between adjacent non-diagonal plots. The grid was always aligned North-South. The plots were not of fixed dimensions, and were defined by all the 'in' trees when sweeping with Basal Area Factor 10 (in ft^2/acre) prism at the plot centre peg. The use of prism, rather than fixed dimension, plots means that mensurational effort was concentrated on the larger size classes. This is consistent with the objective of the inventory, which was concerned with timber resources exploitable in the near future. The relative under-sampling of the smaller size classes detracts from the value of the data for general ecological and silvicultural purposes, as these are also concerned with the dynamics of the forest and its potential post-exploitation regrowth.

All 'in' trees of greater than 8 inches (20 cm.) diameter at reference height were identified in the field, to species level where possible, by fallen leaf and butt slash characteristics. Leaf material was collected for confirmatory and more specific identification by Botany Section staff in base camp. The diameters were measured at reference height, which was at 4.3 feet (1.3 m) above ground level on the uphill side of the tree, except in heavily buttressed trees, for which it was 2.3 feet (70 cm) above the highest buttress-bole junction. Measurement was usually by steel diameter tape, but callipers were also used. Upper stem diameters were measured with Wheeler Penta Prism Optical Callipers. Upper stem diameters were either used to determine the position of the 12 inches (30 cm) or 18 inches (45 cm) diameter top points or, in the larger stems, to give the diameter at the crown point. They were not used in the volume equations but merely to more precisely locate the upper limits of the merchantable log sections (FIDP, 1974 (a)).

In the second and third field seasons of the inventory (1970-71) all 'in' trees with at least one commercial log of 12 feet (3.6 m) length and a minimum diameter of 12 inches (30 cm) were electrically drilled to detect the presence of buttrot. This was because the first season's defect studies showed that hollow decay was widespread and highly variable. The defect results also showed that stemrot without accompanying buttrot was fairly uncommon. Drilling was at reference height, in two perpendicular directions. Very hard-wooded trees, non-commercial species, and trees with poisonous or irritant saps were not drilled. Eventually, over 20,000 trees in Units 2 and 4-8 were successfully drilled. This represents a major effort,as all the drilling equipment, the electric generator and its fuel had to back-packed into the plots from boat or helicopter dropping points.

In addition to these measurements made on the standing forest of all inventory plots, detailed volume and decay studies were carried out on a random selection of the plot clusters. These studies involved the felling and sectioning of all 'in' trees that had at least one 12 feet (3.6 m) commercial log with a minimum overbark diameter of 12 inches (30 cm). All felled trees were sectioned into 12 feet (3.6 m) log lengths, working upwards from the stump (which was taken as 2.3 feet (70 cm) below the reference height) to the crown point or 12 inch (30 cm) top, whichever was lower. Any log which showed hollow or spongy decay was further sectioned into 6 feet (1.8 m) lengths to enable a more accurate estimate of the timber volume lost to the decay. Once felled and sectioned, the logs were measured for size and shape. The area of crossection of decay at all cut heights was measured using transparent square-gridded plastic sheets. Any form defects were also noted, so that the logs could be graded for quality. The measurements on the felled trees enabled the development of accurate volume equations, which were applied to the standing forest measurements collected on the non-felled plots. Trees not felled in the volume and defect studies included those with bee or hornets nests, trees with poisonous or irritant saps, and trees with obviously dangerous tendencies to split. This meant that the largest size classes were rather poorly sampled, as many of the largest trees showed some external sign of stem rot and a tendency to split on felling. In addition, trees on the steepest slopes were sometimes not felled because of their highly asymmetric crowns and their tendency to jump the butts. Some felled trees which had come to rest bridging depressions could not safely be sectioned and were used only for the accurate estimate of gross external volumes. In all these decisions, the defect crew leaders had complete discretion, and safety considerations were paramount.

It was originally intended that 10% of the inventory plots would be used for the volume and decay studies. However, when the scale of the decay problem became apparent, and as the field crews became more adept, the sampling fraction was increased. Eventually 22.5% of all the plot clusters were used.

The volume and decay studies involved the accurate measurement of plots already measured by the standing forest inventory routine, and so constituted an element of field checking in the programme. In addition, the FAO technical personnel checked a random selection of the standing forest inventory plots. The fieldwork appears to have been of high quality, especially considering the size of the project and the difficult field conditions. Species identifications were 97% correct and the volumes of individual trees were generally accurate within 5%. The most disappointing phase of the field operations was in the detection of buttrot by tree drilling, but even here the accuracy was over 87% in the 1800 trees that could be checked by subsequent felling.

4.2.2 Selection of Plots for Soils Work

The FIDP Plan of Operations for the MDF inventory did not include any mention of ecological studies into soil-forest relationships. The use of the FIDP plots for these studies was only seriously considered when the FAO and Forest Department planning was well advanced. However, despite its late inclusion, the personnel of the FIDP, both FAO and Forest Department, gave the Forest Soil Survey all possible assistance and co-operation. The material assistance included full use of base camp facilities, helicopter and ground transport, and access to the field radio network. It was partly because of these logistic advantages that soils work on the FIDP plots was tackled first, so as to run concurrently with the inventory field operations. There were also many useful discussions on the conduct and analysis of the study with FIDP personnel, including visiting FAO experts.

Despite these practical advantages, there were certain drawbacks to the use of the FIDP plots for the soils project. These mainly stemmed from the sampling pattern, which had been designed specifically to economically maximise the precision of the estimates of the immediate commercial timber resources. One disadvantage, which was increasingly apparent during the analysis of the data, was the small size of the individual plots. They were well below the minimal area for floristically diverse forests such as the MDF. Therefore, the high probability of chance spatial exclusion of characteristic, site-compatible species precluded consistent forest type classification. The second disadvantage was more immediately apparent and stemmed from the layout of the plot clusters. In the intricately dissected landscapes of upland Sarawak, the 11.3 chains (230 m) separating diagonally opposite plots in a cluster can cover a considerable range of topographic situations. The earlier studies in Brunei (Ashton, 1964 (a)) indicated that local topography and associated soil changes were influential factors on the variation in the MDF. Because of the internal topographic heterogeneity in the FIDP plot clusters, it was decided to treat the plots separately as individual cases. It was this decision, which still appears to have been unavoidable, that led to the rapid accumulation of large numbers of soil samples in this programme. Another consequence of this decision emerged during the interpretation of the results. This is the chance possibility of high associations between site and forest being apparent using a highly clustered sampling layout in forests dominated by poorly dispersed and more or less contagiously distributed species, such as many dipterocarps.

It was not feasible for the single soils team to attempt to cover all of the inventory plots. Attention was therefore restricted to the randomly selected clusters used for volume and defect studies. As well as having data on decay, these were also the plots on which the standing forest data had been remeasured, and were therefore more reliable.

In the first field season (1969), most of the volume and defect study clusters were visited and sampled by the soils team. In 1970, the increased scope of the inventory operations and the increase in volume and defect sampling intensity, from 10% to over 20%, meant that this was no longer possible. It became necessary to select from among volume and defect clusters for soils work. Mindful of the increasing backlog of soil samples for laboratory analysis, it was decided to concentrate the limited site characterisation capacity on those plots for which the forest data were most complete. The plots chosen were those which the volume and defect field records showed to have two or more felled and fully sectioned trees.

Unfortunately, this basis of selection, although practically sensible, introduced an element of bias that was not fully appreciated at the time. Because of the low number of stems qualifying for felling, many plots in low density forests were discarded. Sampling was therefore biased towards the medium and high density forests. In addition, plots in very rugged terrain tended to be discarded because many trees had not been felled or sectioned because of safety considerations. These tendencies to bias became apparent during the analyses of the data (Table 6.17).

4.2.3 Site Characterisation Procedure

In developing a site characterisation procedure for the FIDP plots, the major considerations were the variable dimensions and the large numbers of the plots. The procedure had to concentrate efforts close to the centre peg of the plot, and had to be fairly rapid and routine.

General site description was straightforward. The ruling slope gradient through the centre peg was measured with an Abney level. The topographic position was described on a clinal categorical scale from ridge crest through upper-, mid- and lower-slope, to valley. The local geology was determined from outcrops, surface stones, soil stones and the geological survey maps. The depth of the discrete litter layer was measured at the centre peg.

In the first season the morphology of the soil at the centre peg was described from a 5 cm. diameter Edelman augering to a depth of one metre or to the lithic contact, whichever was shallower. These auger descriptions were supplemented by full profile descriptions on some plots within each cluster, selected after augering was complete (Baillie, 1971 (a)). In the auger descriptions the only properties that could reliably be described were matrix colour, mottling, texture, and the content and type of soil stones. Topsoil

TABLE 4.1 Summary of site data collected on all FIDP plots

General site characteristics	Soil characteristics (topsoil and subsoil)	
	Morphological	Chemical
Topographic situation	Matrix colour	pH
Slope gradient	Mottles	Organic C
Litter thickness	Stone content	Total N
Geology	Stone type	Reserve P
	Field texture	" Ca
	Structure (topsoil)	" Mg
	Cutans (subsoil)	" K
		Exchangeable Ca
		" Mg
		" K
		CEC
		Free Group III oxides
		% clay
		silt
		sand

TABLE 4.2 Execution of soils work on FIDP plots

	FIDP Operations					Soil Studies	
Field Season	Unit	Location (see Fig. 4.1)	Area (Km^2)	Total number of inventory plot clusters	Number of plot clusters used for volume and defect studies	Number of plots described, sampled and analysed	Number of clusters
1969	1	Upper Rajang	1756	83	13	67	8
	3	Upper Balleh	2249	48	13	88	11
1970	4	Anap-Upper Oya	2055	89	25	76	13
	5	Kakus	2091	83	21	60	13
1971	2, 6-8	North Sarawak	3462	200	41	No soils work on FIDP plots in 1971	
Total			11 613	503	113	291	45

Eventually the soils team visited 49 clusters of plots. By ignoring plots with scant standing forest inventory data, the number of plots described and samples was reduced to 381. As mentioned above, plots with few volume and defect data were also discarded in the second season. Finally, 612 soil samples from 306 plots, on 45 clusters, were submitted for laboratory analysis. Unfortunately, 15 of the subsoil composite soil samples were so stony that there was insufficient fine earth for full laboratory analysis. These plots also had to be discarded. This unfortunately exacerbated the undersampling of the plots on shallower soils and steeper slopes.

The distribution of the 291 plots of the final raw data matrix is summarised in Table 4.2.

4.3 MDF Ecological Plots

4.3.1 MDF Ecological Plots Objectives, Establishment and Original Data Collection

These plots were established in 1963-6 by the Forest Department Botany Section, under the supervision of Dr. P.S. Ashton, then Forest Botanist. The purpose of the plots was to provide detailed data on the full range of forests and environments within the Sarawak MDF. These data are of great value for general description and characterisation of the MDF. They have also been used as the basis for a number of ecological studies of the MDF and its environment.

The plots were subjectively sited so as to cover as wide a range of rock types as possible. Igneous rock outcrops were deliberately oversampled, at the expense of the more extensive Tertiary deposits. In this, the Sarawak plots complement the series previously established in Brunei, which are entirely situated on Tertiary deposits. They also fortuitously complement the later established FIDP plots, which are also almost entirely on Tertiary sedimentary rocks.

105 plots were established at 15 sites throughout the state. The sites were intended to be geologically homogeneous. In general this was achieved, although one site, Bukit Iju, did later prove to be straddling a boundary between rhyolite and greywacke sandstone. The distribution of the sites is shown in Figure 4.1, and the number of plots and permanent plots, and the rock and soil types of the sites, are summarised in Table 4.3. The clustering of plots into sites was partly necessitated by the very limited number

TABLE 4.3 Summary of MDF ecological sites

Site	Location	Total number of 1.5 acre plots	Number of permanent growth increment plots	Geology	Soils	Number of plots recharacterised 1971 - 72
A	Hose Mountains (A1) Kerapa Pila (A2)	2	-	Dacite (A1) Basalt (A2)	RYP - Skeletal (A1) Lateritic (A2)	0
B	Santubong, West Sarawak	2	-	Plateau Group siliceous sandstone	RYP + Skeletal	(2) (No analytical data)
C	Bukit Marsing	30	5	Basalt	Lateritic + Skeletal	12
D	Ulu Dapoi, Tinjar	2	-	Dacite	Gley + Skeletal	0
E	Bok-Tisam P.F., Tinjar	10	-	Slightly calcareous and non-calcareous shales	RYP + Skeletal	6
F	Bako National Park, West Sarawak	4	4	Plateau Group siliceous sandstone	Podzol, RYP + Skeletal	(4) (No analytical data)
G	Bukit Iju, Arip	15*	-	Rhyolite + greywacke	RYP + Skeletal	5
H	Bukit Raya, Rejang	15*	-	Mixed shale and greywacke sandstone	RYP + Skeletal	0
J	Bakong, Miri	5*	-	Non-calcareous shale	RYP	0
K	Yong Khaw, Miri	4*	-	Greywacke sandstone + some shale	RYP	0
L	Lambir Hills, Miri	6	4	Greywacke sandstone	RYP	4
M	Nyabau F.R., Bintulu	5*	4*	Greywacke sandstone + some shale	RYP + Skeletal	2
N	Segan F.R., Bintulu	5	-	Greywacke sandstone and shale	RYP + Skeletal	4
15	TOTAL	105	17			33 (39)

*Indicates that, by 1972, some of these plots had been destroyed by shifting agriculture, logging or road building.

of extensive outcrops of some of the rock types sampled. It also adds flexibility to the data, enabling them to be used for studies of localised variation within the MDF (e.g. Large, 1971). Logistic considerations favour clustering of the plots. However, spatial clustering does complicate the interpretation of the results, as noted above and further discussed in Chapter 6.

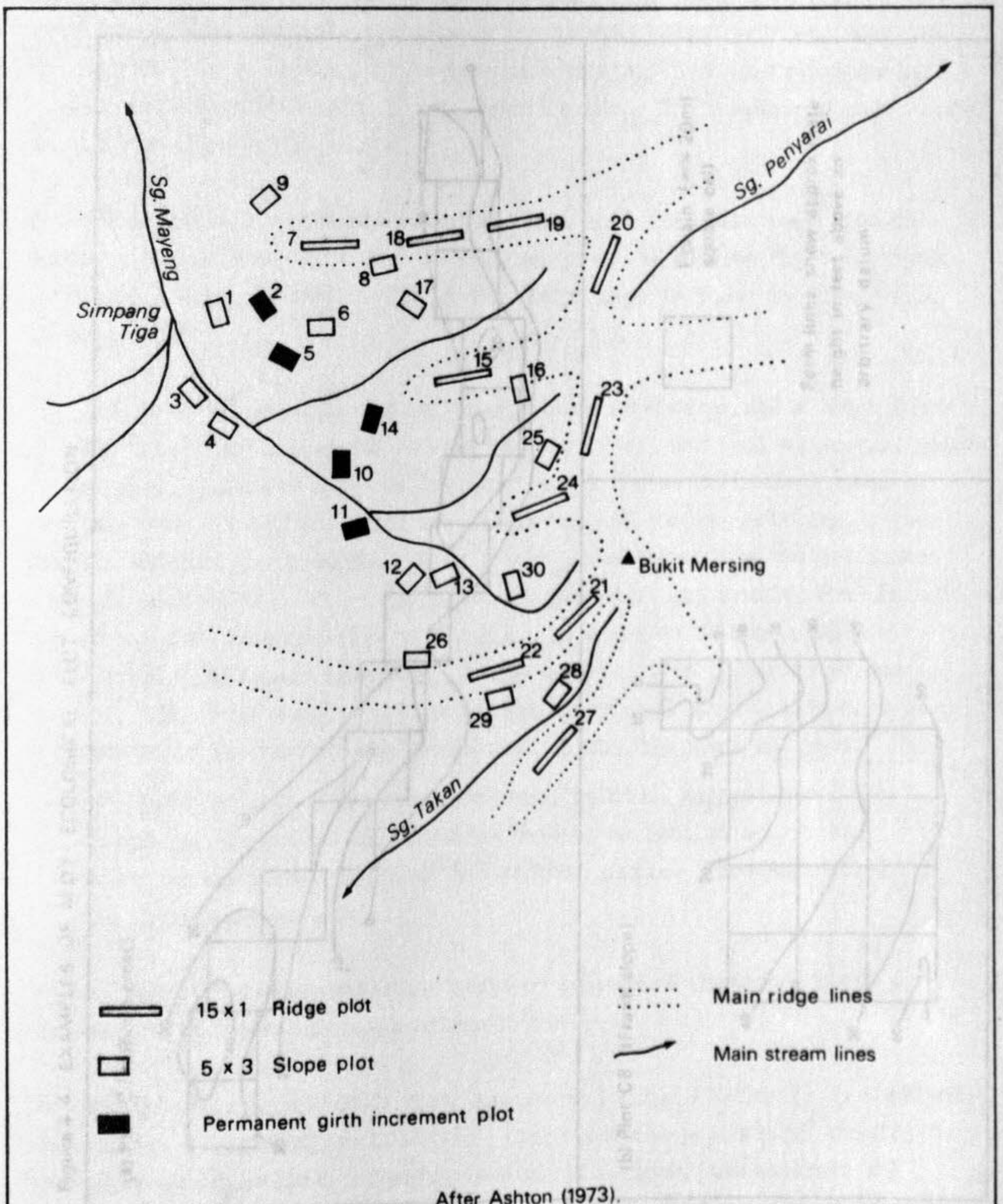
The number of plots at each site appears to have been arbitrary. The plots were sited subjectively so as to give as high a degree of internal geological and topographic homogeneity as possible. The plots are 1.5 acres (0.6 hectares) in area, this being about the largest plot size that can consistently be fitted into a single landscape facet in the intricate topography of upland Sarawak. Even for plots of this size, it is necessary to have plots of variable shape to avoid them trangressing topographic boundaries. The plots are made up of 15 cells, each of one square chain (22 yards or 20 m). For ridge crest plots the 0.1 acre (0.04 hectares) cells were aligned in a 15 x 1 formation, giving long and narrow plots. The cells could be offset if necessary to keep to the crest so that some of the plots had quite a sinuous form. For plots on slopes, the basic formation was 5 x 3 cells, with the long axis running across the slope. These plots also varied in shape in order to avoid hillocks or major drainage lines. Examples of possible plot layouts are shown in Figure 4.4. The plots and cells were marked out by temporary pegs and rentis lines.

All botanical data were collected and booked by 0.1 acre cells, so that the plots could be subdivided, if desired, in later analyses of the data. For all trees of girth greater than 12 inches (30 cm) at reference height (1.3 m. or above the buttress bole junction, whichever is higher), the girth was measured, the height estimated, and leaf and fertile materials, if any, were collected for Herbarium identification. Because the Botany Section team included highly-skilled tree climbers, it was not necessary to rely on fallen leaves, as in the FIDP inventory.

On two of the cells in each plot, chosen subjectively to represent the full range of conditions within the plot, plants of less than 12 inch (30 cm) girth were also measured and identified, including tree saplings, palms and climbers. On the other cells the presence of saplings was recorded, together with visual estimates of their abundance.

At four sites some plots were selected by dynamic studies of the MDF. They were made semi-permanent by marking the angles of the plot boundary with

Figure 4.3: PLOT DISTRIBUTION AT SITE C (Bukit Mersing).



After Ashton (1973).

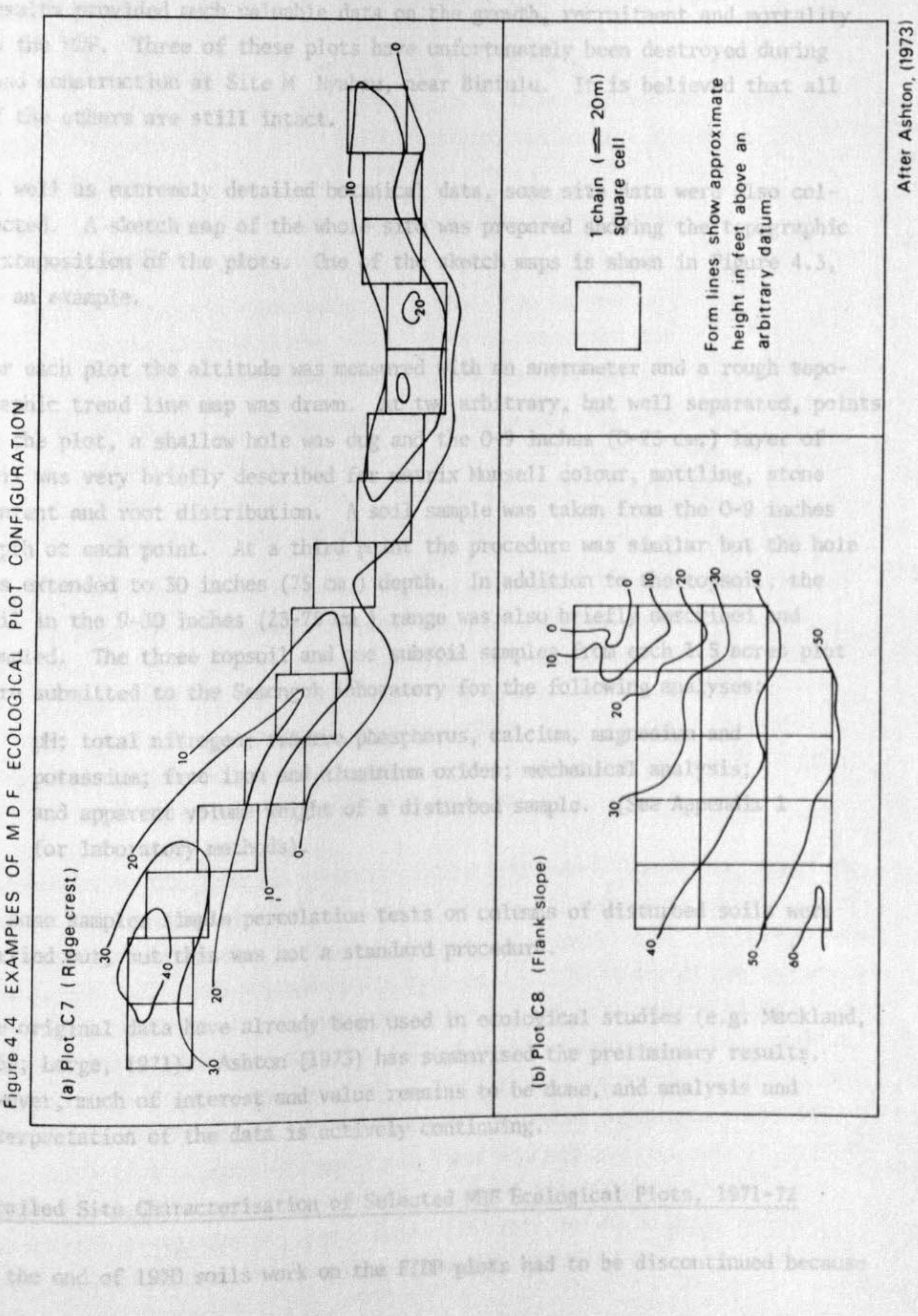


Figure 4.4 EXAMPLES OF M D F ECOLOGICAL PLOT CONFIGURATION

durable belian *(Eusideroxylon zwageri)* pegs, and by marking all of the measured trees with aluminium number tags. These plots were re-measured five and ten years after establishment, and it is hoped that quinquennial re-measurement will be continued for some time. The first five years' results provided much valuable data on the growth, recruitment and mortality in the MDF. Three of these plots have unfortunately been destroyed during road construction at Site M Nyabau, near Bintulu. It is believed that all of the others are still intact.

As well as extremely detailed botanical data, some site data were also collected. A sketch map of the whole site was prepared showing the topographic juxtaposition of the plots. One of the sketch maps is shown in Figure 4.3, as an example.

For each plot the altitude was measured with an anerometer and a rough topographic trend line map was drawn. At two arbitrary, but well separated, points in the plot, a shallow hole was dug and the 0-9 inches (0-23 cm.) layer of soil was very briefly described for matrix Munsell colour, mottling, stone content and root distribution. A soil sample was taken from the 0-9 inches depth at each point. At a third point the procedure was similar but the hole was extended to 30 inches (75 cm) depth. In addition to the topsoil, the soil in the 9-30 inches (23-75 cm) range was also briefly described and sampled. The three topsoil and one subsoil samples from each 1.5 acres plot were submitted to the Semongok laboratory for the following analyses:

> pH; total nitrogen; reserve phosphorus, calcium, magnesium and potassium; free iron and aluminium oxides; mechanical analysis; and apparent volume weight of a disturbed sample. (See Appendix 1 for laboratory methods).

On some samples simple percolation tests on columns of disturbed soils were carried out, but this was not a standard procedure.

The original data have already been used in ecological studies (e.g. Mackland, 1969; Large, 1971). Ashton (1973) has summarised the preliminary results. However, much of interest and value remains to be done, and analysis and interpretation of the data is actively continuing.

4.3.2 Detailed Site Characterisation of Selected MDF Ecological Plots, 1971-72

At the end of 1970 soils work on the FIDP plots had to be discontinued because of the excessive number of soil samples it was generating. Attention was therefore concentrated on a more detailed characterisation of the site conditions of the MDF ecological plots. Particular emphasis was laid on soil physical properties that can be measured simply in the field.

As it was clear that not all of the sites and plots could be visited, because of the shortage of time and because some of them had been destroyed since establishment, the plots for recharacterisation were chosen on the following basis:

(a) The highest priority was given to the semi-permanent girth-increment plots.

(b) Attention was concentrated on the sites located on outcrops of crystalline rocks, so as to complement the concentration on sedimentary rocks of the FIDP plots.

(c) Sites of easy access and with large numbers of extant plots were chosen in preference to others, as this gave a more economical balance between actual fieldwork and the time and cost of access travel.

Eventually 39 plots on 8 sites were recharacterised. Unfortunately, the laboratory data for the two West Sarawak sites on siliceous sandstone are not available, so full data exists for only 33 plots from 6 sites. This can be seen in the final column of Table 4.3. The main sites recharacterised were those on basalt (Bukit Mersing), rhyolite (Bukit Iju), slightly calcareous Neogene shale (Bok-Tisam), Baram Group greywack sandstone and shale (Segan) and Brunei Group greywacke sandstone (Lambir Hills).

Relocation of the plots was sometimes quite difficult. The intact permanent growth plots were no problem, because of the belian angle pegs and the aluminium tree number tags. In order to be sure of relocation of the non-permanent plots, the soils team was always accompanied by at least one of the labourers and by one of the Botany Section tree climbers, who were present at the original establishment of the plot. Their combined memories usually enabled the plot to be located approximately. For final placement the traces of the original rentis lines and correspondence of the local topography with the plot trend line diagram were used. If there was any conflict between personal recollections, the rentis traces, and the trend line diagram, the plot was deemed unlocatable and not used. About six plots had to be discarded for this reason, mostly at the basalt site, Bukit Mersing.

After plot relocation, the centre points of all 15 of the 0.1 acre cells were measured out and pegged. The 0.1 acre cells were the basis of all subsequent site characterisation work, so that the site data could be manipulated as flexibly as the original botanical data. The centre peg of each cell was the main description and sampling point, but there were subsidiary examination and sampling points halfway out along the diagonals of the cell (about 7 m from the centre peg). This is shown in Figure 4.5.

The topographic position of the cell was ranked on a clinal categorical scale, as in the FIDP plots. Litter thickness and ruling slope were measured, and the degrees of microterrace-like stepping and surface stoniness were visually assessed at all five sampling points. A sample of the upper mineral horizon was collected, for bulking and laboratory analysis, at each of the five sampling points.

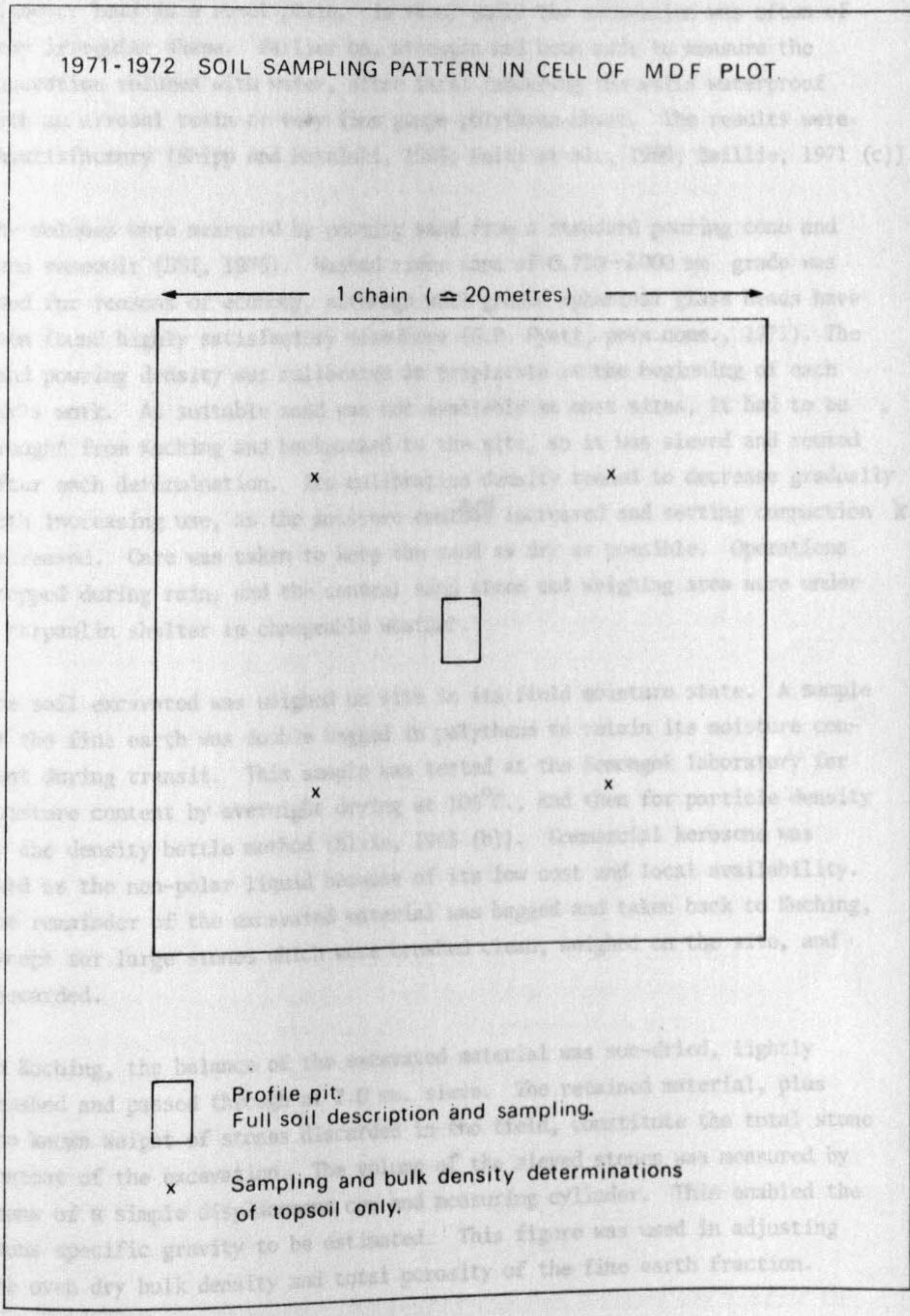
Three topsoil bulk density determinations were made at the centre peg and one at each of the subsidiary sampling points.

A profile pit was then dug at the centre peg to a depth of two metres or to the lithic contact, whichever was shallower. The soil profile was described by natural horizons along conventional soil survey lines (FAO, 1968). This gave data on litter, solum and horizon depth, matrix colour, degree and colour of mottling, field texture, soil structure, presence and development of ped coatings, soil consistency, apparent porosity, root distribution, and the abundance, type, and degree of weathering of any stones.

After profile description, the main subsoil horizon was selected on the basis of horizon thickness, more reddish matrix colours, relatively high clay content and the presence of well developed ped coatings on generally moderately developed blocky structures. The morphological properties of this horizon were taken as representative of the subsoil in subsequent factor analysis. This horizon was sampled to give the 'subsoil' sample for bulking and laboratory analysis. Three bulk density determinations were made in this horizon by cutting back into the described face of the profile pit to make a horizontal step at the level of the upper boundary of the horizon.

All bulk densities were measured by the excavation method. This was preferred to the more rapid coring technique, because it can be used in stony soils, and is therefore better suited to the shallow soils common in MDF areas (Tisdall, 1951; Vomocil, 1957; Blake, 1965 (a); Cunningham et al., 1968).

Figure 4.5


1971-1972 SOIL SAMPLING PATTERN IN CELL OF MDF PLOT
1 chain (≃ 20 metres)
Profile pit.
Full soil description and sampling.
x Sampling and bulk density determinations
of topsoil only.

easily determined substitute for the Plasticity Index, which requires determination of the Atterberg limits (P.J. Beavan, pers.comm., 1971). It gives a rough indication of the clay mineralogy (Franzmeier and Ross, 1968). It was measured by the U.S. Army Corps of Engineers technique (BSI, 1975). The fine earth was mixed with water to a slurry at about the liquid limit. It was then poured into a 5 inches (12 cm) long and 1 inch (2.5 cm) diameter hemi-cylindrical copper trough, the inside surface of which had previously been lubricated with silicone car wax to reduce soil adhesion. The trough and soil were sun-dried until no further soil shrinkage occurred. The linear shrinkage was expressed as a percentage of the dry length. This is contrary to standard practice, in which the shrinkage is expressed as a percentage of the original, wet, length. The relationship between the two modes of expression is not linear, but differs by only a few percent in soils where the COLE is less than about 20%.

Initially, 10 replicate readings with a California Bearing Ratio (CBR) cone penetrometer and with a hand-held shear-vane tester were taken in the topsoil and subsoil at the centre peg of each cell (Davidson, 1965; B.D. Soane, pers.comm., 1971). Both these instruments are designed for testing disturbed materials in civil engineering, and were not very suitable for the rather compact, undisturbed soils of the MDF. These determinations were discontinued because of the high local and operator variability.

The topsoil and subsoil samples for laboratory analysis were bulked from groups of 5 adjacent cells. This matched the subdivision of the plots into three 0.5 acre (0.2 hectare) subplots in some of the floristic analyses of the original forest data (Ashton, 1973). The composite soil samples were submitted to the laboratory for the following analyses:

> pH (water); organic carbon; total nitrogen; reserve phosphorus, calcium, magnesium and potassium; and mechanical analysis. (For laboratory methods, see Appendix I).

From comparison with the list of analyses for the FIDP plot samples, it can be seen that the free iron and aluminium (Group III) oxides and the exchangeable forms of the cationic nutrients were omitted, in the interests of economy of laboratory capacity.

The demands on the laboratory for lengthy chemical analyses were modest compared with those of the FIDP samples. However, the several thousand gravimetric moisture content and particle density determinations, necessary for

TABLE 4.4 Summary of site data collected from MDF ecological plots, 1971-72
Number of determinations per 1.5 acre plot

Field: Property	Replicates per plot	Laboratory: Property	Replicates per plot
Topographic position (visual)	15	Topsoil moisture content	105
Slope gradient (Abney level)	75	Topsoil particle density	75
Litter thickness (cm)	75	Subsoil moisture content	45
Surface stones (visual)	75	Subsoil particle density	15
Microterracing (visual)	75	pH (water) (top soil and subsoil)	3
Soil profile description	15	Organic C (")	3
Topsoil bulk density (sand pouring)	105	Total N (")	3
Subsoil bulk density (")	45	Reserve P (")	3
Topsoil stone content (w/w)	105	" Ca (")	3
Topsoil stone density	105	" Mg (")	3
Subsoil stone content (w/w)	45	" K (")	3
Subsoil stone density	45	Free Group III oxides (topsoil and subsoil)	3
Topsoil COLE	105	Clay % (")	3
Subsoil COLE	45	Silt % (")	3
		Sand % (")	3

the bulk density and porosity calculations, were also carried out at the Semongok laboratory. The Forest Department supplied additional semi-skilled personnel during 1971-72 specifically for these determinations.

The site data collected on the MDF ecological plots are summarised in Table 4.4. In total, about 600 profiles were described and sampled and about 6,000 bulk densities determined in the field.

4.4 Data Recording

All field data collected on the FIDP and MDF ecological plots were recorded using 2H pencils on designed proformae. The bulk density and porosity calculations were done on proformae, and the laboratory data were presented on the standard Semongok results sheets. All this material gave highly legible photocopies, obviating the need for transcription, with its attendant possibilities of error.

The FIDP standing forest inventory and volume and defect study data were also photocopied from the computer printouts. The only material that had to be transcribed by hand to enable subsequent work in Aberdeen was the FIDP tree drilling data. Several errors in the transcription were detected and corrected, and there are probably a few more, although it is hoped that they are not significant.

The MDF ecological plots botanical and original site data were already available at the University of Aberdeen.

ANALYSIS OF DATA

5.1 Introduction

The statistical analyses of the data were aimed at extracting the maximum information of use and interest, rather than testing specific hypotheses. The structures of the data sets were partly determined by the inherited sampling patterns, so that the statistical techniques were selected to suit the data, rather than *vice versa*.

The site data from the FIDP plots were punched and verified by the writer. The remainder of the data were punched and verified by the University of Aberdeen Data Preparation Service. They were checked against the photocopies of the original field and laboratory proformae. As a further check, particularly of the formats, all data sets were subjected to the Data Summary Program, BMD 01.

Because the preparation and checking of the large sets of data were so time-consuming, and because of the writer's unfamiliarity with the statistical and computing skills required, it was decided, at the outset, that the writing of personal programs for the University of Aberdeen's ICL 4-70 computer was not feasible. Instead, extensive use was made of the programs of the Biomedical (BMD) package, prepared by the Health Sciences Faculty of the University of California, Los Angeles (Dixon, 1973), and already available on the Aberdeen computer.

As they were entirely fresh, the data from the FDP plots were analysed first. As experience gained in their analysis influenced some decisions in the analysis of the data from the MDF ecological plots, the analyses are reported below in their approximate chronological order.

The analyses performed on each set of data are summarised in Tables 5.7 and 5.12.

5.2 Analyses of Data from FIDP Plots

5.2.1 Treatment of Site Data

5.2.1.1 Factor analysis of site data

Because of the large number of raw site variables and the high degree of correlation between some of them, it was decided to simplify the site data by factor analysis. This and several subsequent decisions during the course of the factor analysis were intuitive and subjective (Horn, 1967). Without recourse to a large series of parallel analyses, such decisions cannot be objectively tested.

Factor analysis is one of the best known techniques of multivariate statistics. The aim is to extract a reduced number of axes from the multi-dimensional hyperspace that encompasses the original variables. Because the factor space has fewer dimensions than the original variable space, there is inevitably a loss of variance, and hence of information. However, it has often been found that relatively few, well chosen, factor axes can encompass a high proportion of the total original variance. The loss of variance is often an acceptable cost for the benefit of clarification and simplification. This is particularly true if the lost variance is mainly of the non-systematic, error type (Cattel, 1965). Factor analysis is not a single technique, but includes a range of methods, which differ in their criteria for axis selection. In some, the axes are required to be orthogonal (independent), e.g. Principal Component Analysis and Varimax. In others, oblique (correlated) factor axes are permitted.

The loading of an original variable on an extracted factor depends on the angle between the variable and factor axes in variable hyperspace. Interpretation of the physical 'meaning' of the factors is simplified if there are relatively few of the original variables with significant loadings on each factor. This condition is known as simple structure and may be more desirable in some cases than the maximisation of the incorporated proportion of the total initial variance (Harman, 1967; Childs, 1970).

Prior to factor analysis of the FIDP plot data, some of the less satisfactory variables were discarded. These included the soil colour variables because of the rather high operator variability. The qualitative classification of soil drainage status was also discarded because of the difficulty in distinguishing, in auger examination, between hydromorphic mottling and variegated colouring due to incomplete weathering.

The 40 variables remaining were:

Site variables: topographic position; slope gradient; litter depth; solum depth; the grain size and geological age of the parent rock.

Soil variables (both topsoil and subsoil): clay, silt and sand percentages; pH; organic carbon; total nitrogen; reserve phosphorus, calcium, magnesium and potassium; exchangeable calcium, magnesium and potassium; cation exchange capacity; free iron and aluminium oxides; topsoil structure; and the degree of development of subsoil ped coatings.

Although well characterised chemically, this array is weak on soil physical and morphological data.

Another necessary preliminary before factorisation was to discard one of the granulometric variables from each horizon. This is not because the data are unsatifactory. Because the three percentages must sum to 100%, any one of them is linearly dependent on the other two. Inclusion of a linearly dependent variable in the matrix introduces rank deficiency, which has a marked destabilising effect on any subsequent factor analyses. This is a common problem in the analysis of fractional data (e.g. Joreskog et al., 1976).

Initially it had been intended to retain the clay percentage as one variable, because of the predominant physical and chemical activity of the clay fraction, and to substitute the silt:sand ratio as the second. This derived variable was intended to indicate the fineness of the non-clay fine earth. This seemed desirable because the silt and very fine sand fractions appear to have disproportionately important effects on the soil's physical properties, particularly its erodibility (Wischmeier and Mannering, 1969; Wischmeier et al., 1971) and the available moisture capacity (Salter et al., 1966; Salter and Williams, 1969, Hollis et al., 1977).

The silt:sand ratio is an obvious indicator of the fineness of the non-clay fine earth, but it is not the only possibly alternative, nor necessarily the best. It is fortunate that for the soil samples collected during 1969 from the plots in FIDP inventory units 1 and 3, not only were the three major fine earth fractions determined by the pipette method, but the sand was also separated into 5 granulometric fractions by sieving. With these data, it is possible to test which of several parameters derived from the main fine earth fractions gives the best indication of the fineness of the sand fraction.

Taking the topsoil and subsoil data separately and together, the following fine earth parameters; silt %, sand %, silt:sand ratio, silt plus clay:sand ratio, and clay:sand ratio were each correlated against two sand parameters, i.e. the very fine sand:total sand and very fine plus fine sand:total sand ratios. For the ratio variables, the logarithms were also correlated. The results are given in Tables 5.1-5.3.

The generally negative correlations in the second columns of these Tables are due to the fact that, in upland Sarawak soils, sand fractions are generally fine-grained (Huntings, 1974 (a)). This means that the second sand parameter, i.e. very fine plus fine sand:total sand, is generally close to unity. As an indicator of the relative fineness of the sand fraction, the first sand parameter, i.e. very fine sand:total sand, shows greater variation and is more satisfactory. The first columns show that, predictably, the sand becomes increasingly coarse-grained as the sand content increases. However, silt content is also well correlated with the fineness of the sand, and is in fact a superior indicator for the topsoil samples taken separately (Table 5.1). It can be seen that the ratio parameters are inferior to the unmodified fine earth fractions as indicators of sand fineness. The logarithmic transformations do increase the correlation coefficients of the ratio parameters, but not sufficiently to give them preference over the unmodified fine earth parameters.

In order to facilitate the final choice between silt and sand as the second included granulometric variable, the correlation coefficients between the major fine earth fractions for the samples were calculated. The results are tabulated in Table 5.4. They show that for both topsoils and subsoils, the clay and silt fractions are the least correlated pair. Silt was therefore retained in preference to sand, as its inclusion minimised linear dependence and rank deficiency in the data matrix. Silt is also generally the best indicator of the fineness of the sand fraction.

Some of the remaining 38 variables were scored in the field on discrete nominal scales. These were topographic position (scored on a crest-valley scale), parent rock grain size (scaled from wholly shale, through mixtures, to wholly sandstone), parent rock geological age (scaled from Upper Cretaceous to Neogene), topsoil structure (scaled from moderate crumb, through blocky, to stone-dominated), and subsoil ped coating development. Because there are some soils in which the lithic contact is below one metre, and was therefore not encountered in augering, it was necessary to convert the continuous scalar soil depth data to discrete nominal values, taking increments of 20 cm depth as the categorical limits. The sixth class was 'deeper than 1m

TABLE 5.1 Correlations between granulometric parameters (topsoil samples only)

191 topsoil samples from FIDP units 1 and 3

(a)

Fine earth parameters \ Sand Parameters	Very fine sand / Total sand	Very fine + fine sand / Total sand
Silt	.54	-.09
Sand	-.47	.16
Silt/sand	.41	-.12
Silt + clay/sand	.40	-.14
Clay/sand	.37	-.15

(b)

Fine earth parameters \ Sand Parameters	log (Very fine sand / Total sand)	log (Very fine + fine sand / Total sand)
log (silt/sand)	.51	-.12
log (silt + clay/sand)	.49	-.14
log (clay/sand)	.46	-.15

TABLE 5.2 Correlations between granulometric parameters (subsoil samples only)

175 subsoil samples from FIDP units 1 and 3

(a)

Fine earth parameters \ Sand Parameters	Very fine sand / Total sand	Very fine + fine sand / Total sand
Silt	.34	-.26
Sand	-.38	.31
Silt/sand	.23	-.32
Silt + clay/sand	.22	-.33
Clay/sand	.19	-.32

(b)

Fine earth parameters \ Sand Parameters	log (Very fine sand / Total sand)	log (Very fine + fine sand / Total sand)
log (silt/sand)	.38	- .28
log (silt + clay/sand)	.34	- .32
log (clay/sand)	.31	- .31

TABLE 5.3 Correlations between granulometric parameters (all samples)

366 samples from FIDP units 1 and 3

(a)

Fine earth parameters \ Sand parameters	Very fine sand / Total sand	Very fine + fine sand / Total sand
Silt	.44	-.18
Sand	-.42	.24
Silt/sand	.33	-.22
Silt + clay/sand	.31	-.24
Clay/sand	.29	-.24

(b)

Fine earth parameters \ Sand parameters	log (Very fine sand / Total sand)	log (Very fine + fine sand / Total sand)
log (silt/sand)	.45	-.20
log (silt + clay/sand)	.42	-.22
log (clay/sand)	.39	-.22

TABLE 5.4 Correlations between fine earth fractions

366 samples from FIDP units 1 and 3

(a) Topsoil (191 samples)

	Clay	Silt	Sand
Clay	1.00		
Silt	.60	1.00	
Sand	- .90	- .89	1.00

(b) Subsoil (175 samples)

	Clay	Silt	Sand
Clay	1.00		
Silt	.64	1.00	
Sand	- .91	- .90	1.00

All of the discrete nominal scalar scores were transformed to quasi-continuous scalar scores by Ridit analysis (Bross, 1958). The Ridit scores depend on the distribution of the cases between the clinal categories, and are independent of the absolute differences in the physical intensity of the phenomenon being categorised. If a category has few cases, its scalar score will only be slightly higher than that of the subjacent category, even though the physical differences between them may be considerable.

There was a problem of missing data. About 7% of the elements of the 291 x 38 matrix were blank, due to a variety of practical reasons. There did not appear to be any major bias in the pattern of missing data, except for a tendency to undersample shallow soils. There are several methods of substituting missing data that make use of relationships between variables in the existing data (e.g. Beale and Little, 1975; Gleason and Staelin, 1975). Due to shortage of time, however, it was decided to substitute the variable means for the missing values. As factor analysis is based on the correlation matrix, this procedure is statistically conservative, as it diminishes rather than accentuates relationships between variables.

As factor analysis requires data with approximately normal distributions, the final preliminary to factorisation was the qualitative examination of the normality of the complete Ridit-transformed, means-substituted FIDP plot data. This was done by plotting histograms for all the variables. Most of them appeared to be more or less normal, although some of the Ridit-transformed variables appeared irregular, particularly if there are few original categories.

The final, complete 291 x 38 data matrix was subject to exploratory factor analyses using the BMD Principal Components Analysis (orthogonal, with no rotation of the axes), Varimax (orthogonal, but with the axes rotated for the simplest possible structure) and Oblique Simple Structure programs. The greater interpretability of the Oblique Simple Structure factorisation was felt to outweigh possible disadvantages of non-zero correlations between factors, particularly as it appeared that the interfactor correlation coefficients were generally low. Other ecological users have also found that some form of rotated factor analysis gives factors of easier physical interpretation than non-rotated Principal Component Analysis (e.g. Ivimey-Cook and Proctor, 1967).

Although principal component analysis was not adopted, the output of its exploratory run was used to determine the best number of factors for rotation in the oblique simple structure analysis, using the scree test (Cattell, 1952).

The square roots of the eigenvalues of the successively extracted principal components were plotted on a linear scale against factor number. The major break in slope of the descending line is thought to indicate the optimum number of factors. Extraction of factors additional to this will tend to destabilise the analysis by the disruptive fission of real factors and by the incorporation of residual error (Cattell, 1965). For the FIDP data, the scree test showed a major break of slope at about 9 or 10 factors, with a less evident break at Factor 4.

To aid the final choice of the number of factors, the stability of oblique simple structure factor analyses were tested with a variant of Tukey's 'jack-knife' technique (Gray and Schucany, 1972). The general principle is to simulate replication by repeated analysis of a number of subsets of the data, created from the full original data by random deletion of some cases. As a preliminary, the factor analyses were run separately on each half of the full data matrix (McCarthy, 1969). As the results of this were uninterpretable, five larger submatrices were used. Each submatrix consisted of the data from 233 plots (80% of the total). They were formed by the random deletion of one decile (29 plots) from each half of the full data matrix. This was not as exhaustive as the formation of ten submatrices, each consisting of 90% of the full data, as suggested by Pennell (1972). This suggestion was not adopted, because of the time and computer resources it requires.

Each of the five reduced matrices was subject to two oblique simple structure factor analyses, rotating 9 or 10 factors. The final choice was made on the basis of the stability and ease of identification of the common factors. The results are summarised in Table 5.5, from which it can be seen that the 10 factor rotation is more satisfactory. There are only two factors which are not common to all five factorisations.

Oblique simple structure factor analysis, rotating 10 factors, was then run, using the full data matrix. The factor scores for each plot were stored in the computer for the subsequent ecological analyses.

The results of the jack-knife factorisations were also used to validate the final loadings of the variables on the factors. Using the five estimates of each loading from a 10 factor oblique simple structure factorisation of the submatrices, the upper and lower 95% confidence limits of all loadings were calculated. A loading in the final full data factorisation was regarded

TABLE 5.5 Stability of factors in oblique simple structure factor analyses of FIDP data

Number of common factors identified

	9 factor rotation	10 factor rotation
Reduced data matrix		
1	8	9
2	7	9
3	8	9
4	7	8
5	8	9
Number of factors identified in all 5 factorisations	6	8

as validated only if the absolute value of its lower 95% confidence limit equalled or exceeded 0.1 (Pennell, 1972).

5.2.1.2 Analysis of variance of factor scores

In order to determine the extent to which the spatial clustering of the plots affected their factor scores, one-way, univariate analyses of variance of the plot factor scores were performed, taking the clusters and the inventory units as treatments. The analyses taking clusters as treatments were repeated for each inventory unit separately.

5.2.1.3 Site variables

The ten factor scores were used as site variables in the subsequent ecological analyses. However, apart from the geological age of the parent material, the plot data from which the factors are derived consists of variables that are thought to be subject to small and medium scale, rather than regional, variation. This accords with the objectives of the project, but the possibility of major regional trends masking more local effects had to be considered. Climate and historical phytogeography are thought to be elements of the environment most likely to affect forest characteristics at the regional scale encompassed by the FIDP soils plots.

There are undoubtedly considerable variations in the climate within the region, as evidenced by the apparently anomalous but confirmed pocket of low rainfall round Song on the middle Rejang (see Figure 2.1). However, all the plots are in the interior of Central Sarawak. It is thought that moisture stress is rare in this area, and that the climatic variations are not of major ecological significance. Moreover, the local climate of each plot cluster is not known, and thus cannot be used as a variable.

Quaternary phytogeographical history is clearly influential in the distribution of some MDF tree species. Some are restricted to West Sarawak, which was a part of the Sundaland shelf and therefore relatively stable in the Tertiary and Quaternary. Others appear to have migrated North-eastwards out of Sundaland during the Quaternary. These migrations have been spasmodic and there appear to have been long hiatuses. Movement was probably halted by physical barriers such as wide peat-floored valleys or unbroken watershed ridges above 1,000 m. The 'grain' of the phytogeography of the state is roughly parallel to the main drainage systems, particularly in Central

TABLE 5.6 FIDP plots Ridit scorings for geographic location (Phytar)

Area	INVENTORY Unit	Ridit Score
Lupar - Balleh	3	.1433
Balleh - Rejang	1	.3453
Rejang - north bank	1	.4626
Anap - Kakus - Mukah	4 and 5	.7508

Sarawak. There are local variations within the main drainage systems, possibly due to Quaternary fluctuations in sea level and movements of the coast line (Ashton, 1972 (c)).

In order to allow for the main NE-SW phytogeographical gradation, an eleventh site variable was added to the factor scores. The plots were categorised from South west to North east according to the majoi drainage basins. These categories were converted to quasi-continuous scores by the Ridit transformation (Bross, 1958). This variable is referred to as Phytogeographical Area, abbreviated to Phytar. The Ridit scores for Phytar are summarised in Table 5.6.

2.2 Analyses of Site Effects on Forest in FIDP Plots

2.2.1 Site effects on total forest basal area parameters

As the individual FIDP plots are too small to enable consistent forest type classification, the FIDP data were mainly used for the investigation of the site relationships of selected individual species. However, in order to determine whether there is a general edaphic trend in forest stature and economic potential across the range covered by the FIDP plots, the linear relationships between site variables and some basal area parameters of the whole forest were examined.

Using the FIDP inventory field data, the total basal area, the total dipterocarp basal area, the total non-dipterocarp basal area, and the mean basal area per enumerated tree were calculated for each soils plot. These basal area parameters are not satisfactory and give only rough indications of the aerial biomass and economic potential of the forest. As the basal areas are not partitioned into size classes, the parameters give no indication of forest structure. Shortage of time and low expectation of much more satisfactory results precluded further treatment of the inventory data.

Each of the basal area parameters was treated as the dependent variable in stepwise multiple linear regression against the ten plot factor scores as predictor variables. The analysis was repeated in the case of total basal area after the omission of a cluster of plots known to have been inadvertently sited in low stature secondary forest. The regressions were also repeated for all four basal area parameters with the location variable, Phytar, included in the predictors.

As expected, the plotwise regressions proved unsatisfactory. This may be due to the unsatisfactory nature of the basal area parameters and also to the high variation of such small plots. In order to reduce the problem of the small sample size, the regressions were repeated on a cluster basis, using cluster means of the forest parameters and the site variables.

The use of a linear model in these and subsequent regressions needs justification. It has been pointed out that curvilinear models are more realistic descriptions of biotic responses to environmental variation. However, there are problems in the testing of curvilinear relationships in this kind of general, hypothesis-generating investigation.

The first is the choice of curvilinear model for testing. Gaussian curves are probably of the greatest general validity (Beals, 1973; Ihm and van Groenewoud, 1975). However, in a study of plantations of exotic tree species in Brazil, the growth responses to environmental variation were satisfactorily described by Mitscherlich type curves (Bastide and van Goor, 1970). Other curves might prove equally satisfactory, in some situations, but Visser (1969) has shown that the data must be very precise if various asymptotic models are to be differentiated.

A second consideration is that most of the models have only been tested in artificial and simple communities such as plantations. In complex and competitive communities such as tropical rainforests, synecological effects may lead to considerable distortion of response curves (Walter, 1971; Scott, 1974).

In the absence of *a priori* reasons for testing a particular model, there is doubt about the usefulness of indiscriminate curve-fitting (Mead, 1971). A more complex linear model, such as path analysis (Ferrari, 1963; Scott (D.), 1973) might be equally informative.

If MDF responses are actually curvilinear, but only part of the total range is sampled, the incomplete curve may be adequately described by a linear model. This applies if the sampled range is one arm of a Gaussian curve or the non-plateau section of an asymptotic function.

For these various reasons, only linear regressions were attempted in the present project.

2.2.2 Site effects on the distribution of individual species

The FIDP plots are much smaller than the 0.2 hectares that is estimated to be the minimal area for consistent floristic classification in the MDF (Ashton, 1973). The FIDP data were therefore used only for the investigation of the site relationships of some of the commoner tree species, taken separately and without consideration of possible synecological interactions.

The small size of the plots means that there is a strong possibility that a characteristic species, even if quite common, may be spatially excluded from a suitable site merely because of the low number of trees enumerated. The general procedure therefore was to compare the site conditions of plots containing the species in question with the overall FIDP soil plot means, and not with those plots from which the species is absent.

For each of the 39 commonest species, the means of the site variable scores for plots with the species were calculated. They were compared with the means of all 291 FIDP soil plots (zero by definition for the factor analysis scores, and 0.5 by definition for Ridit-transformed variables, such as Phytar) by the 't' test, allowing for unequal variances. This will only reveal specific restrictions in site conditions if the species' range lies well away from the mean of the range of all the FIDP plots. It will not identify restricted ranges if these are centred close to overall FIDP soil plot mean. In order to identify such cases, all site variable/species combinations for which the 't' test results were not significant were tested by calculation of the variance ratios. These compared the variance of the variable for plots containing the species with the variance of the same variable for all FIDP soil plots, making allowance for the large inequalities in sample sizes (Brown and Forsyth, 1974).

The 't' test and variance ratio calculations were repeated on a plot cluster basis, in order to overcome the spatial and site variable score clumping due to the distribution of the plots. The occurrence of a species on just one plot qualified the whole cluster as being 'with' the species. The cluster mean site variable scores were used in the 't' and variance ratio tests.

The 't' tests and variance ratios refer only to the species/site variable combinations individually and independently. It is also useful to somehow combine the results, in order to rank the species for site selectivity and the site variables for their effect on MDF floristic variation. This was done using the combination parameters of Wilks and Shapiro (1968).

Before combining the 't' values, they were all converted, even if not significant, to standard normal deviate values by the transformation of Wallace (1959). This was found to be satisfactory and simple, in comparison with several other formulae (Prescott, 1974). These values, z, were used in the calculation of the combination parameter $\frac{\sum(-z)}{k}$, where k is the number of cases. The standard normal deviate values were converted to one-tail probability values by use of tables (Fisher and Yates, 1963). The probability values, α, were used in the calculation of a second Wilks and Shapiro parameter, $\sum(-2 \ln \alpha)$. Using the species/site variable matrix, the parameters were calculated by rows to give species selectivity, and by columns to give the floristic discriminatory effect of the site variables. The significance levels of the parameter values are obtained by comparison with the Chi-squared tables for 2k degrees of freedom.

The absolute values of the parameters and associated significance levels have to be treated with caution. The data contravenes Wilks' and Shapiro's assumptions of independence in several ways. Due to the use of oblique simple structure factor analysis, the site variables are not independent. The site variable scores for any individual plot are reused for each of the 39 species it contains, so that the species cannot be regarded as wholly independent. Finally, the spatial and site variable scores clustering due to the layout of the plots also contravenes strict independence. This last reservation does not apply to the parameters when calculated on a cluster basis.

These reservations are not thought to invalidate the results, although the significance levels may be inflated. The relative values probably reflect the true rankings of the species for site selectivity, and of the site variables as influences on species distributions.

.2.2.3 Site effects on the basal areas of individual species

As the results of the 't' tests, singly and in combination, indicated a degree of site influence on species distribution, the effects of site conditions on the basal area of individual species were examined. . Basal area combines tree numbers and size, and was taken as an easily calculable indicator of species importance. However, the inflationary effect of single large trees on small plots means that basal area is not a very satisfactory parameter.

The plot basal areas of 14 of the commoner, apparently selective species were taken as the dependent variables in separate stepwise multiple linear regressions against the site variables as predictors. The regressions were repeated on a plot cluster basis, taking the cluster mean of the plot basal areas and the cluster mean site variable scores as the dependent and predictor variables respectively.

Because of the relatively low number of occurrences for some species in comparison with the number of predictor variables, it was suspected that the regressions might be distorted by an approach to full resolution. The 'cleanness of residuals' statistic (= residual sum of squares / (residual degrees of freedom)^2 (Tukey, 1954), was calculated for each step of the regressions. This confirmed that the BMD program's stopping procedure, based on 5% significance level of the F ratios, was conservative and that there was no tendency to incorporate residual error.

The possible reservations about the use of a linear model have been noted above (5.2.2.1). The species tested in these regressions generally had high combined 't' test results, which suggests that the FIDP plots only cover part of their edaphic range. In such cases, the linear model is likely to be a satisfactory approximation to most response curves.

The only effort to check on possible curvilinearity was to plot the basal areas of *Shorea quadrinervis* separately against the site variables that apparently restrict its distribution. This species was chosen because it is apparently very site-selective, but its basal area regression was completely non-significant.

5.2.3 Analyses of Site Effects on Hollow Decay in the MDF

5.2.3.1 Introduction

Loggers in North Sarawak have reported a marked association between stem-rot levels in the MDF and site conditions. If confirmed, this association could arise in several ways. It may be that site effects on forest floristics lead to concentrations of decay-susceptible species. An alternative is that site conditions affect tree longevity, leading to congregations of older trees, which are more liable to decay infection on probability grounds. Another alternative is that site conditions affect intraspecific variation in decay-susceptibility, independently of tree size and age.

In an attempt to distinguish between these alternatives, three separate lines of investigation were followed. The relationships between site conditions and stem rot levels in the forest taken as a whole were examined by multiple linear regression. Interspecific variations in buttrot occurrence, irrespective of site conditions, were examined. Finally, the effects of site conditions on intraspecific variation in the severity of stemrot were examined, using multiple linear regression.

5.2.3.2 Intergeneric and interspecific variation in buttrot occurrence

As this part of the investigation was not concerned with site effects, all of the available FIDP tree drilling data were used. As the trees were drilled only at reference height, only buttrot could be identified. However, the FIDP's more detailed volume and decay sampling program showed that rot in the upper parts of the stem without accompanying buttrot was infrequent in the commoner timber groups (FIDP, 1974 (c)); Panzer, 1975). This indicates that buttrot severity gives a rough guide to the severity of decay in the stem as a whole. In the drilling descriptions spongy heart could not be consistently distinguished from hollow decay, and the two were classed together as unspecified rot. Brittle heart, where it occurred, was almost certainly described as sound.

For a selection of botanical groupings (timber group, genus, section or species) the proportions of all drilled trees showing buttrot were calculated. The asymmetric 95% confidence intervals for these percentages were obtained from tables (Mainland et al., 1956), extrapolating conservatively where necessary. Differences in the percentages of trees showing rot were compared by the Brown and Forsyth (1974) modification of the F ratio, which allows for wide variations in variance and sample size.

Because some of the species and genera that are known to yield highly durable timber had high percentages of rotten trees, the tree size data were also examined. The mean diameters for all drilled, all sound and all rotten trees in each grouping were calculated. The differences between the means for sound and rotten trees within each grouping were tested for significance by the 't' test, with allowance for differences in sample size and variance.

5.2.3.3 Site effects on stemrot severity in the forest as a whole

The results of the analyses described so far indicate that there are apparently marked site effects on the distribution of some important species and that there are considerable interspecific differences in buttrot frequency. In combination, these may give rise to associations between site conditions and the severity of decay in the total forest, as reported by loggers in North Sarawak.

In order to examine this possibility, the severity of stemrot in the whole forest was calculated for those FIDP soil plots on which at least two stems had been completely measured in the volume and defect studies. The plot stemrot severity was taken as the total volume lost to decay, expressed as a percentage of the sum of the total volumes (TSV) of the fully measured trees (FIDP, 1974 (c)). This figure is heavily weighted by the presence of one very large rotten stem in an otherwise sound stand of medium-sized stems.

The plot stemrot severity was taken as the dependent variable in stepwise multiple linear regressions against various sets of predictor variables. One set consisted only of the ten plot factor scores. Another consisted of all the site variables, including Phytar. Because of the known increase in the probability and severity of stemrot with increasing tree age and size, the third and most complete set of predictors consisted of the site variables, including Phytar, and the sum of the total stem volumes of the measured trees.

5.2.3.4 Site effects on intraspecific variation in stemrot severity

The relationships between site conditions and the intraspecific variation in the severity of stemrot were examined.

Nine species were used, as they have a sufficient number of fully measured trees on site characterised defect study plots to avoid any tendency to

TABLE 5.7 Summary of statistical analyses of FIDP data

Objective	Type of Analysis	Input	Variations tested	Result/Output	Text Section refers.
Reduction of granulometric variables	Product moment correlation coefficients	Detailed granulometric data from Units 1 and 3	Various simple and logarithmic ratios	Clay and silt retained. Sand discarded	5.2.1.1
Quasi-normalisation of non-continuous variables	Ridit transformation	Ordered, categorical variables		Quasi-scalar Ridit values for non-continuous variables	5.2.1.1
Simplification and clarification of raw data	Factor analysis	Raw site and soils data with variable means substitutes for missing data	Principal components (for scree test), Varimax, Oblique Simple Structure with 9 and 10 factors rotated.	Plot factor scores for Oblique Simple structure with 10 factors rotated	5.2.1.1
Choice of final number of factors for rotation	Jack-knife factorisations	5 reduced 80% matrices of plot factor scores formed by random deletion of one decile from each half of full plot factor scores matrix.	Oblique simple structure factor analysis with 9 or 10 factors rotated.	Final choice of 10 factors. Validation of factor loadings	5.2.1.1
Determination of clumping of site properties due to spatial proximity within clusters and units	One-way univeriate analyses of variance	Plot factor scores, plot groupings into clusters and samples.	Inventory units treated individually and together.	Estimates of significance of cluster and Unit clumping effect for each factor.	5.2.1.2
Test whether total basal area related to site characteristics	Stepwise multiple linear regression	Plot factor and Phytar scores, and plot overall basal areas.		Estimates of significance of successive site factor contributions up to stopping limit, and multiple R^2	5.2.2.1
Identification of effect of iste properties on distribution of 39 commoner species	(i) t test (ii) Variance ratios	Factor and Phytar scores for plots with species.	Integration of multiple 't' tests by use of Wilks and Shapiro (1968) parameters	Estimates of species site properties' floristic differential effect.	5.2.2.2
Test whether basal area of selected species related to site characteristics	Stepwise multiple linear regressions.	Plot factor and Phytar scores, and plot basal areas for selected species		Estimates of significance of successive site factor contributions up to stopping limit; and multiple R^2	5.2.2.3
Test whether occurrence of stem rot varies significantly between commoner taxonomic groups	Visual comparison of 95% confidence intervals of proportions of rotten trees.	All available FIDP tree drilling data for selected groups		Graphic representation of 95% confidence limits of percentage of trees with buttrot	5.2.3.2
Test whether severity of overall forest stemrot related to site characteristics	Stepwise multiple linear regressions	Cull volume percentage and total stem volume for all trees on plot. Plot factor and Phytar scores		Estimates of significance of successive site factor contributions up to stopping limit, and multiple R^2	5.2.3.3
Test whether severity of stemrot in individual species is related to site characteristics	Stepwise multiple linear regression	Cull volume percentage for individual trees, tree size, and factor and Phytar scores for plots on which they occur		- do -	5.2.3.4

full resolution in multiple linear regression. The selected species were:

Keruing:	*Dipterocarpus caudiferus*
Kapur:	*Dryobalanops aromatica* and *D. oblongifolia*
Yellow merantis:	*Shorea collaris* and *S. faguetioides*
Red merantis:	*Shorea beccariana, S. parvifolia, S. rubra* and *S. sagittata*

The volume loss to stemrot in each measured tree, expressed as a percentage of the tree's total stem volume, was taken as the dependent variable and subjected to stepwise multiple linear regression against various sets of predictor variables. The first set were the factor scores for the plots on which the trees occur. The second set included Phytar. The most complete analyses included a tree size parameter in the predictor variables. One parameter tried was the tree's total stem volume. The second was its basal area.

The possible reservations about the use of the linear model noted above also apply to some extent. However, the *a priori* choice of an appropriate curvilinear model for testing is even less straightforward in these analyses. In complex host-vector-pathogen systems it is thought that quasi-linear or asymptotic responses to edaphic factors are as likely as peaked Gaussian curves.

5.3 Analyses of Data from MDF Ecological Plots

5.3.1. Introduction

Soils fieldwork was completed on only 39 of the original 105 MDF ecological plots during 1971-72. As there are no laboratory data for the 6 West Sarawak plots visited, there are complete 1971-72 site data for only 33 plots (see Table 4.3). Initially analytical effort was concentrated on these data but, because the number of plots eventually seemed too small, the original 1963-66 site data from all 105 ecological plots were re-used for further investigations of site-forest relationships.

Unlike the FIDP plots, the MDF ecological plots had been planned, from the outset, to be of sufficient size to permit consistent floristic classification. 1.5 acre (0.6 ha) plots gives a satisfactory compromise between maximisation of the forest data with the minimum internal environmental heterogeneity. In some of the floristic classifications, subplots of 0.5 acre (0.2 ha) were used. This area is rather low, although the concept of the absolute minimal area is not really applicable in these kinds of forests (Poore, 1968). It was chosen as the maximum subplot size that enabled the integration of the Brunei 1.0 and the Sarawak 1.5 acre plot data into a single matrix.

Both the full 1.5 acre plots and the 0.5 acre subplots were subject to a series of objective floristic classifications, using the 1963-66 forest data (Ashton, 1973). Three methods of classification were used. The best known is Association Analysis, which is a divisive monothetic technique. The array of plots is successively divided according to the presence or absence of the most highly associated species. The relative associations of the species are determined from the summed Chi squared values of the matrix of species consociation (Williams and Lambert, 1959 and 1961). This method has been widely used, including applications to studies of tropical rainforest elsewhere (e.g. Greig-Smith et al., 1967). In the preliminary analyses of the MDF ecological plot data (Ashton, 1973) it was applied to the data from the 105 1.5 acre plots, using the full complement of species, and also using only the 98 most common species. It was also applied to an en- larged matrix of 0.5 acre plots from the Borneo MDF, which included all 315 Sarawak MDF ecological subplots, and also 200 0.5 acre subplots from Brunei, formed by halving Ashton's original one acre plots (Ashton, 1964 (a)).

Another method used was the divisive monothetic technique developed by Crawford and Wishart (1968). This method is economical of computational resources and has been satisfactorily applied in the tropics by its authors (Crawford et al., 1970). However, it has not been widely adopted elsewhere. As with Association Analysis, it was applied to the 105 Sarawak 1.5 acre plots, and to the enlarged matrix of 0.5 acre Borneo MDF plots, using both the full complement of species and a reduced list of the 58 most common species.

The third method tried was Divisive Information Analysis (Williams et al., 1966). This is theoretically the most satisfactory of the three techniques, but it has high computational requirements. It was therefore only attempted once, on a very much enlarged matrix of 0.5 acre plots. This included all the Sarawak and Brunei 0.5 acre MDF plots, and also plots from the Lowland Dipterocarp Forest of West Malaysia, the Peat Swamp Forests of Sarawak, and the Kerangas (heath) Forests of Sarawak.

Details of the methods and their computational artefacts are discussed in Ashton (1973). Since widespread interest in the West in objective numerical methods of classifying ecological data was stimulated by the study of Bray and Curtis in 1959, there have been rapid methodological developments (Beals, 1973). Not all of the techniques used on the MDF ecological plots are now being widely applied, and they may have already been superseded (e.g. Noy-Meir, 1973; Hill et al., 1975). However, there is broad consensus between the various results obtained, and the classifications seem to reflect the same major trends in the physical and biological environment, suggesting that the methods are appropriate.

Because of the larger plot sizes, and because of the pre-existence of these objective floristic classifications, it is possible to use the site data from these plots to investigate the site relationships of the forest as a whole. This is more realistic and satisfactory than the strictly autecological analyses necessitated by the small size of the FIDP plots.

Other workers studying vegetation-site relationships with complex vegetation and site data have used a variety of multivariate statistical strategies. These often involve the use of principal component analysis to clarify and simplify the site data (e.g. Gray and Bunce, 1972), the plant community data (e.g. Hall, 1977) or both (e.g. Barkham and Norris, 1970).

The pre-existing objective floristic classifications of the MDF ecological plots made the use of discriminant analysis possible. This is a technique which objectively compares some multivariate attributes of a set of cases with a pre-determined classification of the cases based on different attributes. Using the hyperspace that is defined by the new attributes, the method generates the linear function that best discriminates between the classification groups and it also indicates the concordance between the classification and the new attributes (van de Geer, 1971). It has been used in soil survey and classification studies (Oertel, 1961; Kimura and Swindale, 1967; Webster and Burrough, 1974; Burrough and Webster, 1976). An application to the classification of Scandinavian podzols, using factor scores rather than raw data is reported by Jauhainen (1976). Discriminant analysis has also been used in the determination of the soil properties which most affected the performance of *Pinus elliottii* in the south-eastern U.S.A. (White and Mead, 1971). The application to determine the degree of association between complex sclerophyllous bush communities and the underlying geology in Western Australia seems similar in principle to its present application to Sarawak MDF data. The difference is that there the known geology of the test sites formed the predetermined classification, and it was the botanical data that were used to generate discriminant function (Nielsen et al., 1973).

In its application to the MDF ecological plots data, the BMD Stepwise Multiple Discriminant Analysis program first locates the centroids of the floristic classification groups in site variable hyperspace. It then calculates the position of each of the plots or subplots in the hyperspace, using the plot's edaphic data, and determines the floristic group centroid to which the plot or subplot is edaphically closest. If the plot is closest to the centroid of its original floristic group, the floristic and site variable classifications may be regarded as in agreement. If the plot or subplot is closer to the centroid of another floristic group, the classifications 'disagree' and the plot or subplot may be regarded as edaphically misclassified. The program also determines the size and significance of the individial contributions of the site variables to the discriminant function. As with the Stepwise Multiple Linear Regression program, the course of this procedure is unique only if the site variables are orthogonal. Because of the correlations between the factor scores or the raw data variables, both of which are used as site variables, the course of these discriminant analyses are not unique.

Finally, the program also calculates the relative contributions of the successive orthogonal canonical variables in accounting for the dispersion of the floristic group centroids. This indicates the degree to which the forest can be interpreted in terms of a few orthogonal environmental clines even if the physical interpretation of the canonical variables is obscure.

Discriminant analysis was repeated for a variety of combinations of floristic classifications and site variables. These are described in detail in Sections 5.3.2 and 5.3.3, and summarised in Table 5.12.

5.3.2 Analyses Using 1971-72 Site Data

5.3.2.1 Factor analysis of site data

Because there were more variables per MDF ecological plot than for the FIDP plots, the need to clarify and simplify the raw data by factor analysis was even more pressing. As described above (Section 4.3.2), the site and forest data had been collected to enable each 0.5 acre subplot to be treated as a separate case. This was fortunate, as there were so many variables in the raw data that, if the 1.5 acre plots had been indivisible, there would have been more attributes than cases, a condition that does not permit satisfactory and stable factor analysis.

Including morphological data from the profile descriptions, there were initially over 60 primary variables. Some of these are subject to rapid change, e.g. moisture contents, and were discarded. Others are not of great interest except as intermediates in the calculation of derived variables, e.g. particle density is mainly required for the calculation of total porosity. These variables were also discarded. Others are clearly duplicated measurements of the same property, such as the measurement of stone contents in the bulk density excavations and the visual assessment of stone abundance in the same horizons in the profile descriptions. Table 5.8 summarises the comparison of these methods of estimating soil stoniness. Despite their qualitative nature, the visual assessments are preferred because they summarise the appearance of the whole width of the pit face, whereas each bulk density excavation only samples about 0.002 m^3 of soil. Moreover, the excavations are not randomly sited, as care was taken to avoid large stones. This accounts for the zero stone content values in horizons described as very stony.

After this preliminary culling, there were 51 primary variables remaining. They were:

Site: Topographic position; slope gradient; microterracing; surface stoniness; depth of litter; depth to lithic and paralithic contacts; acidity and geological age of parent rock.

Soil: (repeated for top- and subsoils):
Horizon depth; matrix hue and (value + chroma); mottles; structure type and strength; ped coatings; root density; stone frequency (visual assessment); clay, silt and sand percentages; coefficient of linear expansion (COLE): oven-dry bulk density; total porosity; pH; organic carbon; total nitrogen; reserve phosphorus, calcium, magnesium and potassium.

TABLE 5.8 Comparison of estimates of stoniness (1971-2 MDF ecological plot data)

Visual assessment of stone frequency in horizon description	Estimates of stone content (w/w) by sieving and weighing excavated material in bulk density determinations.			Number of horizons (Stone content estimations)
	Mean	s.d.	Range	
Absent	1.13	3.82	0 - 25.51	111 (333)
Few	6.20	10.40	0 - 31.76	49 (147)
Common	11.28	9.57	0 - 44.51	71 (213)
Many	16.43	12.06	0 - 65.71	99 (297)
Abundant	19.56	11.49	1.69 - 44.67	61 (183)

Of these, the following were not originally measured on continuous scales:

Topographic position; microterracing; surface stoniness; acidity and geological age of parent rock; mottles; structure; ped coatings; root density; and stone frequency.

All of these were scored in discrete categories on nominal scales.

For some of them this is straightforward, but the procedure requires amplification for the others. Topographic position was interpreted along a cline from crest to lower slope, as in the FIDP plots. The acidity of the parent rock was assessed on the approximate silica contents as gauged from the geochemical data, summarised in Table 5.9, available from similar rocks. Based on this, the parent rocks of the plots were divided into 5 groups, i.e.

basalt; shale; mixed shale and greywacke; greywacke; rhyolite.

Mottles were assessed with respect to the combination of frequency, size and contrast, but not colour. The scale ran from zero through few, fine and faint to abundant, coarse, prominent.

Structures were interpreted according to their presumed indications of profile age, stability and degree of development. The topsoil structure cline ran from moderate crumb, through blocky, to stone-obscured structures. The scale for subsoil structures was similar, except that simple crumb structures were not encountered. There were some compound structures in the subsoils of the basalt-derived Lateritic soils, in which weak blocky peds crumbled to give weak-moderate crumbs.

Because the profile pits were dug to two metres if necessary, there was no necessity to convert the depth data into categorical values, as done for the FIDP data. Soil matrix Munsell hue was treated as a discrete nominal variable. Scores ran from 2.5 for 2.5 YR to 12.5 for 2.5 Y. The variable (value + chroma) was preferred to the simplification of values and chromas adopted from Northcote by I.M. Scott (1973).

The clinal categorical variables were converted to quasi-continuous scalar values by the Ridit transformation (Bross, 1958).

As the data matrix was complete, there was no missing data problem. Before starting factor analysis, a correlation matrix of the 51 variables was drawn up. As expected it showed some pairs of very highly correlated variables. These were:

TABLE 5.9 Chemical composition of some Sarawak rocks

Rock Type	SiO_2	TiO_2	Al_2O_3	Fe_2O_3	FeO	MnO	MgO	CaO	Na_2O	K_2O	P_2O_5	Reference
Basalt (Bt Mersing)	46.57	3.03	13.08	7.90	8.37	0.03	5.07	8.33	2.68	2.82	0.61	Leichti *et al* (1960. p.242)
Calcareous Shale (North Sarawak)	53.43	n.d.	22.86		n.d.	n.d.	1.41	8.06	n.d.	n.d.	tr.	Haile (1962, p.135)
Neogene Shale (North Sarawak)	60.52	n.d.	27.05		n.d.	n.d.	0.71	0.26	n.d.	n.d.	n.d.	
Cretaceous Shale (West Sarawak)	60.1	0.99	21.6	5.36		n.d.	1.53	tr.	n.d.	2.24	n.d.	Andriesse (1975, p.30)
Dacite (Usan Apau)	64.04	0.35	14.21	0.35	2.93	0.09	1.10	4.90	5.01	3.29	0.12	Kirk (1957, p.83)
Paleogenic greywacke sandstone (Central Sarawak)	70.94	0.40	13.19	2.69	1.17	0.03	0.49	1.79	4.07	1.68	0.24	Wolfenden (1960, p.39)
Rhyolite (Bt Arip)	77.24	0.21	11.19	1.52	tr.	tr.	0.18	0.26	2.33	5.35	0.09	Wolfenden (1960, p.55)

tr = trace n.d. = no determination

Surface stoniness and topsoil stone frequency (r = 0.884)

Depths to lithic and paralithic contacts (r = 0.904)

Dry bulk density and total porosity (r = -0.987 for topsoils, r = -0.983 for subsoils)

Such high degrees of correlation are almost equivalent to linear dependence, and lead to rank deficiency in the data matrix, with unfavourable effects on factor analysis. Consequently, the surface stoniness, depth to paralithic contact, and dry bulk density (topsoil and subsoil) variables were discarded.

As with the FIDP data, it was necessary to omit one of the fine earth granulometric variables because of linear dependence and rank deficiency considerations. On the basis of experience with the FIDP data (see Tables 5.1 - 5.4), sand contents were discarded and the clay and silt variables retained.

The procedure for the factor analysis of the final 45 variable data matrix was similar to that used for the FIDP data. Principal component analysis was performed and the square roots of the eigenvalues plotted on a linear scale against factor numbers. This 'scree·test' showed a major break of slope at about Component 11 or 12. There was also a subsidiary, but distinct, break at Component 7 or 8. Because of this equivocal result, eight exploratory oblique simple structure factor analyses were run, rotating successively 6-13 factors. The analyses with 6-10 factors were rejected because of the undue amalgamation of factors. Physical variables such as porosity and COLE were incorporated in with the first, general soil fertility, factor. The 13 factor analysis appeared to be subject to disruptive, trivial fission of factors, and was also rejected.

The 'jack-knife' procedure was again employed to finalise the choice between the 11 or 12 factor analyses. Five reduced (80%) data matrices were formed by random omission of one plot in five. Each of the reduced matrices was successively subjected to 11 and 12 oblique simple structure factor analyses. The stabilities of the factorisations were compared by calculating the proportion of loadings in the analysis of the full data matrix that were validated by the procedure of Pennell (1972). In this, a loading is only validated if the lower absolute 95% confidence limit exceeds 0.1. The results are summarised in Table 5.10. There is very little difference between the two sets of factorisations. However, it was noted during the desk calculations of the loading validities, that the majority of the high value loadings

TABLE 5.10 Oblique simple structure factor stability.
MDF ecological subplots 1971-2 data

Loading size in factorisation of full data matrix / Number of factors rotated	Percentage of loadings validated	
	$\lvert 0.1 - 0.25 \rvert$	$>\lvert 0.25 \rvert$
11	36	90
12	34	90

(i.e. with absolute values greater than 0.25) in the full matrix factorisation that are not validated occur on the smaller, higher number factors. On the basis of this, and its marginal superiority in Table 5.10, the 11 factor rotation was preferred.

Oblique simple structure factor analysis, rotating 11 factors, was re-run on the full raw data matrix. The subplot factor scores were stored as site variables for the subsequent ecological investigations.

5.3.2.2 Analysis of variance of factor scores

The spatial contiguity of the subplots of each 1.5 acre plot was expected to have a strong clustering effect on the factor scores, particularly for factors with validated loadings by topographic variables. Clustering of scores within sites was also expected because of the spatial proximity and geological similarity of the plots.

To test the magnitude and significance of these clustering effects, one-way univariate analyses of variance were carried out on the subplot factor scores, taking the plot and site groupings as treatments.

5.3.2.3 Site variables

As mentioned earlier (see 5.2.1.3), there is a historical phytogeographical gradation running from South west to North east across the state. In order to allow for this, a phytogeographical area (Phytar) variable was added to the eleven factor scores. The need for such a variable was more acute for these plots than for the FIDP plots. This is because they cover a wider geographic range. Also the geological age of the parent rock does not run parallel to the phytogeographical gradation, as in the FIDP plots. This is because some of the plots are on igneous rock outcrops, which post-date the sedimentary rocks in which they are emplaced. The procedure for calculating Phytar scores is basically the same as in the FIDP plots. The plots are assigned to ordered categories according to major drainage systems. These are converted to quasi-continuous scalar scores by the Ridit transformation (Bross, 1958).

Unlike the FIDP plots, the MDF ecological plots are not all situated in the interior. There are some within 2 kilometres of the coast. It is probable

Analysis and the Crawford and Wishart techniques. Again the course of the analyses might have been somewhat different had the original array consisted of only the 33 plots with the 1971-72 site data. As with the subplots, it was necessary to reinterpret the classification dendrograms to reduce the number and increase the size of the groups. In fact, the cutoff was taken at two levels, giving 7 and 3 groups for each of the classification methods. Two levels were taken because, for the 7 groups classification, the group size seemed too small, whereas 3 seemed an excessively low number of groups. As before, the discriminant analyses were repeated with and without the inclusion of the locational variables in the predictors.

5.3.3. Analyses Using Original 1963-66 Site Data

5.3.3.1 Introduction

The results obtained from the 1971-72 data were inconclusive in some respects, probably because of the low number of plots. It was therefore decided to re-examine the site data collected under the supervision of Dr. P.S. Ashton in 1963-66, when the plots were originally established.

These data have already been used for some preliminary investigations of relationships between forest variation and site conditions (see Ashton (1973) and section 3.1.2).

As only one subsoil sample was taken for laboratory analysis from each 1.5 acre plot, there is no possibility of complete site data for separate 0.5 acre subplots. The statistical analyses were therefore confined to the floristic classifications of the 1.5 acre plots.

The statistical procedure followed was similar to that for the analyses of the 1971-72 data. The raw site data were clarified and simplified by oblique simple structure factor analysis. The plot factor scores were then used, together with locational variables, in discriminant analyses, using pre-existing floristic classifications. The discriminant analyses were also repeated using the raw site data.

5.3.3.2 Factor analysis of site data

The 1963-66 site data consisted of 27 variables. They were:

Plot: Topographic position; altitude; and parent and rock acidity.

Soil: (topsoil (mean of 3 determinations) and subsoil (one determination):
Sand, silt and clay percentages; pH; total nitrogen; reserve phosphorus, calcium, magnesium and potassium; free iron and aluminium (Group III) oxides; volume weight.

There were also Munsell codings for subsoil matrix colours.

The topographic position was assessed from the sketch map of the site and the trend line map of the plot. Field experience in 1971-72 showed this to be satisfactory for assigning plots to one of four categories running from crest to lower slope. The parent rocks were assigned to one of the five categories on an acidity scale, similar to that used for the 1971-72 data. This was based on the silica contents of similar rocks, as summarised in Table 5.9. Of the parent rocks not encountered in the 1971-72 data, dacite was grouped with mixed shale and sandstone in category 3, and the siliceous Plateau Group sandstone was classed with rhyolite in category 5.

These ordered categorical scores were converted to quasi-continuous scalar values by the Ridit transformation (Bross, 1958).

Altitude data were collected with an anerometer when the plots were established. Since then, some of the sites have been covered by newly issued, contoured 1:50,000 map sheets in the Lands and Survey Department/U.K. Directorate of Overseas Surveys series. The contours and spot heights on these show the original plot altitude data to be somewhat inaccurate. However, the data were retained for factor analysis, as not all of the sites are covered by the new mapping.

As with the other raw data sets, it was necessary to omit one of the fine earth granulometric variables in order to avoid linear dependence and rank deficiency. A preliminary correlation matrix, part of which is given in Table 5.11, showed that clay and silt were the least correlated pair of variables, so sand contents were omitted from the data. This result confirmed that the untested omission of the sand content variables from the 1971-72 data, based on experience with the FIDP plot data, was probably correct.

TABLE 5.11 Correlation coefficients between granulometric fractions for 105 1.5 acre MDF ecological plots (1963-6 site data)

(a) Topsoil

	Sand	Silt	Clay
Sand	1.000		
Silt	- .773	1.000	
Clay	- .842	.319	1.000

(b) Subsoil

	Sand	Silt	Clay
Sand	1.000		
Silt	- .847	1.000	
Clay	- .870	.477	1.000

The 25 variable matrix was subject to principal component analysis. A scree test was performed, plotting the square roots of the eigenvalues against component numbers on a linear scale. This showed the main break of slope at about factor 4-5.

Preliminary oblique simple structure factor analyses were run, rotating 4, 5 or 6 factors. The 6 factor analysis was rejected because it was difficult to interpret and appeared to be subject to trivial, disruptive fission.

To enable a final choice between the 4 or 5 factor analyses, the 'jack-knife' technique was again employed. Five reduced (84 plots) matrices were formed by the random deletion of one plot in five. Each of the reduced matrices was subject to two oblique simple structure factor analyses, rotating 4 or 5 factors. Visual inspection of the results showed the 4 factor analyses to be unstable and unsatisfactory, as it was not possible to consistently interpret and identify the four factors. In contrast, when 5 factors were rotated, it was quite possible to identify all of the factors in every run.

The results of the jack-knife factorisations were used to validate the factor loadings. As before, a factor loading was accepted as valid only if its lower 95% confidence interval limit had an absolute value greater than 0.1 (Pennell, 1972).

The oblique simple structure factor analysis of the full data matrix was re-run, rotating five factors. The plot factor scores were stored as site variables for the subsequent discriminant analyses.

5.3.3.3 Site variables

As with the 1971-72 data, it was felt necessary to add locational variables to allow for major phytogeographical and climatic trends. The locational scores were calculated on the same basis as for the 1971-72 data. The phytogeographical area (Phytar) scores were again calculated by the Ridit transformation of drainage basin categories. The second locational variable, Seadist, was again the shortest straight line distance to the coast.

No analyses of variance of the plot factor scores were run. It was assumed that the geological homogeneity of the sites, and the spatial proximity of the plots within the sites, would give clustering effects similar to those in the 1971-72 data.

5.3.3.4 Discriminant analyses

The 105 1.5 acre plots had previously been floristically classified by the Association Analysis and Crawford and Wishart techniques (see Section 5.3.1). Shortage of time precluded the use of the Crawford and Wishart results, and attention was concentrated on the classification produced by Association Analysis, which had generally given the most site-compatible groupings in the analyses of the 1971-72 data. One set of discriminant analyses was performed using the final groupings of the Association Analysis classification. The second set was performed using fewer and larger groups formed by stopping the bifuraction process at a higher value of the divisive statistic.

At each level of floristic subdivision, two discriminant analyses were run. In the first the predictor variables were the five plot factor scores and the two locational variables. In the second, the analysis was run with the 25 raw site data variables and the two locational variables as the predictors.

As mentioned earlier, the course of stepwise multiple discriminant analysis is not unique if the predictor variables are not orthogonal. The degree of intercorrelation between some of the raw site variables is considerably higher than between the oblique factors, so that the discriminant analysis based on the raw data need to be interpreted with greater caution.

TABLE 5.12 Summary of statistical analyses of MDF ecological plot data

Objective	Type of Analysis	Input	Variations	Result/Output	Text Section Refers.
A. 1971-1972 data (99 x 0.5 acre subplots)					
Quasi-normalisation of clininal categorical variables	Ridit transformation	Clinal, categorical variables		Quasi-scalar Ridit values	5.3.2.1
Simplification and clarification of raw data.	Factor analysis	Raw site and soils data (less sand percentages) for 99 x 0.5 acre subplots	Principal components, (for 'scree test'), Oblique simple structure with 6-13 factors rotated.	Plot factor scores for oblique simple structure factor analysis with 11 factors rotated	5.3.2.1
Validation of factor loadings	'Jack-knife' factor analysis	5 matrices of 80% raw data by random omission of one subplot in five.		Validated factor loadings	5.3.2.1
Determination of clumping effect due to spatial proximity and within-site geological homogeneity	One-way univariate analysis of variance	Subplot factor scores		Estimates of statistical significance of 'plot and 'site' clustering effects	5.3.2.2
Analysis of relationships between site properties and floristic classification of 0.5 acre subplots.	Stepwise Discriminant Analysis	Subplot factor scores, and floristic groups of subplots	Floristic classifications produced by Association Analysis, Information Analysis and Crawford and Wishart techniques used. Analyses run with and without locational variables	(a) Number of subplots for which floristic and site properties classifications 'agree' (b) Estimates of relative proportions of site properties in affecting floristic classification. (c) Number of orthogonal canonical variables required to account for bulk of floristic group dispersion	5.2.3.4
Analysis of relations between site properties and floristic classification of 1.5 acre plots.	Stepwise Discriminant Analysis	Plot means of subplot factor scores, and floristic groups of plots	Floristic groupings produced by Association Analysis and Crawford and Wishart techniques, at two levels of subdivision, used. Analyses run with and without locational variables	- do -	5.3.2.4
B. Original 1963-6 data (105 x 1.5 acre plots)					
Quasi-normalisation of clinal categorical variables	Ridit transformations	Clinal categorical variables		Quasi-scalar Ridit values	5.3.3.2
Elimination of one granulometric variable	Product moment correlations between granulometric variables	Granulometric variables		Sand omitted from raw data	5.3.3.2
Simplification and clarification of raw data	Factor analysis	Raw site and soil data	Principal Component Analysis (for 'scree test'). Oblique Simple Structure, with 4, 5 or 6 factors rotated	Plot factor scores	5.3.3.2
Choice of number of factors to be rotated, and validation of factor loadings	Jack-knife factorisations	5 reduced raw site and soil data matrices for 84 plots, by random omission of one plot in five.	Oblique simple structure with 4 or 5 factors rotated.	Confidence limits for factor loadings. Choice of 5 factor analysis.	5.3.3.2
Analysis of relationships between site properties and floristic classification of plots	Stepwise Discriminant Analysis	Plot raw data, Plot factor scores, locational variables. Floristic groupings by Association Analysis.	Floristic groupings at 2 levels of subdivision by Association Analysis used; each run with raw data and with factor scores.	(a) Number of plots for which floristic and site properties classifications 'agree' (b) Estimates of relative influence of site properties on floristic classification. (c) Number of orthogonal canonical variables required to account for bulk of floristic group dispersion.	5.3.3.4

CHAPTER 6

RESULTS AND DISCUSSION:

I: SITE EFFECTS ON MDF FLORISTIC AND PHYSIOGNOMIC VARIATION

6.1 Introduction

The results from the MDF ecological plots are treated before those from the FIDP plots. This is a reversal of the chronological order of the fieldwork and of the statistical analyses, and the sequence of description so far in this account. It was done because it was felt to be more satisfactory to move from consideration of the broad range of forest types and site conditions covered by the MDF ecological plots to the more restricted range of FIDP plots, rather than *vice versa*. Also, the reversed order means that discussion moves from the site relationships of forest types to those of individual species, which also seems more satisfactory.

In the following sections, each of the three factor analyses are physically interpreted. This kind of interpretation is inevitably subjective but it appears to be essential for the comprehension of ecological relationships involving the factors. The element of subjectivity is reduced by the simple structure of the factors.

Any set of factors is unique to the particular data from which they are derived. It is hoped that the sampling programmes in this project have been extensive enough for the factors to characterise site conditions in the Sarawak MDF in general.

6.2 MDF Ecological Plot Results

6.2.1 Results Using 1971-72 Site Data

6.2.1.1 Factor analysis of site data

The validated factor loadings for the oblique simple structure factor analysis of the site data from the 99 subplots characterised in the 1971-72 fieldwork are given in Table 6.1. Table 6.2 shows the correlations between the factors. The analysis incorporated almost 81% of the total original variance, which is satisfactorily high (Childs, 1970). Only two variables, subsoil mottles and subsoil root density, have communalities of less than 0.5

TABLE 6.1 Oblique simple structure factor analysis of 99 x 0.5 acre MDF ecological subplots. 1971-2 site data validated loadings.

Factor	1	2	3	4	5	6	7	8	9†	10	11†	Cumulative
Proportion of total variance (%)	43.9	11.4	6.6	4.6	3.7	2.7	2.2	1.9	1.6	1.3	1.0	80.9
Variable												Final communality
Site:												
Topography			-.382				-.260		-.368	-.206	-.175	.690
Slope		.232		.208		.464						.572
Surface stepping						.951						.856
Litter depth	-.548				.281							.882
Soil depth		-.259		-.191	.294					.444		.855
Parent material acidity	-.538	-.251						-.183				.919
Parent material age			.218								-.698	.967
Topsoil:												
Depth								.745				.626
Hue				.199	-.154	-.122					-.783	.800
Value + chroma			.813		-.168							.693
Mottling						.200	-.250	-.345				.586
Structure		.296	.286					.385				.644
Cutans								.454		-.238		.777
Roots		-.328		-.208				-.249	.411			.778
Stones	.302		-.192		-.192			.348		-.241		.869
Clay		.234		.242					.234		.610	.958
Silt				.973								.888
COLE				.245							.665	.900
Total porosity		-.226	-.328			.157			.201		.569	.839
pH			-.530	.248	-.394							.800
Organic C		-.202	-.335	.305					.332		.400	.903
Total N			-.344	.305					.273		.284	.922
Reserve P	.517		-.190					.243				.939
Reserve Ca	.544		-.365					.225		-.152		.951
Reserve Mg	.344	.248	-.241				-.212	.334				.944
Reserve K		.839						.150				.845
Subsoil:												
Depth										.768		.595
Hue				.130	-.379	-.212	.232				-.554	.841
Value + Chroma		.264	.331	.236				.300	-.262	.286		.796
Mottles				.234				.305				.458
Structure							.867					.750
Cutans					.649							.535
Roots									.527			.425
Stones	.142	.183				.160				-.345	.282	.890
Clay		.408		.239			.262		.275		.455	.922
Silt				.853						-.219		.864
COLE	.306	.292									.554	.842
Total porosity				.222						-.215	.632	.939
pH			-.520					.276	-.207		.336	.826
Organic C	.363									-.355		.890
Total N	.383	.195		.220	-.211		.122			-.163		.912
Reserve P	.397											.798
Reserve Ca	.539		-.189					.210		-.202	.230	.983
Reserve Mg	.309	.281					-.242	.243		-.201		.884
Reserve K		.900										.836
Factor designation	Fertility	K	Drainage	Silt	Cutans	Surface wash	Structure	Topsoil stones	Organic matter	Depth	Porosity	

† Original factor loading signs reversed in these factors

TABLE 6.2 Oblique simple structure factor analysis of 99 x 0.5 acres MDF ecological subplots

Factor correlations

Factor	1	2	3	4	5	6	7	8	9†	10	11†
1	1.000										
2	.252	1.000									
3	-.298	-	1.000								
4	-	.371	-	1.000							
5	-.306	-.260	-	-.204	1.000						
6	-	-	-.181	-	-.188	1.000					
7	.174	.233	-	-	-	-.179	1.000				
8	.362	.297	-.166	.264	-.238	.219	.151	1.000			
9†	-	-	-	-	-	.160	-	.169	1.000		
10	-.420		.167	-.295	.352	-	-	-.327	.156	1.000	
11†	.282	-	-.211	.198	-	.282	-	.354	.475	-.185	1.000

values of r <0.150 are not shown

† signs of correlation coefficients involving these factors reversed where necessary.

Factor 1 accounts for more than half of the systematic variance. It is heavily loaded by parent rock acidity and the reserve nutrients, except for potassium. This factor reflects the general reserve mineral nutrient status of the soils. The high negative loading by litter depth shows the role of moderately high nutrient status in the prevention of the accumulation of thick mor-like litter layers in the Red Yellow Podzolic and Lateritic soils. This contrasts with the thick litter layers found in the less fertile Podzols. The moderate positive loadings by the soil stone content variables indicate the importance of freshly weathered rock in the replenishment of soil reserve nutrients. Although there is no validated loading by the soil depth variable on this factor, there is a negative correlation with Factor 10, the soil depth factor, also indicating the association between freshly weathered parent rock and general chemical fertility. There is also, predictably, a moderate positive correlation with Factor 8, the topsoil stone content factor. There are moderate negative correlations with Factors 3 (drainage) and 5 (cutans), and a moderate positive correlation with Factor 11 (porosity).

Factor 2 reflects another, but more restricted, facet of soil chemical fertility. There are very high loadings by reserve potassium levels, and moderate loadings by clay and reserve magnesium contents. This factor is thought to be related to the importance of micaceous minerals in the parent material and of illitic clay minerals in the soil. The moderate loadings by topsoil porosity (negative) and subsoil COLE (positive) reinforce this interpretation. There are moderate positive correlations with Factors 1 (general fertility), 4 (silt), 7 (structure) and 8 (topsoil stone content). There is a moderate negative correlation with Factor 5 (cutans), which is unexpected.

Factor 3 is rather complex but appears to be related to soil drainage, particularly in the topsoil. The high (value + chroma) loadings and the negative loading by topographic position (the scores of which increase from crest to lower slope positions) are directly related to drainage. There are no validated loadings by the mottling variables. This may be an indication that mottling in the soils is due as much to incomplete rock weathering as hydromorphism. The moderate negative loadings by all the nutrients in the topsoil, by subsoil reserve calcium, and particularly by soil pH, probably reflect the more intense leaching regimes of the well-drained soils of upper slopes. This is also shown in the moderate negative correlation with Factor 1 (general fertility). There is also a moderate negative correlation with Factor 11 (porosity), which accords with the moderate negative validated loading by topsoil porosity on Factor 3. At first sight, these negative relationships with porosity are surprising, but it should be noted that it is the total porosity that has been used, calculated from bulk density, moisture content and particle specific gravity. In contrast, it is expected that air porosity and aeration status are higher, not lower, on the well-drained soils of the upper slopes and crests.

The high loadings by silt on Factor 4 are accompanied by moderate loadings by clay contents and topsoil COLE. The moderate positive loadings by topsoil organic matter and subsoil total nitrogen may reflect the structural role of organic matter and its effect on the difficulty of the dispersion of clay particles in mechanical analysis. The moderate positive loadings by Munsell hues indicate that high silt contents tend to be associated with the yellower soils, derived from sedimentary rocks, rather than the redder soils derived from crystalline rocks. This interpretation is strengthened by the positive correlation between this factor and Factor 2 (potassium), which is clearly related to the importance of the 2:1 lattice shale-derived clay minerals. Factor 4 has a moderate positive correlation with Factor 8 (topsoil stone content), and a moderate negative correlation with Factor 10 (soil depth). This agrees with the low negative validated loading by the soil depth variable on Factor 4.

Factor 5 has a high negative loading by the subsoil cutan (ped coating) variable. The low negative loadings by both Munsell hue variables indicate that cutans are more apparent in the redder soils. This is contrary to expectations, as cutans are normally thought to be more characteristic of the Red Yellow Podzolic than the redder Lateritic soils. However, it does accord with the moderate negative correlation between Factors 2 and 5 noted above. Cutan development is related to overall soil development and site stability, as evidenced by the moderate loadings by the soil and litter depth variables, the moderate positive correlation with Factor 10 (soil depth), and the moderate negative correlation with Factor 8 (topsoil stone content). The moderate negative correlations with Factors 1 (general fertility) and 2 (potassium) are probably related to the increased leaching associated with the development of the cutans in particular, and of the soil profile in general.

Factor 6 seems to reflect the intensity of surface wash processes, with high loadings by the surface stepping (microterracing) and slope angle variables. The absence of a validated loading by the soil depth variable, and a significant correlation with Factor 10 (soil depth) suggests that surface wash may not be a major erosion process in the MDF. There is a moderate positive correlation with Factor 11 (porosity), although the interpretation of this is obscure.

Factor 7 combines a high positive loading by subsoil structure development with a moderate positive loading by subsoil clay content. The significance of the loadings by the colour variables and the moderate negative loadings by the reserve magnesium variables is difficult to determine. The moderate positive correlations with Factors 1 (general fertility), 2 (potassium) and 4 (silt) are also indications of the tendency for subsoil structures to be more apparent in fine textured soils.

Factor 8 is referred to as the topsoil stone content factor, although topsoil stone content is not the variable with the heaviest loading. Some of the more heavily loaded variables, such as topsoil structure, were assessed in such a way in the field that stone-obscured structures scored highly and therefore reflect stone content. The moderate negative loadings by the mottling variables on this factor are inconsistent with the notion that mottling in upland Sarawak soils is mainly due to incomplete weathering. As well as the loadings by the morphological variables, there are moderate loadings by the reserve mineral nutrients. These loadings are due to the release of these nutrients by weathering. In view of the several variable loadings in common, the moderate positive correlation with Factor 1 (general fertility) is expected. The moderate positive correlations with Factors 2 (potassium) and 4 (silt) are also predictable, as are the negative correlations with Factors 5 (cutans) and 10 (soil depth). The moderate positive correlation with Factor 11 (porosity) is less clear. Factor 8 is regarded as the least satisfactory of the eleven, because its structure is far from simple, with a multiplicity of low but validated loadings. Its high degree of overlap with Factor 1 and the high degree of correlation with other factors are also unsatisfactory.

Factor 9 is referred to as the organic matter factor. It could be called the root density factor, as the root density variables have heavier loadings than the organic carbon and total nitrogen variables. Moreover, these organic matter variables are more heavily loaded on Factor 3 (drainage), although negatively. The negative loading by topographic position indicates that rooting densities are higher in the better drained soils of the upper slopes and ridge crests. The role of aeration in rooting density may be shown by the high positive correlation with Factor 11 (porosity).

Factor 10 is an unequivocal reflection of soil depth. The high positive loadings by soil depth and the thickness of the main subsoil horizon and the negative loadings by the stone content variables confirm this. The negative loadings by subsoil clay content, some of the reserve mineral nutrients and topographic position show that depths tend to be greater in the coarse textured, more leached soils of the crests and upper slopes. This is also shown by the negative correlations with Factors 1 (general fertility), 8 (topsoil stone content), and 4 (silt). The positive correlation with Factor 5 (cutans), which reflects general soil development and site stability, is also as expected.

Factor 11 is clearly associated with the friable, porous structures of the soils derived from crystalline rocks. As well as high loadings by porosity, there is a high positive loading by parent material geological age and high negative loadings by the Munsell hue variables. This and the absence of any validated loadings for parent material acidity confirms that high scores for this factor are registered by subplots on the reddish coloured soils derived from both basalt and rhyolite. The high positive loadings by COLE must be interpreted in conjunction with the high clay loadings. The predominantly kaolinitic clay minerals in these soils would generally be expected to give lower COLE values than the 2:1 lattice clay minerals in the soils derived from sedimentary rocks. The numerical preponderance of the more fertile Lateritic soils is thought to account for the positive loading by subsoil reserve calcium. It may also be due to the beneficial effect of this cation on the maintenance of friable and porous soil structures. The preponderance of Lateritic soils also accounts for the positive correlations with Factors 1 and 8, the general chemical fertility factors. There is also a negative correlation with Factor 3 (drainage and leaching) and a positive correlation with Factor 9 (organic matter).

Overall this factorisation is not wholly satisfactory. A high proportion of the initial total variance is accounted for. This is probably due to the predominance in the data of soil properties, such as the reserve nutrients, which are related to soil parent materials. However, the structure is not particularly simple or interpretable. The apparent overlap between Factors 1 and 8 is especially unsatisfactory. However, in the preliminary factorisations, reduction of the number of rotated factors tended to amalgamate Factors 1 and 11, rather than Factors 1 and 8. As it seems desirable that soil porosity should be accommodated on a factor separate from general chemical fertility, reduction of the number of factors does not give a more satisfactory solution.

6.2.1.2 Analysis of variance of factor scores

The F ratios from the univariate one-way analyses of variance of the subplot factor scores are summarised in Table 6.3. It can be seen that the spatial contiguity of the subplots, the topographic homogeneity of the plots and the geological homogeneity of the sites combine to give very powerful clustering effects. The scores for all factors are highly agglomerated for the plot 'treatment'. All factors except 7 (structure) and 9 (organic matter) are also highly agglomerated for the site 'treatment'. Factors in which parent material plays an important role, i.e. Factors 1, 2, 5, (6) 8, 10 and 11, have higher F ratios for the site rather than the plot 'treatments'. The reverse is true for the factors in which local topography is an important influence, i.e. Factors 3, 4, (7) and 9.

6.2.1.3 Results of discriminant analyses

The results of the stepwise multiple discriminant analyses, using various floristic classifications as the initial groupings, are summarised in Table 6.4. At first glance, the results appear to demonstrate a high degree of association between forest types and site conditions. At most, only about 40% of the subplots require reclassification. Few canonical variables are required to account for the bulk of the variance of the centroids of the groups.

Association Analysis appears to produce the most site-compatible floristic classification, with only just over 20% of the subplots needing to be re-classified on edaphic grounds. This is thought to be a low proportion considering the complex forest and site conditions. However, part of the higher degree of site-compatability by this particular floristic classification may be due to there being fewer groups, and hence wider separations of the group centroids, than in the other classifications. The classification produced by the computationally expensive Divisive Information Analysis is clearly less site-compatible than either of those produced by the Crawford and Wishart technique.

The results of the discriminant analysis starting from the Association Analysis floristic classification and using the subplot factor and locational variable scores are examined in more detail in Table 6.5. It shows that high degree of site-compatibility is partly an artefact of the layout and

TABLE 6.3 Summary of F ratios from one-way analyses of variance of factor scores of 99 x 0.5 acre MDFecological subplots

Factor \ d.f.	'Plot' effect	'Site' effect
d.f.	32, 66	5, 93
1	13.703***	37.362***
2	12.528***	18.972***
3	19.860***	12.149***
4	17.367***	12.571***
5	6.903***	14.745***
6	3.794***	6.516***
7	2.774***	1.934 ns
8	4.569***	14.542***
9	7.668***	4.352**
10	3.841***	17.132***
11	34.868***	54.134***

TABLE 6.4 Stepwise discriminant analysis of 99 x 0.5 acre MDF ecological subplots

Botanical classification	No. of groups	Environmental variables used	No. of plots reclassified (out of 99)	Significant environmental variables: p <0.001***	p <0.01**	p <0.05*	No. of canonical variables to account for 90% of dispersion
Association Analysis	6	Plot scores on Factors 1-11	22	Factor 2 (K) Factor 10 (depth) Factor 5 (cutans) Factor 11 (porosity)	Factor 1 (Fertility)	Factor 3 (drainage) Factor 4 (silt)	1
		Factor scores + geographical location	22	Sea distance Phytar Factor 1 (fertility)	Factor 8 (stones)	Factor 3 (drainage)	1
DIVINF	8	Plot scores on Factors 1-11	43	Factor 1 (fertility) Factor 4 (silt) Factor 11 (porosity) Factor 2 (K) Factor 3 (drainage)	Factor 5 (cutans)		3
		Factor scores + geographical location	41	Sea distance Phytar Factor 1 (fertility) Factor 4 (silt)	Factor 3 (drainage)	Factor 2 (K)	3
Crawford-Wishart (All species)	10	Plot scores on Factors 1-11	38	Factor 5 (cutans) Factor 11 (porosity) Factor 2 (K) Factor 3 (drainage) Factor 4 (silt)	Factor 1 (fertility)	Factor 9 (o.m) Factor 7 (structure)	4
		Factor scores + geographical location	36	Sea distance Phytar Factor 1 (fertility)	Factor 3 (drainage)	Factor 4 (silt) Factor 8 (stones) Factor 5 (cutans) Factor 6 (surface wash)	4
Crawford-Wishart (58 species)	8	Plot scores on Factors 1-11	34	Factor 8 (stones) Factor 2 (K) Factor 11 (porosity) Factor 1 (fertility) Factor 4 (silt)	Factor 3 (drainage)	Factor 10 (depth)	2
		Factor scores + geographical location	31	Sea distance Phytar Factor 8 (stones) Factor 1 (fertility)	Factor 4 (silt)	Factor 2 (K)	2

TABLE 6.5 Discriminant analysis of 99 x 0.5 acre MDF ecological subplots, using scores on Factors 1-11 and location scores. Original floristic grouping by Association Analysis

Initial Association Analysis group			Edaphically reclassified plots	
Group	No. of plots	Component plots	Number Reclassified	Plots reclassified (new group assignment)
1	17	G 4-b,c; 8-a,b 13-a,b,c; 14-a,b,c 15-b,c L 5-a,b M 1-c N 3-b,c	5	G 15-b (5) L 5-a,b (5) N 3-b,c (4)
2	15	G 15-a L 3-a,b,c; 4-a 5-c M 1-a,b; 2-a,b,c N 3-9; 4-b,c; 5-c	8	G 15-a (5) L 3-a,c (5) 5-c (4) M 2-a (4) 2-c (5) N 4-c (5) 5-c (1)
3	7	G 4-a; 8-c L 4-b,c N 1-a,b,c	7	G 4-a (1) G 8-c (2) L 4-b (2) L 4-c (5) N 1-a (1) N 1-b (5) N 1-c (2)
4	2	L 2-a,b	0	
5	2	N 5-a,b	0	
6	56	C 2;3;5;6; 7;10;11;14; 15;16;19;27 E 1;2;3;4; 9;10 L 2-c N 4-a	2	C 2-b (5) C 10-c (4)
TOTAL	99		22	

clustering of the subplots. The floristic classification tends to group together subplots from the same plots and sites. Given such groups to start with, and also the strong clustering of subplot factor scores by plots and sites, a degree of apparent correspondence between forest types and site conditions is inevitable, and need not betoken any causal relationships. Moreover, it is the geographically heterogeneous groups, 1, 2 and 3, that suffer the greatest degree of disruption in the discriminant analysis. It is noticeable that in the case of Group 1, the rejected subplots are mostly those from minority sites.

However, the correspondence is not entirely artificial. The largest floristic group, i.e. Group 6, might be expected to lose more outliers than the other groups. In fact it remains almost completely intact. Although it contains many plots on Lateritic soils derived from basalt at Site C (Bukit Mersing), the group is geographically fairly heterogeneous. Moreover, the plots from the minority sites are not preferentially reclassified during the discriminant analysis.

Table 6.4 shows that, when the locational variables are included in the predictors, they are invariably the first incorporated in the discriminant function. As well as indicating regional phytogeographic and climatic effects, the high significance of the locational variables is thought to be another effect of the spatial clumping in the floristic classifications. Because the locational scores for all plots at one site are identical, the locational variables are the most highly clumped of all the site variables, and are therefore the first incorporated. However, there are strong clumping tendencies in the subplot factor scores. In the absence of the locational variables, the factor scores are able to account for almost as much of the floristic variance as when the locational variables are included.

The inclusion of the locational variables, with their role in totally accounting for the clumping tendency in the floristic classification, generally means that the other site variables are reduced in significance. Factor 1 (general fertility) is an exception to this, and its contribution to the discriminant function maintains or increases its significance when the locational variables are included. This is not due to independence of this factor from spatial clumping effects, as can be seen from its high plot and site F ratios in Table 6.3. It is thought to indicate a strong influence by this factor on forest floristic composition, independent of spatial proximity.

These spatial considerations complicate the interpretation of the contributions by the other, non-locational, site variables. Apart from Factor 1, the most consistently significant contributing variables are Factors 3 (drainage) and Factor 8 (stone content and fertility). As noted above, Factor 8 cannot be regarded as truly independent of Factor 1. Its contribution is therefore thought to be another manifestation of the importance of soil fertility. The contribution of Factor 3 may indicate an important floristic determinant role for soil drainage and aeration. However, there is a high loading by soil pH on this factor. This suggests that soil pH, and possible labile aluminium are influential on forest composition. Factors 2 (potassium) and 4 (silt) are significant in some of the discriminant analyses. The other factors are generally insignificant. It appears that parent rock-related aspects of chemical fertility are more important floristic determinants than soil physical conditions or topographic factors, except soil drainage and aeration.

Because the spatial proximity considerations complicate interpretation of the subplot discriminant analysis, the procedure was repeated on a full 1.5 acre plot basis. This eliminates the plot effect shown in the analyses of variance of the subplot factor scores in Table 6.3. Two levels of subdivision in the floristic classifications of the 1.5 acre plots produced by Association Analysis and the Crawford and Wishart technique are used as the initial groupings. The means of the factor scores of the three component subplots are taken as the plot factor scores. The results are summarised in Table 6.6. They show again a strong correspondence between the floristic classifications and site conditions, with only 13-36% of the plots requiring reclassification. The Crawford and Wishart classification appears to be the more site-compatible at Level 2. The Association Analysis classification is more site-compatible at Level 3. Details of the discriminant analysis using the Level 2 Association Analysis classification, and including the locational variables in the predictors, are given in Table 6.7. This shows that part of the spatial clustering distortion noted in the subplot analyses has been eliminated. The floristic classification still tends to group together plots from the same sites. However, the edaphic reclassification does not, in this case, seem to preferentially reclassify plots from minority sites.

This is confirmed by the reduced importance of the locational variables in Table 6.6, compared with Table 6.4. In these full-plot analyses, sea distance, with its climatic implications, is the more important locational

TABLE 6.6 Stepwise discriminant analyses of 33 x 5.1 acre MDF ecological plots (1971-2 site data)

Botanical classification	No. of groups	Environmental variables used	No. of plots reclassified (out of 33)	Significant environmental variables: $p < 0.001$***	$p < 0.01$**	$p < 0.05$*	No. of canonical variables to account for 90% of dispersion
Association Analysis (Level 2)	7	Plot scores on Factors 1-11	12	Factor 8 (stones) Factor 1 (fertility)	Factor 2 (K)		2
		Factor scores + geographical location	9	Factor 8 (stones) Phytar Factor 1 (fertility)	Factor 2 (K)		2
Association Analysis (Level 3)	3	Plot scores on Factors 1-11	4	Factor 8 (stones) Factor 2 (K)	Factor 5 (cutans)	Factor 11 (porosity)	1
		Factor scores + geographical location	4	Sea distance Factor 8 (stones)	Factor 2 (K)		1
Crawford-Wishart (Level 2)	7	Plot scores on Factors 1-11	11	Factor 10 (depth)	Factor 4 (silt)	Factor 11 (porosity)	1
		Factor scores + geographical location	4	Sea distance	Phytar Factor 4 (silt) Factor 3 (drainage)	Factor 1 (fertility)	2
Crawford-Wishart (Level 3)	3	Plot scores on Factors 1-11	9	Factor 2 (K)	Factor 10 (depth)		2
		Factor scores + geographical location	7	Factor 2 (K)	Factor 10 (depth)	Factor 3 (drainage)	2

TABLE 6.7 Discriminant analysis of 33 x 1.5 acre MDF ecological plots, using Factor 1-11 and location scores. Original floristic grouping by Association Analysis

Initial Association Analysis group			Edaphically reclassified plots	
Group	No. of plots	Component plots	Number Reclassified	Plots reclassified (new group assignment)
1	5	G 4,13,15 N 3,4	3	G 4 (4), G 15 (2) N 3 (2)
2	7	G 8,14 M 1,2 L 3,4,5	4	G 14 (1) M 1 (1) L 4 (4), L 5 (3)
3	2	E 1,2	0	-
4	2	N 1,5	1	N 1 (6)
5	4	E 3,4,9,10	1	E 3 (1)
6	1	L 2	0	
7	12	C 2,3,5,6,7,10,11, 14,15,15,19,27	0	-
TOTAL	33		9	

variable. This may be due to the absence of any West Sarawak plots from the array, as this truncates a considerable part of the NE-SW phytogeographical range of the Sarawak MDF.

Amongst the non-locational site variables, the factors reflecting soil chemical fertility are again predominant. It is noticeable that Factor 2 (potassium) is more important in some of the analyses than the indicators of general soil fertility, Factors 1 and 8. Factors oriented towards soil physical conditions, e.g. Factors 3 (drainage), 5 (cutans), 10 (depth) and 11 (porosity) appear to be more important than in the subplot-based analyses.

The plot-based analyses provide some confirmation that the strong association between forest type and site conditions found in the subplot-bases analyses is not entirely artificial and due to spatial clumping. However, the number of plots (33) is rather low and does not allow firm conclusions.

6.2.2 Results Using 1963-66 Site Data

6.2.2.1 Factor analysis of site data

The validated loadings for the oblique simple structure factor analysis of the 25 selected site variables from the 105 1.5 acre plots are shown in Table 6.8. The analysis incorporates almost 69% of the total original variance. This is less than in the factorisation of the 1971-72 data, but still seems to be satisfactory (Childs, 1970). Only 2 out of the 25 variables have communalities of less than 0.4.

The low communality for altitude is thought to be partly due to errors in the data. It has been shown that the properties of soils in the region vary systematically with altitude (e.g. Beckett and Hopkinson, 1965; Askew, 1964; Whitmore and Burnham, 1969). However, the altitudinal variation is probably not significant in the narrow range covered by all but a few of these plots.

Subsoil (value + chroma) is the second variable with a low communality. This is unfortunate, as this variable had a high communality in the factorisation of the 1971-72 data, and its validated loading contributed to the interpretation of the drainage-related factor. The low communality in this factorisation is probably due to its high local variability and its undersampling in the data collection.

TABLE 6.8 Oblique simple structure factor analysis of 105 x 1.5 acre MDF ecological plots. 1963-6 data.

Validated loadings

Factor	1	2†	3	4	5†	
Proportion of total variance	.430	.131	.071	.034	.031	Cumulative .688
Variable						Final communality
Site:						
Topography				.280	.429	.449
Parent rock acidity	-.190		-.259		-.580	.643
Altitude				-.241		.139
Topsoil:						
Silt		-.594	.231		.205	.516
Clay			.136	.825		.801
Bulk density	-.184			-.520	-.386	.693
pH	.309	.669				.734
Total N	.598			.278	.299	.812
Reserve P	.527				.612	.967
Reserve Ca	.916					.787
Reserve Mg	.805		.239			.837
Reserve K			.863			.835
Group III oxides					.775	.695
Subsoil:						
Silt		-.638	.180	.190		.614
Clay		-.267		.573		.498
Bulk density	-.385			-.541		.835
Hue		-.189	-.150		-.809	.697
Value + Chroma	-.234	-.333	-.301			.382
pH		.724				.616
Total N	.600				.279	.731
Reserve P	.438				.694	.961
Reserve Ca	.573	.225				.629
Reserve Mg	.680		.273			.664
Reserve K			.859			.736
Group III oxides				.126	.868	.923
Factor name	Fertility	pH	K	Clay	Group III	

† Signs of loadings on these factors are reversed

TABLE 6.9 Oblique simple structure factor analysis of 105 x 1.5 acre MDF ecological plots

Factor correlations

	1	2 †	3	4	5 †
1	1.000				
2	.305	1.000			
3	.303	- .160	1.000		
4	.118	- .211	.200	1.000	
5	.629	.196	.344	.352	1.000

† signs of correlation coefficients involving these factors are reversed where necessary.

The factor correlations are summarised in Table 6.9. They are generally higher than those in the factorisation of the 1971-72 data.

Factor 1 is the general chemical fertility factor, closely related to the parent rock. It accounts for almost two thirds of the systematic variance. There are high loadings by all of the reserve nutrients except potassium. The fertile soils scoring highly on this factor are those derived from basalt. They are also characterised by friable and porous soil structures, thus accounting for the negative loadings by the bulk density variables. This factor has a high positive correlation with Factor 5 (Group III), which is also a basalt-related factor. There are moderate positive correlations with Factors 2 (pH) and 3 (potassium). This factor corresponds closely with Factors 1 and 8 in the analysis of the 1971-72 data.

After sign reversal, Factor 2 has high positive loadings by the soil pH variables and a moderate positive loading by subsoil reserve calcium. It is thought that this factor is related to the calcareous nature of some of the parent materials, particularly at Bok-Tisam (site E). This interpretation is corroborated by the high negative loadings by the silt variables and the moderate negative loadings by the subsoil clay and colour variables. These indicate that the soils with low scores on this factor are brightly coloured, reddish soils derived from basalt. Their clay fractions are difficult to disperse and consequently give high silt determinations. There is a moderate positive correlation with Factor 1 (general fertility).

Factor 3 has high positive loadings by reserve potassium and moderate positive loadings by reserve magnesium. This factor is clearly related to shale parent materials, calcereous or otherwise, and to the presence of illitic clay minerals. The moderate positive loadings by the silt and clay variables and the moderate negative loadings by the subsoil colour variables corroborate this interpretation. The positive correlation with Factor 5 (Group III) is higher than was anticipated. This factor clearly corresponds closely with Factor 2 in the analysis of the 1971-72 data.

Factor 4 reflects the physical effects of the clay fraction, separately from its association with higher chemical fertility. There are high positive loadings by the clay variables, but none by the reserve mineral nutrients. The high negative loadings by the bulk density variables are as expected (Baver, 1956). The concentration of the free iron and aluminium (Group III) oxides in the clay fraction is shown by the moderate positive loading by subsoil Group III oxides, and by the positive correlation with Factor 5 (Group III). This association also reflects the role of these oxides in maintaining friable, porous soil structures. The moderate loadings by the topographical variables show the general increase in clay contents downslope.

Factor 5 is clearly related to basaltic parent materials, even more strongly than Factor 1, with which it is highly correlated. This is shown by the high loadings by parent rock acidity (negative), reserve phosphorus, Group III oxides and subsoil Munsell hue (all positive). The high positive Group III oxide and moderate negative loadings by topsoil bulk density suggest that this factor is more related to the physical aspects of the basalt-derived soils. Their relatively high chemical fertility is accounted for in Factor 1. However, the high loading by phosphorus, and possibly also that by nitrogen, may be ecologically very important. The positive loading by topographic position on this factor is due to the higher proportion of mid- and lower slope plots at Bukit Mersing than at the sites on sedimentary rocks. There are positive correlations with Factors 3 (potassium) and 4 (clay), as well as with Factor 1.

This factorisation appears to be satisfactory and useful. It accounts for a high proportion of the original variance, and yet produces a simple and interpretable structure. The identification of the various aspects of soil fertility is particularly helpful. In the separation of general fertility (Factor 1), pH and calcareous parent material (Factor 2), potassium reserves (Factor 3) and the specifically basaltic inheritance (Factor 5), it is noticeable that phosphorus is the most complex of the major nutrients, with high loadings on two factors (1 and 5).

Although this factorisation is the most satisfactory completed in this project, it should be noted that the input data are the simplest, and that they have a satisfactory structure, with only 25 attributes for 105 cases.

Due to lack of time, the plot factor scores were not subjected to analyses of variance. It is expected that the spatial proximity and geological homogeneity within the sites will produce the same degree of clustering apparent in the second column of Table 6.3. Because of the preponderance of lithomorphic soil variables in the data, the site clustering effects will be of the same order as those of Factors 1-4 and 10-11 in Table 6.3.

TABLE 6.10 Stepwise discriminant analyses of 105 x 1.5 acre MDF ecological plots (1963-6 site data)

Botanical Classification	No. of groups	Environmental variables used	Number of plots reclassified	Significant variables $p < 0.001$***	$p < 0.01$ **	$p < 0.05$*	Number of canonical variables to account for 90% of dispersion
Association Analysis (Level 1)	19	25 raw variables + sea distance + Phytar	19	Parent material acidity Phytar Subsoil Group III oxides Sea distance Altitude Subsoil bulk density Subsoil total N Topsoil pH	Topsoil silt	Subsoil reserve P	5
		Plot scores on Factors 1 - 5 + sea distance + Phytar	26	Phytar Factor 5 (Group III) Sea distance Factor 2 (pH) Factor 4 (Clay)		Factor 3 (K)	3
Association Analysis (Level 2)	8	25 raw variables + sea distance + Phytar	14	Subsoil Group III oxides Phytar Parent material acidity Sea distance Subsoil bulk density Subsoil pH	Altitude	Topsoil clay Topsoil reserve Mg Subsoil total N Topsoil bulk density	3
		Plot scores on Factors 1 - 5 + sea distance + Phytar	17	Factor 5 (Group III) Phytar Sea distance Factor 2 (pH)	Factor 4 (clay) Factor 3 (K)		3

TABLE 6.11 Discriminant analyses of 105 1½ acre plots; Association Analysis Level 2

Initial Group	Association Analysis Groups		Plots edaphically reclassified by Discriminant Analysis, using 25 raw variables + location		Plots edaphically reclassified by Discriminant Analysis, using 5 factor scores + location	
	No. of plots	Component plots	Number reclassified	Plots reclassified (+new group assignment)	Number reclassified	Plots reclassified (+ new group assignment)
1	16	G 1-10,12,13,15 K 1 N 3,4	3	G 12 (5) G 13 (5) G 15 (2)	3	G 12 (2) G 13 (5) G 15 (5)
2	15	G 11, 14 K 3, 4 L 1-6 M 1-5	3	G 11 (1) G 14 (1) K 4 (5)	3	G 11 (1) G 14 (1) M 2 (5)
3	12	H 1-9,11,14,15	0	-	0	-
4	6	C 20 E 1,2 H 10,12,13	5	C 20 (8) E 1 (7), E2 (7) H 10 (3), H13 (3)	6	C 20 (8) E 1 (7), E2 (7) H 10 (3) H12 (3), H13 (3)
5	3	N 1,2,5	0	-	0	-
6	9	A 1 B 1,2 D 1 F 1-4 K 2	2	A1 (4) B1 (2)	3	A1 (4) B1 (2) B2 (4)
7	13	E 3-10 J 1-5	0	-	0	-
8	31	A 2 C 1-30	1	C19 (7)	2	C11 (4) C19 (4)
TOTAL	105		14		17	

6.2.2.2 Results of discriminant analyses

Table 6.10 summarises the results of the discrimanant analyses starting from the floristic groupings produced at two levels of subdivision in the Association Analysis classification of the 1.5 acre plots. The discriminant analyses were carried out with the plot factor and locational scores, and then repeated using the 25 raw data variables, transformed by Ridit analysis if necessary, and locational scores.

Earlier impressions of strong correspondence between forest types and site conditions are confirmed by these results, with only 13-25% of the plots needing to be reclassified. At both levels of floristic subdivision the analyses using the 25 variables raw data were able to form a discriminant function that required fewer plots to be reclassified than those using the factor scores. This is probably due to the 31% of the original total variance of the site data that was lost in the factorisation process. As some of the lost variance is incorporated into a more floristically compatible discriminant function, it cannot all be regarded as true random error variance.

Table 6.11 gives details of the discriminant analyses starting from the Association Analysis Level 2 groups. It can be seen that, once again, the apparent correspondence between forest types and site conditions is partly artificial and due to the coincidental spatial clustering in the floristic classification and the site variables. It is the floristic groups that are geographically heterogeneous which are most edaphically redistributed. The reclassified plots tend to be assigned to the groups containing the majority of plots from the same site. This is strikingly illustrated by the disruption of floristic group 4, the plots of which are almost entirely dispersed, using either set of predictor variables.

As with the analysis of the 1971-72 data on a 1.5 acre plot basis (see Tables 6.6 and 6.7), spatial proximity does not account for all of the apparent correspondence. This is shown by order and significance levels of the incorporation of site variables into the discriminant functions, as summarised in Table 6.10. Although the locational variables are always highly significant, they are generally only incorporated after a non-locational site variable, often one that is related to the acidity of the parent material.

When the plot factor scores are used, Factor 5 (Group III) is consistently the most significant. This could be due to its high phosphorus loading.

However, this is gainsaid by the consistent and extremely significant contributions by the parent material acidity and subsoil Group III oxide variables when the raw data are used. This contrasts with the inconsistent and barely significant contribution by subsoil reserve phosphorus. At both levels of floristic subdivision the second factor incorporated is Factor 2 (pH). When the raw data are used as input, the pH variables are incorporated at high levels of significance.

The combination of the significant contributions by Group III oxides and pH variables are taken to indicate that soil labile aluminium status is ecologically important. However, in the absence of direct measurements of aluminium levels, this conclusion is speculative. Indirect effects, such as phosphorus or trace element immobilisation, may also be important.

6.2.3. Comparison of Results from MDF Ecological Plots

The three sets of results agree that, starting with wholly floristic subdivisions of sets of MDF plots, discriminant analysis using only site data involves relatively little reclassification of the plots. Even allowing for the distorting effect of the spatial, floristic and edaphic clustering of plots, these results seem to indicate that there are real associations between MDF floristic composition and general site conditions. The results concur that, as floristic determinants, site characteristics closely related to the underlying geology are predominant over the locally more variable topomorphic characteristics. This predominance in part reflects the preponderance of lithomorphic variables in the input site data, particularly the number of reserve nutrient variables.

At a more detailed level, the differences in sample size and intensity of site characterisation between the 1963-66 and 1971-72 data sets lead to considerably divergent results. In the 1971-72 data results, general reserve mineral nutrient status and, less consistently, reserve potassium status are the main floristic influences. The 1963-66 data results give no prominence at all to general site fertility or to individual cationic nutrients. They indicate that the alkalinity of the parent rock and the quantities of pedogenic free iron and aluminium oxides are the most influential characteristics. It is unfortunate that the determination of Group III oxides was omitted from the laboratory analyses requested for the 1971-72 samples. All the results concur that soil pH, either as a raw variable or as a major loading on a

The origin of the subsoil organic matter, which is loaded on this factor, is not clear. The high loading by nitrogen and the positive correlation with Factor 1 (shale) make it unlikely that it is due to the incipient and invisible formation of an illuvial spodic horizon. The release of occluded forms of organic matter by the weathering of carbonaceous shales is another possible origin (Kirk, 1957; Andriesse, 1969 (c)). This alternative is supported by the moderate negative correlation with Factor 8 (depth), but not by the loadings by nitrogen and reserve phosphorus. A third possibility is that the organic matter is root detritus and that this factor reflects the intensity of subsoil rooting. The nitrogen and reserve phosphorus loadings support this origin, but not the positive correlation with Factor 1 (shale), as subsoil rooting densities are normally higher in coarser-textured soils.

The positive loadings by soil and litter depths, and the negative loadings by stone contents and topsoil structure make Factor 8 clearly a reflection of soil depth. The loading by topsoil structure is due to the fact that the final category in the clinal scale on which the structures were assessed was 'stone-obscured'. The separation of this factor from Factor 5 (slope), and the modest degree of correlation between them are noted above. This factor also has moderate negative correlations with the factors that relate to the degree of weathering, i.e. Factors 4 (topsoil phosphorus) and 7 (subsoil organic matter). There is no correlation with Factor 1 (shale).

Factor 9 has positive loadings only by the exchangeable calcium variables. The exchangeable and reserve forms of calcium are poorly correlated and are loaded on separate factors, as are those of potassium and magnesium. Factor 9 has a moderate correlation, and that negative, with only one of the factors that have reserve calcium loadings, i.e. Factor 1 (shale). The physical and chemical basis of this relationship is obscure.

Factor 10 has high loadings by reserve magnesium and a moderate loading by subsoil reserve potassium. The moderate positive loading by parent rock geological age indicates that reserve magnesium levels are slightly higher in soils derived from the Paleogene sediments in Central Sarawak. This factor is highly correlated with Factor 6 (exchangeable magnesium) and moderately correlated with Factor 1 (shale), confirming that this factor is closely linked to soil parent materials.

In general, this factorisation is more interpretable than that of the 1971-72

MDF ecological plot data, although a lower proportion of the total variance is incorporated.

The multi-dimensional complexity of the factorisation is greater than expected, considering the restricted range of soils sampled. It is clear that the soils cannot be adequately summarised on a simple shale-sandstone cline, as Factor 1, the main parent material factor, accounts for only 23% of the total, and 40% of the systematic variance.

In some respects this factorisation is similar to those of the wider-ranging MDF data. Common features include the primary separation of a major parent material-related factor with heavy loadings by the reserve mineral nutrients, the separation of soil pH from the cationic nutrients, even the exchangeable forms, and the complex loading of reserve phosphorus on several factors.

Features related to the exchangeable cations are obviously peculiar to this factorisation. The low communalities and the unfortunate loss of information on these variables has been noted. It appears that there is a considerable probabilistic element in their variances. It is also noticeable that the topographic position variable does not load on to the soil pH factor or on to any of the factors with exchangeable cation loadings, suggesting that there is no marked catenary trend in exchangeable base status. This contrasts with the factorisation of the 1971-72 MDF ecological plot data, in which soil pH and topographic position loaded on the same factor.

Another feature peculiar to this FIDP factorisation is the amalgamation of reserve potassium with the first, general reserve nutrient factor. In the MDF ecological plots the reserve potassium factor was generated because the data comes from soils derived from sedimentary and igneous rocks. As the FIDP plots are all on sedimentary parent materials, the need for this as a separate factor disappears. Another peculiar feature is the separation of reserve magnesium from the other reserve mineral nutrients.

6.3.2 Analyses of Variance of Factor Scores

The F ratios of the one-way univariate analyses of variance of the plot factor scores, with grouping into clusters and inventory units taken as treatments, are summarised in Table 6.14. The ratios are extrely significant throughout, except for Factor 9 (exchangeable calcium) in the cluster treatment.

TABLE 6.14 Summary of F ratios from one-way analyses of variance of all FIDP Plot Factor scores

Factor \ d.f.	'Unit' effect 3,287	'cluster' effect 44,246
1	17.201 ***	11.117 ***
2	13.081 ***	3.842 ***
3	47.234 ***	12.147 ***
4	51.674 ***	9.848 ***
5	8.065 ***	3.390 ***
6	18.394 ***	8.734 ***
7	17.305 ***	5.165 ***
8	13.460 ***	3.239 ***
9	2.120 ns	3.382 ***
10	24.624 ***	11.466 ***

*** $p < 0.001$ ns not significant

TABLE 6.15 Summary of F ratios of cluster effect in one-way analyses of variance of FIDP plot factor scores, by units

Factor \ d.f.	Unit 1	Unit 3	Unit 4	Unit 5
d.f.	7,59	10,76	12,62	10,49
1	20.945 ***	6.346 ***	9.286 ***	5.940 ***
2	6.461 ***	1.151 ns	2.532 **	2.736 **
3	3.020 *	7.813 ***	2.855 **	8.733 ***
4	3.391 **	9.527 ***	3.947 ***	3.351 **
5	4.216 **	0.926 ns	1.652 ns	4.587 ***
6	12.116 ***	2.370 *	10.750 ***	4.803 ***
7	7.321 ***	1.641 ns	12.131 ***	9.828 ***
8	2.524 *	1.797 ns	2.202 *	3.906 ***
9	1.260 ns	5.058 ***	4.674 ***	3.502 **
10	12.011 ***	5.163 ***	4.063 ***	9.234 ***

*** p <0.001   ** p <0.01   * p <0.05   ns not significant

The F ratios of the analyses of variance of the plot factor scores grouped by clusters, with each inventory unit taken separately, are summarised in Table 6.15. The spatial clumping effect is again very significant.

The clumping effect is generally most marked for those factors which have loadings by lithomorphic variables such as granulometric fractions and the reserve mineral nutrients, i.e. Factors 1, 3, 7 and 10. The factors with loadings by topsoil organic matter, exchangeable cation and topographic variables show lower F ratios and higher within-cluster heterogeneity. It was the topographic heterogeneity of the clusters that prompted the decision to treat the plots as individual cases. Factor 6, although loaded heavily by exchangeable magnesium, has high F ratios and low hererogeneity, possibly because of the loading by silt content, a granulometric and rather lithomorphic variable.

It should be noted that the heterogeneity of these factors is only relative, and all factors show strong clumping effects. This suggests that all site properties, even those with higher local heterogeneity, oscillate within an envelope of values that is primarily determined by the soil parent material of the plot cluster.

The highly significant clumping of the plot factor scores presents the same problem of ecological interpretation that was encountered in the MDF ecological plots. With strongly clumped site properties and contagiously distributed tree species, there is the possibility of apparent site-forest associations that may be coincidental rather than causal.

6.3.3 Site Effects on Total Forest Basal Area

In the separate multiple linear regressions of total forest basal area, total dipterocarp basal area, total non-dipterocarp basal area and mean basal area against the plot factor scores, no predictors achieved the required significance level to enter a regression function ($p < 0.05$). All multiple R^2 values were zero. Omission of one cluster of plots known to have been inadvertently sited in low stature secondary forest did not alter this result when the analyses were re-run for the total forest basal area and dipterocarp basal area.

The locational variable Phytar was added to the predictors and the regressions repeated. The results are summarised in Table 6.16. They show that there is a highly significant geographical effect. All of the basal area parameters show marked increases from South to North. No such marked increase in forest stature was apparent during fieldwork, nor is it confirmed by the results of the full forest inventory (FIDP, 1974 (c)). The result appears to be an artefact of a bias in the sampling pattern. The bias is thought to stem from the measures to economise on laboratory requirements during the second (1970) field season and the decision to restrict soils work to plots with ample forest data. This had the effect of biassing the sampling pattern towards high and medium stature forests, as plots in these stands are more likely to have high numbers of enumerated and felled trees. The bias is not large, as can be seen in Table 6.17, but is nonetheless thought to be the main cause of the massive Phytar effect.

In stepwise multiple regression with non-orthogonal predictor variables, the relative magnitude of the increments in multiple R^2 with the successive inclusion of predictors into the regression function is not a precise indication of the relative importance of the variables. However, the increments are given in Table 6.16 in order to show the size of the locational effect. They also show that the other predictors can contribute significantly once the systematic locational element of the variance is accounted for. The significant non-locational variables are able to account for between 21% and 36% of the non-locational variance of the forest parameters. The consistent positive effects of Factors 4 (topsoil phosphorus) and 7 (subsoil organic matter, including phosphorus) and the consistent negative effect of Factor 8 (depth) indicate that the basal area parameters are partly associated with nutrient status, particularly phosphorus. The small but consistent negative effect of Factor 5 (slope) confirms the visual impression that the forests of steep flank slopes are of lesser stature than those of the gentler upper slopes and ridge crests. A similar relationship has been noted in the Lowland Dipterocarp Forests of West Malaysia (Wyatt-Smith, 1960). There is also a consistent negative effect by Factor 6 (exchangeable magnesium).

The regressions were repeated on a cluster mean basis for three of the parameters, with the locational Phytar variable included in the predictors. The results are summarised in Table 6.18. They differ strikingly from those of the plot-based regressions. The proportions of the total variance accounted for are considerably lower, probably because there is no significant locational effect. However, the significant non-locational predictors do have

TABLE 6.16 Multiple regression analyses total forest basal area against plot factor scores and phytogeographical location

(Individual plot basis)

Forest parameter	Significant site variables (with incremental multiple R^2)	Total multiple R^2 (variance accounted for by significant variables)
Total basal area	+ Phytar (0.673)***	
	+ Factor 4 (0.054)***	
	+ Factor 7 (0.016)***	
	- Factor 6 (0.025)***	
	- Factor 5 (0.005)***	
	- Factor 8 (0.002)*	0.774
Basal area of dipterocarps	+ Phytar (0.592)***	
	+ Factor 4 (0.044)***	
	- Factor 3 (0.015)***	
	- Factor 6 (0.009)***	
	+ Factor 7 (0.014)***	
	- Factor 5 (0.006)***	
	- Factor 8 (0.003)*	0.682
Basal area of non-dipterocarps	+ Phytar (0.511)***	
	+ Factor 4 (0.047)***	
	+ Factor 7 (0.020)***	
	- Factor 6 (0.020)***	
	- Factor 1 (0.011)***	
	+ Factor 3 (0.005)*	0.614
Mean basal area	+ Phytar (0.695)***	
	+ Factor 4 (0.070)***	
	+ Factor 7 (0.018)***	
	- Factor 6 (0.009)***	
	- Factor 8 (0.008)***	
	- Factor 2 (0.003)**	
	- Factor 5 (0.003)**	0.805

*** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$

for F value to enter regression equation.

Signs relate to value of R at point of entry.

TABLE 6.17 Bias introduced into sampling by rejecting low volume plots from soil studies

	Unit 3 (South)	Unit 1 (Central)	Units 4 + 5 (North)
All plots			
Total forest area (km^2)	225	176	414
% high density forest	66	74	68
Net industrial stemwood volume in high density forest (m^3/ha)	138	158	138
Soil plots			
Trees/ plot	12.2	9.9	13.2

Inventory data from FIDP (1974 (a))

TABLE 6.18 Stepwise multiple regression analysis of total forest basal area against cluster mean factor scores and phytogeographic location. (Plot cluster basis)

Forest parameter	Multiple R^2	Significant site factors $P < 0.001$ ***	$P < 0.01$ **	$P < 0.05$*
Total basal area	.216		-Factor 3 (pH)	Factor 10 (Reserve Mg)
Dipterocarp basal area	.189			Factor 10 (Reserve Mg) -Factor 3 (pH)
Non-Dipterocarp basal area	0			

higher multiple R^2 values than in the plot-based analyses. The significant non-locational predictors differ from those in the plot-based analyses, with a negative effect by Factor 3 (pH) and a positive effect by Factor 10 (reserve magnesium). The latter is to some extent at variance with the consistent negative effect by Factor 6 (exchangeable magnesium) noted in the plot-based regressions.

These considerable differences, the sampling bias, and the other deficiencies already noted cast doubts on the value of these regression results. These misgivings are reinforced by the intrinsically unsatisfactory nature of basal area as an indicator of forest physiognomy. There are also problems caused by the small sample size when the plots are treated individually.

6.3.4 Site Effects on the Distributions of Individual Species

The results of the 't' tests, which compare the factor scores of plots containing enumerated trees of 39 of the commoner MDF tree species with the whole range of the FIDP soils plots, are abstracted in Table 6.19. Only results achieving statistical significance are shown. The 't' tests cannot identify a restricted factor score range, if that range is centred close to overall FIDP plot means. These are identified by variance ratios.

The visual impression given by Table 6.19 is that there are more significant results than would be predicted by pure chance. This is confirmed in Table 6.20 which summarises the significance levels of the 't' tests. Even without the results from the suspect Phytar variable, statistically significant 't' test results are 2.5 - 7 times as frequent as considerations of pure chance predict. Further confirmation comes from the highly significant marginal totals of the two Wilks and Shapiro (1968) parameters, that were used to assess the combined effect of the multiple individual 't' tests. These parameters achieve extremely significant values for 8 of the 11 site variables, and significant values for 25 of the 39 species. However, the absolute values and associated significance levels for these parameters are somewhat suspect, because of the contraventions of independence in the data (see section 5.2.2.2).

These results are striking but may exaggerate the effect of site conditions on species distribution. Exaggeration is possible because of the spatial clustering of the plot factor scores, as shown by the analyses of variance (see Tables 6.14 and 6.15), in combination with the more or less clumped distribution of many of the species.

TABLE 6.19 Site effects on distribution of individual species (Individual plot basis)

Species	No. of plots	Phytar	1 Shale	2 Topsoil organic	3 pH	4 Topsoil P	5 Slope	6 Exchange Mg	7 Subsoil organic	8 Depth	9 Exchange Ca	10 Reserve Mg	Σ(-2lnα)	$\frac{\Sigma Z}{\sqrt{K}}$	
		Site factors													
Dacryodes incurvata	11										High*		21.55	0.095	
Santiria grandiflora	12	North**											22.61	-0.757	
Elateriospermum tapos	47			Low**		High**	High*				(Midrange)*		49.06***	-3.249**	
Eusideroxylon zwageri	30							High**	High*		High*	High**	52.91***	-3.161*	
Koompassia malaccensis	42							Low***				Low*	35.65*	2.123*	
Millettia vasta	19						High*						17.13	1.266	
Artocarpus anisophylles	12							(Midrange)**					23.90	-0.649	
Dipterocarpus acutangulus	22		Low*		Low*			Low***	Low***	High*		Low**	76.10***	-4.764***	4
Dipterocarpus caudiferus	26	North***	Low*					High**			High**	High***	69.64***	-3.989***	5
Dipterocarpus globosus	13				High ***				(Midrange)***		(Midrange)***		45.75**	-3.102**	
Dipterocarpus mundus	9				Low***		Low*			High***		Low**	66.40**	-3.737***	6
Dipterocarpus pachyphyllus	23	North**				Low*			(Midrange)***				42.41**	-2.423*	
Dryobalanops aromatica	45	North***		High*	Low*	Low***		Low*		Low***	(Midrange)***	Low*	94.55***	-6.747***	2
Dryobalanops beccarii	22	South*						Low**				Low***	55.40***	-2.566*	
Dryobalanops lanceolata	11	North*	Low*						(Midrange)**	Low*			44.17**	-2.492*	
Dryobalanops oblongifolia	52		High***	Low***	Low*			(Midrange)***		Low***	Low***		92.62***	-5.766***	3
Parashorea smythiesii	27					(Midrange)*	Low*		(Midrange)**				23.23	-0.293	
Shorea ochracea	9							Low***					26.31	-0.219	
Shorea collaris	44						High**	(Midrange)**			(Midrange)**		33.00	0.353	
Shorea dolichocarpa	19	North*		High*		Low**	Low*				(Midrange)**		50.67***	-2.446*	
Shorea faguetiana	14							Low**		High*			35.90*	-2.501*	
Shorea faguetioides	43							Low***		High**		Low**	52.08***	-2.953**	
Shorea amplexicaulis	7							Low**			(Midrange)*		32.30	-1.898	
Shorea argentifolia	9			Low*									29.40	-0.508	
Shorea beccariana	24												15.65	0.439	
Shorea ferruginea	18		High **		Low***			(Midrange)***					52.01***	-3.168**	
Shorea macroptera	38	South*			Low*			Low***				Low**	57.46***	-2.589**	
Shorea myrionerva	15		(Midrange)*								(Midrange)**		36.07*	-2.200*	
Shorea parviofolia	88	South*				High***			High*		Low **		50.70***	-3.144**	
Shorea pauciflora	15					Low**	High*				(Midrange)**		39.61*	-2.209*	
Shorea pinanga	22	North*		(Midrange)**							Low*		28.78	-1.885	
Shorea quadrinervis	19	North**	Low**			Low*		Low***	Low**	High***		Low***	114.71***	-7.826***	1
Shorea rubra	41							Low*					27.82	-0.105	
Shorea sagittata	46	North*		Low*				High*					46.48**	-2.903**	
Shorea scaberrima	23							Low*				Low*	26.11	-0.247	
Shorea atrinervosa	8			Low**	High**			Low**				Low**	59.57***	-3.792***	
Shorea havilandii	10	South*							(Midrange)**				14.56	1.505	
Shorea laevis	11			(Midrange)*		Low*		Low**	Low*		(Midrange)***	Low**	47.83***	-2.795**	
Shorea superba	7		Low**	Low**		Low*			Low*		(Midrange)**		55.07***	-4.200***	
Σ(-2lnα)		168.16***	147.37***	145.37***	165.84***	146.24***	107.24*	263.32***	118.12**	170.73***	104.83*	233.00***			
$\frac{\Sigma Z}{\sqrt{K}}$		-4.589***	-2.952	-2.449*	-4.958***	-2.842**	-2.079*	-9.328***	-2.619**	-4.854***	-1.268	-8.199***			

High and Low range preferences identified by 't' test on difference of factor scores of plots 'with' from zero

Midrange preferences identified by variance ratios of factor scores of plots 'without'/plots 'with'

*** p <0.001   ** p <0.01   * p <0.05

TABLE 6.20 Significance levels in plot-based analysis of site effects on species distribution

Number (and proportion) of 't' tests achieving significance levels:

	$p < 0.001$	$p < 0.01$	$p < 0.05$
(a) Factors 1-10 + Phytar; high and low results (11 x 39)			
	26(0.061)	58 (0.135)	102 (0.238)
(b) Factors 1-10; High and low results (10 x 39)			
	24(0.061)	56 (0.144)	94 (0.241)

TABLE 6.21 Site effects on distribution of individual species (Plot cluster basis)

Species	Occurrence (No. of clusters)	Site Factors 1: Geographic area	1: Shale	2: Topsoil organic	3: pH	4: Topsoil P	5: Slope	6: Exchange Mg	7: Subsoil organic	8: Depth	9: Exchange Ca	10: Reserve Mg	$\Sigma(-2\ln\alpha)$	$\frac{\Sigma Z}{\sqrt{K}}$
Dacryodes incurvata	10			(Midrange)**									19.13	0.290
Santiria grandifolia	9												15.20	0.754
Elateriospermum tapos	24	South**	High*	Low*		High**	(Midrange)**		High**	Low*			52.82***	-2.454*
Eusideroxylon zwageri	13												23.94	0.329
Koompassia malaccensis	24		High*	Low*			(Midrange)*					(Midrange)*	35.14*	2.135*
Millettia vasta	11												12.98	1.326
Artocarpus anisophylles	10												21.22	0.152
Dipterocarpus acutangulus	11							Low**				(Midrange)*	31.64	-1.607
Dipterocarpus caudiferus	12	(Midrange)*				(Midrange)*		High*		Low*		High*	34.93*	-1.897
Dipterocarpus globosus	6X				High*		(Midrange)*						26.80	-0.753
Dipterocarpus mundus	4X							(Midrange)*				(Midrange)*	27.48	-0.498
Dipterocarpus pachyphyllus	17	(Midrange)*										High*	31.02	-1.318
Dryobalanops aromatica	21							(Midrange)***				Low*	40.98**	-2.536*
Dryobalanops beccarii	10	South*					(Midrange)*	Low*				Low*	36.24*	-1.683
Dryobalanops lanceolata	6X												24.70	-0.726
Dryobalanops oblongifolia	19	South*	High*	Low*		High*	(Midrange)*		High*			(Midrange)*	48.48***	-2.649**
Parashorea smythiesii	13				High*	(Midrange)*							31.24	-1.054
Shorea ochracea	9X						(Midrange)*	Low***	(Midrange)**				27.70	-0.553
Shorea collaris	18		High*				(Midrange)**	(Midrange)*					35.62*	-1.906
Shorea dolichocarpa	14							(Midrange)*					18.73	0.836
Shorea faguetiana	13												21.42	0.014
Shorea faguetioides	22												24.37	0.048
Shorea amplexicaulis	8X							Low*					36.18*	-2.725**
Shorea argentifolia	8X												12.22	1.477
Shorea beccariana	13												17.98	0.059
Shorea ferruginea	11				Low**		(Midrange)*						29.41	-0.627
Shorea macroptera	19							Low**				Low*	35.73*	-1.100
Shorea myrionerva	11											High*	29.37	-1.482
Shorea parvifolia	31	South*		(Midrange)*		High**			High*	Low*			46.55**	-3.082***
Shorea pauciflora	11			(Midrange)*									25.52	-1.340
Shorea pinanga	14			(Midrange)*									18.53	0.252
Shorea quadrinervis	14	North*				Low*							39.33*	-2.227*
Shorea rubra	24												13.02	1.441
Shorea sagittata	23		Low***	(Midrange)**									43.08**	2.205*
Shorea scaberrima	19												21.43	0.892
Shorea atrinervosa	4X				Low*	High*							25.69	-0.313
Shorea havilandii	7X												25.53	-0.172
Shorea laevis	5X		Low*									Low*	20.67	0.234
Shorea superba	3X												21.03	0.406
$\Sigma(-2\ln\alpha)$		125.46***	109.88 *	83.33	112.16**	105.05*	54.45	135.82***	89.98	88.58	70.94	122.37***		
$\frac{\Sigma Z}{\sqrt{K}}$		-3.770***	-1.452	0.679	-2.698**	-1.593	1.080	-3.670***	-0.836	-0.562	0.394	-2.919**		

High and low preferences identified by t test on differences of means between clusters 'with' and 'without'

Midrange preferences identified by variance ratios of factor score means of clusters 'without'/'with'

__ Underlining indicates that the effect confirms one found in plot-wise analysis (see Table 6.8)

*** p <0.001 ** p <0.01 * p <0.05

TABLE 6.22 Significance levels in cluster-based analysis of site effects on species distribution

	Number (and proportions) of 't' tests achieving significance levels:		
	$p < 0.001$	$p < 0.01$	$p < 0.05$
(a) Factors 1-10 + Phytar, high and low values only (11 x 39)			
	2(0.004)	9(0.021)	41(0.096)
(b) Factors 1-10; high and low values only (10 x 39)			
	2(0.005)	8(0.021)	37(0.095)

To overcome this, the 't' values and the variance ratios were recalculated on a plot cluster basis. The results are abstracted in Table 6.21 and the significance levels of the 't' values are summarised in Table 6.22. The results are less positive than those of the plot-based analyses. The frequencies of the significance levels in Table 6.22 are very close to the two-tailed probability expectations. It is thought that the averaging process smooths out and artificially diminishes some real site effects, particularly those involving the locally variable factors. For this reason, it is felt that the clusterwise results do not contradict the conclusion that there are marked site effects on species distribution. There are two pointers tending to confirm this. The Wilks and Shapiro parameters for the combination of 't' tests are higher and more significant than predictable by pure chance considerations although, as noted above, the absolute values and significance levels of these parameters may be suspect. Additional corroboration comes from the fact that 26 of the 41 (63%) significant 't' test results in Table 6.21 are confirmations of interactions identified in Table 6.19. In contrast, only 2 of the 26 (8%) apparently significant variance ratio results overlap. The restricted midrange distributions in Tables 6.19 and 6.21 are thought to be largely artificial, and are not considered further.

Although the absolute values and significance levels of the Wilks and Shapiro combination parameters may be suspect, it is thought that their relative values do indicate the relative site selectivity amongst the species, and the relative influence on forest floristics amongst the site variables. The rankings of the site variables and the more selective species are given in Table 6.23.

It is noticeable that the site variables with the highest within-cluster variances (see Table 6.14) are the most affected in the process of cluster averaging, and are relatively demoted from their rankings in the plot-based analysis. These are factors with validated loadings by topographic variables, i.e. Factors 8 (depth), 2 (topsoil organic matter) and 5 (slope). Otherwise the rankings of the variables in the two analyses are very similar.

In general, factors that reflect chemical fertility, rather than site physical conditions, appear to be more important as influences on species distribution. It is clear that it is not the major plant nutrients such as nitrogen, phosphorus and potassium that are the major determinants, because Factors 1 (shale), 2 (topsoil organic matter), 4 (topsoil phosphorus) and 7 (subsoil organic matter, including phosphorus) are consistently outranked by Factors 6 and 10

TABLE 6.23 Summary of rankings of site variables and species in site/species interaction tables

(a) Relative influence of site variables

Plots (Table 6.19)		Clusters (Table 6.21)	
6	(Exchangeable magnesium) x++	6	(Exchangeable Mg) x
10	(Reserve magnesium) x++		Phytar
8	(Depth)	10	(Reserve Mg) x+
	Phytar	3	(pH) x+
3	(pH)	1	(Shale) x
1	(Shale)	4	(Topsoil P) x
4	(Topsoil phosphorus) x+	7	(Subsoil o.m.)
2	(Topsoil organic matter)	8	(Depth)
7	(Subsoil organic matter	2	(Topsoil o.m.)
5	(Slope)	9	(Exchangeable Ca)
9	(Exchangeable calcium)	5	(Slope)

(b) Relative site selectivity of species

Plots	Clusters
Shorea quadrinervis x++	Elateriospermum tapos x
Dryobalanops aromatica x++	Dryobalanops oblongifolia x
Dryobalanops oblongifolia x++	Shorea parvifolia xx
Dipterocarpus acutangulus x++	Shorea sagittata x
Dipterocarpus caudiferus x++	Dryobalanops aromatica x
Dipterocarpus mundus xx	Shorea quadrinervis x
Shorea atrinervosa	Shorea amplexicaulis x
Shorea macroptera	Dryobalanops beccarii
Dryobalanops beccarii	Shorea macroptera
Shorea superba	Shorea collaris
Eusideroxylon zwageri	Koompassia malaccensis
Shorea faguetioides x+	Dipterocarpus caudiferus
S. parvifolia	
Elat. tapos	
Dipt. globosus xx	
Shorea laevis x+	
Shorea superba x+	

(exchangeable and reserve magnesium), and 3 (pH). The apparent importance of magnesium is striking and unexpected. However, it should be noted that the magnesium variables have higher communalities than the other cationic nutrients, which have lost higher proportions of their total original variance during factor analysis. Factors 6 and 10 are also the most highly correlated pair of factors, so that there may also be an element of mutual reinforcement, and hence an inflation of magnesium's role.

The important role for the pH factor corroborates the findings from the MDF ecological plots.

Phosphorus is probably an important determinant, although apparently of lesser rank than magnesium and pH. The apparent unimportance of calcium may be partly artificial, as the calcium variables have low communalities and the greater part of their total variance has been lost in the factorisation. However, there are factors with validated calcium loadings, and these are clearly not important. This suggests that the strong magnesium effect is a direct one, and not primarily effective through antagonism to calcium uptake.

Of the factors with validated loadings by topographic variables, Factor 8 (depth) outranks Factors 2 (topsoil organic matter) and 5 (slope).

It should be noted that the high ranking of the locational variable, Phytar, in both analyses is thought to be artificial, and due to the bias in sampling.

The plot- and cluster-based analyses differ more in their rankings of species for selectivity than they do of site variables for importance. Species with particularly clumped distributions may occur on a sufficient number of individual plots to give significant summation parameters, but are found on too few clusters to be able to maintain their rankings against more dispersed species. The three keruing *(Dipterocarpus)* species are thought to illustrate this effect. It may also operate to some extent in the selangan batu species *(Shorea atrinervosa* and *S. superba)*. These are less widespread than the keruings, and it may just be too few occurrences rather than highly clumped distributions that eliminates them from the list of more selective species in the cluster-based analysis. The upgrading of *Elateriospermum tapos, Shorea parvifolia, S. sagittata* and *S. collaris* in the cluster-based analysis is thought to be mainly due to their high frequencies, as they are among the most widespread species in the MDF of Central Sarawak (FIDP, 1974 (c)).

Some of the most selective species in Table 6.23 also show high degrees of association in the MDF ecological plot data. It was the presence or absence of some of these species that were the criteria of subdivision in the objective floristic classifications, such as those produced by Association Analysis and the Crawford and Wishart technique. Species consistently used as criteria in these classifications include *Dryobalanops aromatica, D. lanceolata, Shorea macroptera, S. quadrinervis, S. dolichocarpa, S. pauciflora, Elateriospermum tapos* and *Koompassia malaccensis* (Ashton, 1973). This implies that the species that best distinguish consistently identified forest types are also among the most selective with respect to site conditions. This indirectly confirms the effect of site conditions on the distribution of forest types.

Table 6.24 summarises the site preferences of 15 of the more selective species. The unexpectedly important influence of magnesium is apparent. Soil reserve phosphorus status is a consistent factor in the distribution of three species. Factor 1, with its connotations of general reserve cation status, soil texture and other parent material effects is a consistently significant influence on the distribution of only two species.

Several factors complicate comparison of these results with earlier work on the site restrictions of the same species. The first is the possibility of ecotypic variation within species. This appears to be demonstrated by *Dryobalanops oblongifolia*. In West Malaysia this is a relatively unimportant species, very characteristic of imperfectly drained soils of lower slopes and alluvial terraces (Watson, 1935; Vincent, 1961; Lee, 1967; Poore, 1968; Whitmore, 1973). In Central Sarawak it is widespread and found on shale soils in a wide range of topographic situations. The restriction to heavy textured soils and the fact that Sarawak's climate is generally moister than that of West Malaysia may combine to give equivalent soil moisture regimes for the species' habitat in the two areas. However, it seems more likely that the two populations are distinct, in their edaphic requirements and other characteristics (P.S. Ashton, pers.comm., 1976). Another example of possible ecotypic variation is in *Dipterocarpus globosus*. In Brunei this species is reported to be restricted to very coarse-textured Red Yellow Podzolic soils on sandstone ridges (Ashton, 1964 (b)). In the FIDP plot results it does not give a significant 't' value for Factor 1 (shale), but it shows a consistent preference for soils with higher pH values.

Another factor complicating comparison with earlier work is the greater intensity of site characterisation on the FIDP plots. Earlier workers did

TABLE 6.24 Summary of site preferences of selective species

Timber group	Species	Significant site factors: Plotwise	Significant site factors: Clusterwise	Consistent site preferences
Non-Dipterocarps	Elateriospermum tapos	2(L)**, 4(H)**, 5(H)*	P(S)**, 1(H)*, 2(L)*, 4(H)** 7(H)**, 8(L)**	Low topsoil organic matter, High topsoil phosphorus
	Eusideroxylon zwageri	6(H)** 7(H)*, 9(H)* 10(H)**	-	Inconsistent
	Koompassia malaccensis	6(L)*** 10(L)*	1(H)*, 2(L)*	Inconsistent
Keruing	Dipterocarpus acutangulus	1(L)*, 3(L)*, 6(L)*** 7(L)**, 8(H)*, 10(L)**	6(L)*	Low magnesium
	D. caudiferus	P(N)**, 1(L)*, 6(H)** 9(H)**, 10(H)***	6(H)*, 10(H)*	High magnesium
Kapur	Dryobalanops aromatica	P(N)***, 2(H)* 3(L)* 4(L)***, 6(L)*, 8(L)***, 10(L)*	10(L)*	Low Reserve magnesium
	D. beccarii	P(S)*, 6(L)** 10(L)***	P(S)*, 6(L)*, 10(L)*	Low magnesium
	D oblongifolia	1(H)***, 2(L)***, 3(L)* 8(L)***, 9(L)***	P(S)*, 1(H)*, 2(L)*, 4(H)* 7(H)*	Shale soils with low t soil organic matter leve
Yellow meranti	Shorea collaris	5(H)**	1(H)*	Inconsistent
	S. faguetioides	6(L)***, 8(H)** 10(L)**	-	Possibly deep, low magnesium soils
Red meranti	Shorea macroptera	P(S)*, 3(L)*, G(L)*** 10(L)**	6(L)*, 10(L)*	Low magnesium
	S. parvifolia	P(S)*, 4(H)***, 7(H)* 9(L)**	P(S)*, 4(H)**, 7(H)*, 8(L)*	High topsoil phosphoru High subsoil organic matter
	S. sagittata	P(N)*, 2(L)*, 6(H)*	1(L)***	Inconsistent
	S. quadrinervis	P(N)**, 1(L)**, 4(L)* 6(L)**, 7(L)**, 8(H)***, 10(L)***	P(N)*, 4(L)*	Low topsoil phosphorus
Selangan batu	Shorea superba	1(L)**, 2(L)**, 4(L)* 7(L)*	1(L)*	Sandstone soils

P = Geographical location (Phytar). *** p <0.001 ** p <0.01 * p <0.05

(H) high (L) low (N) north (S) south significant t tests not have access to extensive data on soil chemical characteristics. Their descriptions of specific site preferences were necessarily confined to topography, soil parent material and major variations in soil profile morphology. This is shown by the case of *Dryobalanops beccarii*. In Sabah this species is reported as being characteristically found in, or on the fringes of, heath forest and shows a clear restriction to deep and coarse textured soils, some of which are Podzols (Fox, 1971). The species is more abundant further south. Although regarded as a component of the MDF in Brunei and Sarawak, it exhibits the same preference for coarse textured soils (Ashton, 1964 (b) and 1968). In the FIDP plot results, it shows no interaction with the main soil texture factor (Factor 1). However, a strong and consistent congregation on sites of low magnesium status is apparent. This case is further complicated by possible misidentifications, as this species is easily confused with *D. aromatica* (Ashton, 1964 (b)). The strong North-South polarisation and allopatrism reported for these two species (FIDP, 1974 (c)) may be due to inconsistent identification, as other workers have found them growing together on coarse textured soils (P.S. Ashton, pers.comm., 1977).

Because of the sampling bias, there is a greater probability for all species of enumeration on the soil plots in the northern inventory units than in the south (see Table 6.17). Consequently, any significant 't' test results for the Phytar variable that purport to show a species being restricted to northern areas are suspect. Conversely, results showing a restriction in range to southern areas are achieved against the bias, and are therefore thought to be real, except possibly in the complex case of *Dryobalanops beccarii*. *Shorea parvifolia* is the most important species with such a restriction to the southern part of the FIDP range. The greater abundance of this species in Central Sarawak is confirmed by the full results of the FIDP inventory (1974 (c)), and had been noted earlier (Ashton, 1968).

6.3.5 Site Effects on the Basal Areas of Selected Individual Species

Table 6.25 summarises the results of the stepwise multiple linear regressions of the plot basal areas of 11 selected species against the plot values of the site variables. Ten of the species examined are those with apparently high site selectivities, as shown in Table 6.23. *Dipterocarpus pachyphyllus* was added to the list as it is the most widespread of the keruing species, which are otherwise poorly represented.

The results generally show little compatibility with the high site selectivities.

TABLE 6.25 Stepwise multiple regression of individual species basal area on site variables (Individual plot basis)

Species	Number of plots	Multiple R^2	Significant site factors		
			$p < 0.001$***	$p < 0.01$**	$p < 0.05$*
Elateriospermum tapos	47	.088			+Factor 10 (Reserve Mg)
Koompassia malaccensis	42	.194	+ Phytar		-Factor 3 (pH)
Dipterocarpus caudiferus	26	.408		+ Phytar	-Factor 8 (depth)
Dipterocarpus pachyphyllus	23	.196			-Factor 5 (slope) +Factor 10 (Reserve Mg)
Dryobalanops aromatica	45	0			
Dryobalanops oblongifolia	52	.110			+Factor 1 (shale) +Factor 7 (subsoil o.m.)
Shorea collaris	44	.187	-Factor 3 (pH)		
Shorea faguetioides	43	.062			+Factor 2 (Topsoil o.m.)
Shorea macroptera	38	0			
Shorea parvifolia	88	.108		+Factor 3 (pH)	
Shorea quadrinervis	19	0			
Shorea sagittata	46	0			

Site conditions seem to have little influence over the basal areas of some species with apparently highly restricted edaphic ranges. This can be seen in the low values for the final multiple R^2 for species such as *Dryobalanops aromatica, D. oblongifolia,* and *Shorea quadrinervis*. The highest final multiple R^2 value is that of *Dipterocarpus caudiferus,* which is only moderately site selective in Table 6.23. However, even for this species, site conditions account for less than half of the total basal area variance.

As well as the generally low multiple R^2 values, and the considerably different rankings of the species, the plotwise basal area regressions also differ from the selectivity results as to the identification of the critical site variables. Thus Factors 1 (shale) and 5 (slope) appear to be influential on the distribution of the yellow meranti species *Shorea collaris*, but in the plotwise basal area regression only Factor 3 (pH) achieves the significance level necessary for entry into a regression function.

These incompatible and unsatisfactory results are thought to be mainly due to the very small sample size when basal areas are on an individual plot basis. As there are often only one or two stems of a species on a plot, the plot basal area values for the species are greatly affected by the stage of development of a few individual trees. They are, therefore, very much the consequence of local chance events.

Another factor contributing to the poor results is the possible inapplicability of the linear model. In order to partly check on this, the distribution of plot factor scores and basal areas of *Shorea quadrinervis* are examined in more detail. According to Table 6.23 this is a highly selective species, which appears to be consistently restricted to soils of low phosphorus status. Low levels of both forms of magnesium also appear to be important in the plot-based analysis of site effects on its distribution. However, the regression shows no significant site effects on its plot basal area values. In order to see whether this is due to a curvilinear response curve to site factors, the plot basal areas were graphically plotted against the plot scores for Factors 4 (topsoil phosphorus), 7 (subsoil organic matter, including phosphorus), 6 and 10 (exchangeable and reserve magnesium). The results are shown in Figure 6.1. It appears that the insignificant regression results are due to the wide dispersion of the basal area values, rather than to an underlying and untested curvilinear relationship. However, only univariate relationships were examined, and there is still the possibility that multivariate curvilinear models may be more appropriate.

Figure 6.1

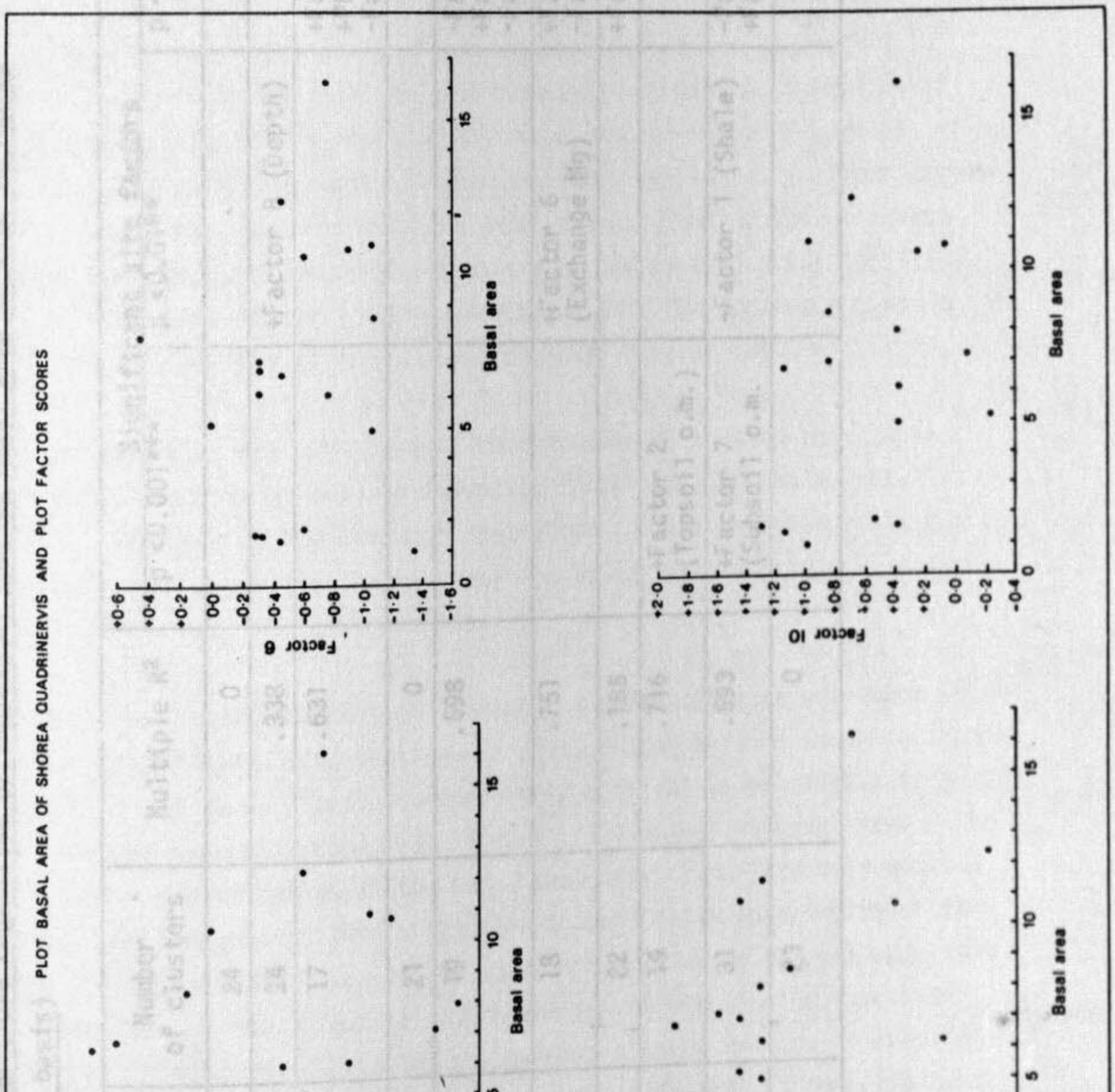

PLOT BASAL AREA OF SHOREA QUADRINERVIS AND PLOT FACTOR SCORES
Factor 4
Factor 6
Factor 7
Factor 10
Basal area

TABLE 6.26 Stepwise multiple regression of individual species basal area on site variables (Cluster basis)

Species	Number of clusters	Multiple R^2	Significant site factors $p < 0.001$***	$p < 0.01$**	$p < 0.05$*
Elateriospermum tapos	24	0			
Koompassia malaccensis	24	.338		+Factor 8 (Depth)	
Dipterocarpus pachyphyllus	17	.631			+Factor 4 (P) +Phytar -Factor 1 (Shale)
Dryobalanops aromatica	21	0			
Dryobalanops oblongifolia	19	.598			-Factor 2 (Topsoil o.m.) +Factor 10 (Reserve Mg) -Factor 6 (Exchange Mg)
Shorea collaris	18	.751		+Factor 6 (Exchange Mg)	+Factor 9 (Exchange Ca) -Factor 3 (pH)
Shorea faguetioides	22	.185			+Factor 5 (slope)
Shorea macroptera	19	.716	+Factor 2 (Topsoil o.m.)		
Shorea parvifolia	31	.593	+Factor 7 (Subsoil o.m.	-Factor 1 (Shale)	-Factor 3 (pH) +Factor 10 (Reserve Mg)
Shorea sagittata	23	0			

The multiple linear regression of the basal areas of nine of the species against site variables were repeated on a cluster basis. *Dipterocarpus caudiferus* and *Shorea quadrinervis* were omitted because they occurred on insufficient clusters to prevent an approach to full resolution.

The results of the regressions for the other species are summarised in Table 6.26. It appears that the smoothing of the basal areas for individual species, by taking the cluster means, considerably reduces the error variance. The multiple regressions account for considerably higher proportions of the basal area variance for most species than do the plot-based regressions. Calculation of the 'cleanness of residuals' statistic (Tukey, 1954) at each step of the regressions showed that the greater success is not due to the low numbers of cases and a tendency towards full resolution.

Although generally more successful, the clusterwise species basal area regressions are just as hard to reconcile in detail with the selectivity results. Thus two of the five most selective species in Table 6.21, i.e. *Elateriospermum tapos* and *Dryobalanops aromatica*, give multiple R^2 values of zero in the basal area regressions.

Similarly, correspondence between the most significant site variables in the selectivity and basal area analyses is poor, as can be seen in comparison of Tables 6.24 and 6.26. Variables apparently critical in delimiting a species range are not generally those significantly affecting its basal area. The significant site variables in the basal area regressions are very heterogeneous. Soil magnesium levels (Factors 6 and 10) are less important than in the selectivity results. In the case of *Dryobalanops oblongifolia*, the interpretation of the effect of soil magnesium on the cluster values of basal area is obscure, as the two magnesium-dominated factors (6 and 10) contribute significantly to the regression function, but in opposite senses.

Soil depth does not appear to have a consistently significant effect on species basal area. It may be that the possible restriction of rooting volume and increased vulnerability to moisture stress on shallow soils is offset by the superior mineral nutrition due to the proximity of weathering rock.

6.3.6 Discussion of FIDP Plot Results

Before comparison of the results from the FIDP plots with those from the MDF ecological plots, or discussion of their significance, the deficiencies of the data and their treatment are summarised.

The site data suffer from a scarcity of soil physical or morphological characteristics, because of the use of the auger in the first field season. Although relatively plentiful, the interpretation of the chemical data is complicated by the fixed sampling depths, which enables confounding by variation in solum depth and in the abundance of freshly weathered rock. The forest data are limited in value for ecological purposes, because of the small sizes of the plots. Both the site and forest data are affected by an unconscious sampling bias, of unknown but apparently significant magnitude. The interpretation of both site and forest data and their interactions are complicated by the tightly clustered distribution of individual plots.

There are also misgivings about the statistical treatment of the data. The use of factor analysis requires more or less normally distributed data. The normality of the data was only tested by visual assessment of univariate histograms, and may be doubtful, particularly for the Ridit-transformed variables. The choice of the oblique simple structure form of factor analysis, with its disadvantage of non-zero factor correlations, was arbitrary. The alternatives were not examined in detail. The identification of site restrictions on species distribution by individual 't' tests for every site factor/species combination is crude and unsatisfactory, as it does not allow for interspecific or interfactor effects. The attempts to integrate the 't' tests by calculation of the parameters of Wilks and Shapiro (1968) is not strictly valid, as the 't' values matrix contravenes the authors' assumptions of independence on several counts. There are also doubts about the application of the linear model in the multiple regressions.

However, despite these reservations, it is felt that the size and comprehensiveness of the data set make the results, particularly those relating to site effects on species distribution, of some value. In general it is felt that there are sufficient internally compatible results to justify the conclusion that there are marked site influences on the distribution, and possibly also the vigour, of many of the commoner MDF species. There are also species which are apparently distributed more or less independently of site conditions, within the range covered by the FIDP plots.

The site data is heavily weighted towards the chemical aspects of soil fertility.

These therefore appear to be the dominant influences on species distribution. There is sufficient geological variation within the plots for the lithomorphic aspects of fertility to be important. However, it is noticeable that it is not the general fertility factor which ranks highest, but rather the reserve magnesium (10) and soil pH (3) factors. The effect of parent material is not overriding, and the more locally heterogeneous factors are also important. These include depth, topsoil organic matter and the topsoil exchangeable cations. The exchangeable magnesium factor is apparently the most influential of all. Although primarily loaded by exchangeable cation variables, the analyses of variance show this factor as having low within-cluster variability, possibly due to the silt loadings. The prominence of the magnesium factors is unexpected. It may be partly artificial due to the high communalities of the magnesium variables and the high correlation between the magnesium-loaded factors.

Of the physico-morphological factors, soil depth (Factor 8) is consistently more important than slope angle and topographic position (Factor 5).

Because of the general inadequacy of basal area as a parameter of forest structure, and also because of the very small plot sizes, the multiple regression analyses of basal areas are not very satisfactory. This applies to the basal areas of the forest as a whole and of individual species. These FIDP results tentatively indicate that site conditions have more effect on the forest's floristic composition than its basal area. Similarly, for individual species, site conditions influence distributions more than local basal areas.

6.4 Discussion of Site Effects on Floristic Variation in the MDF

The considerable differences between the MDF ecological and FIDP plots in plot size and distribution, range of forest and soil types sampled, the intensity of forest and site characterisation, and in the deficiences of the data and their analysis, inevitably lead to some inconsistencies between their results.

The general conclusion from examination of each set of results separately was that there are marked but complex associations between MDF floristic variation and site conditions. There is sufficient agreement between the results to strengthen, rather than weaken, this conclusion.

One of the main areas of agreement is on the identification of site-sensitive species. Several of the highly associated species, whose presence or absence serve as criteria for the objective floristic subdivision of the MDF ecological plots, rank highly for site selectivity in the FIDP results. They include *Shorea quadrinervis*, *Dryobalanops aromatica* and *Elateriospermum tapos*.

There is less agreement on the identity of the most important site characteristics as floristic determinants. This is largely due to the differences in the range of site conditions and forest types sampled. For the geologically heterogeneous MDF ecological plots, soil parent material and closely associated properties are predominant. As the FIDP plots are confined to sedimentary rocks, their geological range is narrower. Nonetheless, there is evidently sufficient geological variety for some lithomorphic site properties to be important as floristic determinants. However, in the FIDP plots, some of the locally variable site characteristics are also important.

The relative importance of the locally variable site properties in determining forest floristics is further increased if plots from only a single locality and rock type are considered. No such studies are included in the present project, but this effect is shown by some of Ashton's work. In the Brunei studies, topographic position and soil drainage were of major importance (Ashton, 1964 (a); Austin et al, 1972). Similarly, in the floristic ordinations of geologically homogeneous single site groups of the Sarawak MDF ecological plots, altitude and similar topographically related variables sometimes appear to be critical (Ashton, 1973).

This illustrates the importance of sampling range and variability in determining the ranking of site properties as floristic influences in the Borneo MDF.

The importance of sampling range is clearly shown by the results of some further analyses of the 1963-66 MDF ecological plot data, recently completed in Aberdeen. If the whole range of plots is used, reserve phosphorus is the site variable most highly correlated with the first and most important axis of a Reciprocal Averaging floristic ordination of the plots. If the basalt-derived plots are excluded, reserve magnesium and potassium become the most significant site variables (C. Legg, pers.comm., 1978).

If similar considerations apply in other tropical rainforests, generalised rankings of different site properties as forest influences are suspect, unless the range of sampling is specified. A common generalisation in the literature is that soil physical conditions are more important than chemical fertility in tropical rainforest (e.g. Holdridge et al., 1971). This is valid only in some areas and at certain scales of sampling. The results also suggest that Whitmore's (1975) ranking of topography above other site characteristics as an influence in the tropical rainforest is not universally valid, although he is considering physiognomy as well as floristics.

In the identification of specific site properties, the MDF ecological and FIDP plot results are consistent that soil pH is a major floristic determinant. The interpretation of soil pH is complex, as it can affect plant growth in a variety of ways. However, from the FIDP results, it appears that it is not acting as an indicator of exchangeable base status in general, or of exchangeable calcium in particular. It loads mainly on its own factor, that is separate and more or less independent of the factors with exchangeable cation loadings. It may be acting through its effect on phosphorus availability. In all of the factor analyses, pH and reserve phosphorus are independent and do not have validated loadings on the same factor. Another possibility is that pH is acting through its effect on trace element availability (Bleeker and Austin, 1972). The preferred interpretation is that pH is effective mainly as an indicator of soil labile aluminium status. This is supported to some extent by the significance of the Group III (free iron and aluminium oxides) variables in the MDF ecological plot results. However, this may also be due to effects on phosphorus availability. Aluminium is known to be phytotoxic (Jackson, 1967; Kamprath, 1972). Aluminium toxicity has been noted in agricultural crops on upland Sarawak soils (de Waard and Sutton, 1960). Exchangeable aluminium levels and aluminium toxicity are known to increase with decreasing soil pH values, although the relationship is complex and varies with soil type (Brenes and Pearson, 1973).

Floristically, the main general reserve nutrient factor is not the most significant of the lithomorphic site properties. In the MDF ecological plots it is outranked either by the Group III oxide or the reserve potassium factor. In the FIDP plots the magnesium factors consistently outrank the main reserve nutrient factor.

As discussed above, magnesium's role may be artificially inflated by the statistical analyses. However, magnesium is confirmed to be important in the recent reanalysis of the 1963-66 MDF ecological plot data (C. Legg, pers.comm., 1978). Magnesium may be acting indirectly, through its antagonistic effect on the uptake of other cations (Acosta et al., 1975). This is gainsaid by the consistent unimportance of the exchangeable calcium factor as a floristic determinant in the FIDP plot results. The importance of the reserve as well as exchangeable magnesium factors also suggests that the element's effect is direct. Magnesium plays a crucial role in plant carbon metabolism, both as an ingredient of chlorophyll and in its effect on respiration.

Ashton's (1973) preliminary results from the MDF ecological plots showed reserve phosphorus to be the single most important soil characteristic as a floristic determinant. In his initial interpretation, Ashton suggests that phosphorus is critical at low levels, but its importance declines above reserve levels of 100-150 ppm.

This finding cannot be directly tested by the present results, either from the MDF ecological or FIDP plots. Both sets of data contain many reserve phosphorus values above 150 ppm. Any effect is likely to be considerably diluted by the large number of plots in which the variable is thought to be floristically irrelevant. Furthermore, in the factorisations of both sets of site data, reserve phosphorus is one of the more complex raw data variables, with validated loadings on several factors. The factors with reserve phosphorus loadings generally appear to be moderately significant as floristic determinants. When raw site variables, rather than factor scores, are used for the whole range of MDF ecological plots (Table 6.10), the reserve phosphorus variables are apparently unimportant. However, the phosphorus uptake by the forest may be as much affected by solubilisation and fixation phenomena as by the size of the soil reserve. It is possible, therefore, that the floristic significance of the pH and Group III oxide variables is partly due to their effects on phosphorus immobilisation.

The site characteristics with high local topomorphic and probabilistic variation are of some importance in the FIDP plot results, but are completely subordinate to the less variable lithomorphic properties in the MDF ecological plot results. The heterogeneous properties include topographic, morphological, topsoil organic matter and the topsoil exchangeable cation variables. As determinants of species distribution in the FIDP plots, the most important of these are exchangeable magnesium and soil depth. The ranking of soil depth above topographic position was as unexpected as the importance of magnesium. Soil depth's importance may be due to the ecological importance of occasional periods of moisture stress, which are more frequent on shallow soils with low available moisture capacities (Brunig, 1971; Baillie, 1976 (a)). It may also be acting as indicator of site stability. The necessity of relatively stable site conditions for the full development of dipterocarp forests, especially those with significant contents of shade-bearing, slow-growing and heavy timber species has been noted (e.g. Cousens, 1965; Lee, 1967). This interpretation of soil depth, and also its possible dual role both as a determinant of, and a response to, forest processes are discussed further in Chapter 8. This interpretation should not be exaggerated because the species expected to be most affected by site stability, such as belian *(Eusideroxylon zwageri)* and the selangan batu section of *Shorea*, do not show significant interactions with depth in Tables 6.19 and 6.21.

Except for magnesium, the exchangeable cations appear to be unimportant, as does topsoil organic matter. These are variable site properties and their apparent insignificance may be partly due to inadequate sampling intensity (P.H. Nye, pers.comm., 1977).

A chemical factor of possible importance in these forests, but for which there are no data for the present project's plots, is silicon. It is known that quite significant levels of water-extractable silica are found in upland Sarawak soils (Andriesse, 1975). The physiological role of silicon in the MDF is obscure, but many common dipterocarps accumulate significant quantities in their timbers (Balan Menon, 1965; Murthy, 1965; Burgess, 1965). This suggests that silica is not an entirely inert load in the transpiration stream (Jones and Handreck, 1967). The dipterocarps are probably not as silicophilic as some graminaceous species. Sugar cane, for instance, shows marked responses to siliceous fertilisers (Wong and Halais, 1970; D'Hoore and Coulter, 1972). These effects may be complex, and due more to reduced phosphate and trace element fixation than directly to silicon nutrition.

The interpretation of the results is complicated by the spatial clustering of both sets of plots. Clustered sampling designs are commonly used for forest inventories in difficult terrain (Loetsch et al., 1973). They are satisfactory for the estimation of exploitable timber volumes, as can be seen in the results of the FIDP inventory (FIDP, 1974 (b) and (c)). However, they do influence and limit the ecological interpretation of the data.

Some confirmation of the project's tentative conclusions come from the results of the MDF experimental inventory blocks in the Bok-Tisam P.F. in North Sarawak. These blocks do not suffer from complications of spatial clustering to the same degree. They were established in 1966 by the Forest Department's Working Plans and Botany sections. The results have been reported by Ashton (1973).

The blocks are laid out non-contiguously along two subparallel lines, that run approximately across the geological strike of the Baram and Brunei groups of sedimentary rocks of the area. The lines are about 12 - 20 km apart. Each block measured 48 x 5 chains (965 x 100 m approximately), and all the data were collected so that the analyses could be carried out on the basis of plot sizes of 0.5 acres or multiples thereof, as required. The forest data collected was restricted to trees assumed to be in the upper canopy, with a lower size limit of 4 feet gbh (approximately equivalent to 40 cm dbh). The original site data were derived from the geological map (Haile, 1962) and from a semi-detailed conventional soil survey transect along the two base lines (Ebon, 1967). Much more detailed site characterisation of four of the blocks was carried out by the Forest Soil Survey in 1969-70. The non-availability of some laboratory data has so far prevented more detailed analysis of forest-site relationships in these blocks.

The blocks were subdivided floristically by Association Analysis, using a range of plot sizes. Plots of 1.5 or 2.0 acres (0.6 and 0.8 ha) seemed to be the most satisfactory (Middleton, 1969).

Despite their limited extent and distribution, the blocks cover a considerable range of sedimentary rock types. The distribution of the main floristically defined forest types is more related to the underlying geology than to the conventional soil survey mapping units. Some of the blocks are geologically homogeneous, but at least two of them straddle boundaries separating lithologically distinct rock formations. In these blocks there are marked floristic changes at, or close to, the geological boundaries. This confirms the conclusion from the MDF ecological and FIDP plot results about the predominance of lithomorphic site variables in geologically heterogeneous samples.

Although providing welcome general confirmation of the project conclusions, the Bok-Tisam results also show that there is a considerable element of non-edaphic floristic variation in the MDF. This is seen in comparison of the floristic classification of the forest on outcrops of the same geological formation on the two lines. The forests are usually separated in the floristic classifications. However, the dendrogram structure of the Association Analysis classification shows them to be related. The floristic differences may be due to non-edaphic variation in the forest over the 12 - 20 km separating the lines, but it could also be partly due to lithological variation within the geological formations. These are partly defined and differentiated on palaeontological grounds (Haile, 1962).

The Bok-Tisam data were also used in conjunction with experimental aerial photography, taken with a variety of films, filters and scales, to explore the possibility of aerial photographic identification of objectively defined floristic subdivisions of the MDF. In general it proved difficult to reconcile the imagery with the ground enumeration data. The identification by canopy appearance of individual species and forest types was generally unsuccessful. It was possible to distinguish the main geological, and hence the main soil, boundaries. This was due mainly to their topographic expression, and not to their effects on the upper canopy appearance (Ashton, 1973).

This result suggests that detailed variation in MDF floristics and physiognomy are only tenuously related. This indirectly confirms some of the project results. In general, site conditions affect forest floristics more than physiognomy. This is true at whole forest and individual species level. Overall floristic composition is apparently more site-sensitive than total forest basal area. Similarly, individual species distributions generally appear to be more site responsive than are their basal areas. For both total forest and individual species, the critical site factors are different for floristics/distribution from those for basal areas.

CHAPTER 7

RESULTS AND DISCUSSION:
II: SITE EFFECTS ON VARIATION IN HOLLOW DECAY

7.1 Introduction

The investigation of this aspect of the site relationships of the MDF is confined to the data from the FIDP plots. The site variables used are the factor and locational scores that have been calculated for these plots (Sections 5.2.1.3 and 6.3.1).

7.2 Site Effects on Overall Forest Stemrot Severity

The results of the plot-based multiple regressions of the plot values for total forest percentage stemrot severity against combinations of site and tree size variables as predictors are summarised in Table 7.1. Because of the low number of trees felled on all but a few plots, the stemrot severity values can be greatly inflated by the presence of a single very large and rotten stem. In this respect these values are similar to the plot values for total forest basal area, which also have high error variance (section 6.3.3).

There are also parallels in the two sets of results,as can be seen by comparison of Tables 7.1 and 6.16. The results in Table 7.1 show that there is a considerable distortion due to the sampling bias. The higher timber volumes of the soil plots in the northern inventory units mean that there is a higher probability of including large and rotten trees. Decay frequency and severity are therefore likely to be higher. However, the Phytar effect cannot be entirely attributed to the higher stature of the sampled forests in the north, as the final multiple R^2 value with the factor scores and Phytar as predictors is higher than with factor scores and the plot total stem timber volume (TSV). Also when Phytar and TSV are both included as predictors, Phytar is the first variable to enter the regression, and its presence does not preclude the entry of TSV.

Once the locational and/or timber volume element of the stemrot severity variance is accounted for, the other site variables make significant but small contributions to the regression function. The soil properties associated with high overall stemrot levels are fine texture, high reserve nutrient fertility, high levels of topsoil phosphorus, and low levels of exchangeable magnesium. These are also the factors which apparently affect plot total basal areas (see Table 6.16).

Because of the high error variance of the plot stemrot severity values, the regressions were repeated on a cluster mean basis. The results are summarised in Table 7.2. The final values of multiple R^2 are lower than in the corresponding plot-based analyses. However, the locational variable, Phytar, does not enter the function, and the non-locational site variables account for higher proportions of the stemrot severity variance than in the plot-based regressions. Apart from a weak negative effect by Factor 6 (exchangeable magnesium) the significant variables differ from those in the plotwise regressions. It is noticeable that the floristically insignificant Factor 9 (exchangeable calcium) is the first variable to enter the function. The weak effect of Factor 1 (shale) in the opposite sense to that in the plot results is inexplicable, and rather detracts from the credibility of all of these results.

As in the plot-based regressions, there are parallels between the cluster-based regressions of total forest basal area and stemrot severity. Similarities include lower final multiple R^2 values than in the plotwise regressions, the disappearance of Phytar as a significant contributor, the higher contributions from the non-locational site variables, and the inconsistency between the plot- and cluster-based analyses on the identification of the significant variables.

7.3 Interspecific Variation in Buttrot Frequency

The intergeneric and interspecific variations in the frequency of buttrot are summarised in Tables 7.3 - 7.8 and in Figures 7.1 - 7.2. The generic totals in Table 7.3 include trees that were only identified to genus level, and also trees of rare species, so that they are higher than the marginal totals in Tables 7.4 - 7.7.

As expected, there are large and very significant differences between and within the genera. Of the main commercial timber groups, the keruings (*Dipterocarpus spp.*) are generally the soundest and the yellow meranti section of the genus *Shorea* the most decayed.

The buttrot frequency results cannot simply be graded according to timber

TABLE 7.1 Stepwise multiple regression of plot total forest stermrot severity on site factors and total stem volume

257 plots

Predictor variables used	Multiple R^2	Significant predictor variables: $p < 0.001$***	$p < 0.01$**	$p < 0.05$*
Plot scores for Factors 1 - 10	.027			-Factor 6 (Exchange Mg)
10 Factor scores + Phytar	.400	Phytar -Factor 10 (Reserve Mg) +Factor 1 (Shale) -Factor 6 (Exchange Mg)	+Factor 4 (Topsoil P)	
10 Factor scores + plot total stem volume	.340	+TSV -Factor 6 (Exchange Mg)		
10 Factor scores + Phytar + plot total stem volume	.422	+Phytar, TSV -Factor 10 (Reserve Mg) -Factor 6 (Exchange Mg) +Factor 1 (Shale)		+Factor 4 (Topsoil P)

TABLE 7.2 Stepwise multiple regression of cluster total forest stemrot severity volume on site factors and total stem volume

45 clusters

Predictor variables used	Multiple R^2	Significant predictor variables		
		$p < 0.001$***	$p < 0.01$**	$p < 0.05$*
Mean scores on Factors 1 - 10 +Phytar	.207		-Factor 9 (Exchange Ca) -Factor 1 (Shale)	-Factor 2 (Topsoil o.m.)
Mean Factor scores +Phytar +Total stem volume	.313		-Factor 9 (Exchange Ca) +TSV	-Factor 6 (Exchange Mg)

properties, and must be interpreted together with the tree size data. In fact, the interpretation is problematical and appears to require some assumptions about the role of hollow decay in tree mortality and MDF dynamics. Taking the buttrot and drh data together, at least five groups are discernible.

The first group includes species capable of reaching great size and in which buttrot is infrequent. This group includes the genera *Hopea* and *Parashorea* in Table 7.3, several *Dipterocarpus* species (7.4), *Dryobalanops lanceolata* (7.5), *Shorea leptoclados* (7.7), *S. ochracea* and *S. superba* (7.8). For some of these species, their freedom from decay in the standing forest can be attributed to their resistant timbers, e.g. the selangan batu species *Shorea superba*. In others the cut timber is not notably durable, and the cause of their relative freedom from decay in the standing forest is uncertain.

The second group contains those species which also contain many trees of great size, but in which buttrot is frequent. This group includes species which are known for the density and durability of their timbers, such as the selangan batu section of the *Shorea* genus (except *S. superba*), *S. curtisii* in the dark red meranti section of the same genus, and, especially, *Eusideroxylon zwageri* (belian). These are characteristically shade-bearing and slow growing species, and their large stems are of considerable age. They appear to survive for long periods after decay infection. Massive growing stems are found which have been reduced to thin-walled hollow pipes.

The third group consists of species which also have high buttrot frequencies, but which contain few trees of great size. This group includes many of the yellow meranti *Shorea* species. The diameter differences between the sound and rotten trees in these species tend to be smaller and less significant than in the other groups. As these are medium density timber species that are capable of quite rapid growth in the gap and building phases of forest development (Whitmore, 1975), it is thought that decay may play a significant part in their tree mortality.

The fourth group is also characterised by generally small size, but their buttrot frequencies are low. This group includes species such as *Elateriospermum tapos*, which are characteristically understorey species. It is thought that decay is relatively unimportant in the mortality and population dynamics of these species.

The final group includes the red meranti section of the genus *Shorea* and most of the kapurs *(Dryobalanops spp.)*, and therefore contains a major part of the commercial timber resources of the Sarawak MDF. These are upper canopy species, and individual stems can reach great size, but in lower proportions than in the species of the first and second groups. They show an intermediate buttrot pattern, with about half of the extractable stems showing some decay. This gives an indication of the frequency of decay in the MDF and why it is a major practical and economic problem in exploitation of these forests.

As noted above, the proportions of trees with buttrot are not consistently associated with timber properties. Durability is often associated with high density timber, as in *Shorea superba* (selangan batu). However, in these results there are several exceptions to this trend. *Dryobalanops lanceolata*, for example, is apparently the least buttrot susceptible of the kapurs, yet it is also the species with the lowest reported timber specific gravity in the genus. The densest timber in this genus comes from *D. oblongifolia*, which also shows the highest buttrot frequency. This apparent anomaly cannot be attributed to differences in tree size and age patterns, because the sounder but lighter species, *D. lanceolata*, actually reaches considerably greater sizes than the others.

Dark timber colours are often associated with high specific gravity and durability. As colour and durability are both largely due to the presence of secondary metabolites, this association is to be expected. However, the association is by no means invariable. Although the yellow meranti section of the genus *Shorea* are generally less durable than the darker coloured red merantis, both groups are generally less durable than the white merantis. Similarly, within the red merantis, species with dark coloured timbers are not consistently more durable than the light red merantis.

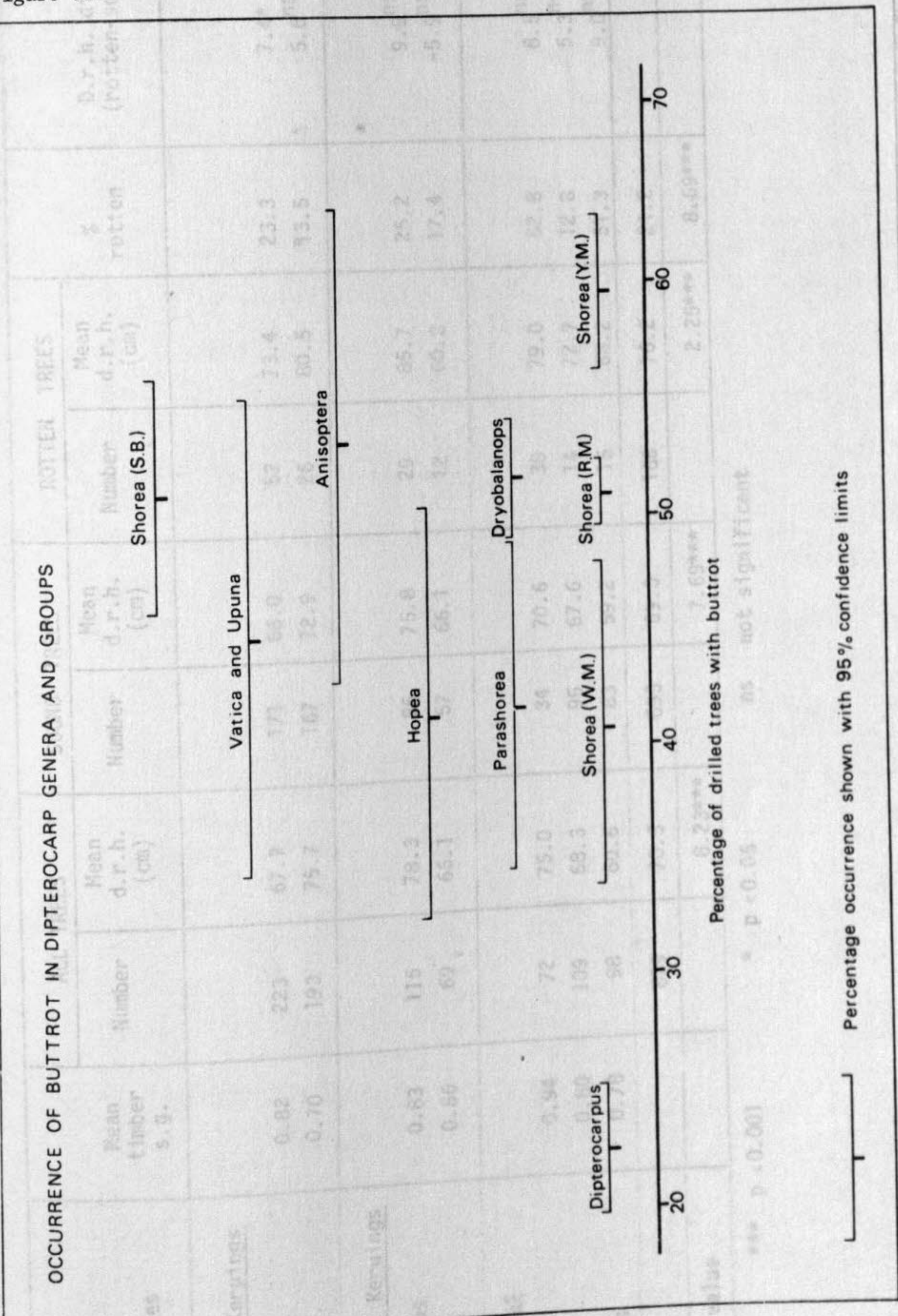
Some of the light coloured but durable timbers, such as those of the white meranti section of the *Shoreas*, have high silica contents. The keruings *(Dipterocarpus spp.)* also combine low buttrot frequencies (Table 7.4) with highly siliceous timbers (Murthy, 1965; Jongebloed and Jutte, 1965). Subterranean termites and other insects may be important as vectors in the transmission and entry of the buttrot fungi (Panzer, 1975). The association between high silica content and resistance may therefore be due to the mechanical deterrence and impedance to insect attack that is afforded by the silica grains (Ong and Lee, 1972). However, it is thought that the main cause of the enhanced resistance is due to the high levels of polyphenolic secondary metabolites that often go with high silica contents (Scurfield et al., 1974; Southwell and Bultmann, 1971).

TABLE 7.3 Buttrot occurrence in dipterocarp genera and sections

s/section	Timber density description	ALL TREES Number	ALL TREES Mean D.r.h. (cm)	SOUND TREES Number	SOUND TREES Mean D.r.h. (cm)	ROTTEN TREES Number	ROTTEN TREES Mean D.r.h. (cm)	% rotten	D.r.h. difference (rotten - sound) (cm)
ptera	Medium-heavy	105	81.0	49	77.4	56	84.1	53.3	6.7 ns
rocarpus	Medium-heavy	1254	70.1	972	68.7	282	74.8	22.5	6.1***
alanops	Medium-heavy	1471	76.2	710	73.2	761	79.1	51.7	5.9***
	Medium-heavy	133	57.3	78	54.1	55	61.9	41.4	7.8 ns
shorea	Medium-heavy	228	71.8	133	67.6	95	77.8	41.7	10.2**
ea te meranti)	Medium heavy	201	86.1	119	79.6	82	95.4	40.8	15.7***
ea low meranti)	Medium-heavy	954	66.6	385	62.6	569	69.4	59.6	6.8***
rea d meranti)	Heavy (D.R.M.) Medium (L.R.M.)	5380	72.8	2638	67.6	2742	77.8	51.0	10.2***
rea elangan batu)	Heavy - very heavy	424	78.0	207	73.5	217	82.3	51.2	8.7**
tica and Upuna	Heavy and very heavy	100	47.5	55	44.9	45	50.7	45.0	5.8*
tal/mean		10250	72.5	5346	68.3	4904	77.0	47.8	8.7***
dified F value			36.28***		18.40***		20.36***	51.59***	

*** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$ ns not significant

Figure 7.1



OCCURRENCE OF BUTTROT IN DIPTEROCARP GENERA AND GROUPS
Shorea (S.B.)
Vatica and Upuna
Anisoptera
Hopea
Parashorea
Dryobalanops
Shorea (W.M.)
Shorea (R.M.)
Shorea (Y.M.)
Dipterocarpus
20
30
40
50
60
70
Percentage of drilled trees with buttrot
Percentage occurrence shown with 95% confidence limits

TABLE 7.4 Buttrot occurrence in Dipterocarpus (Keruing) species

Species	Mean timber s.g.	ALL TREES Number	ALL TREES Mean d.r.h. (cm)	SOUND TREES Number	SOUND TREES Mean d.r.h. (cm)	ROTTEN TREES Number	ROTTEN TREES Mean d.r.h. (cm)	% rotten	D.r.h. difference (rotten-sound) (cm)
Lightweight Keruings									
D acutangulus	0.82	223	67.7	171	66.0	52	73.4	23.3	7.4*
D caudiferus	0.70	193	75.7	167	72.9	26	80.5	13.5	5.6^{ns}
Medium weight Keruings									
D pachyphyllus	0.83	115	78.3	86	75.8	29	85.7	25.2	9.9^{ns}
D verrucosus	0.86	69	65.1	57	66.1	12	60.2	17.4	-5.9^{ns}
Heavy Keruings									
D. crinitus	0.94	72	75.0	34	70.6	38	79.0	52.8	8.5^{ns}
D. mundus	0.80	109	68.3	95	67.6	14	72.7	12.8	5.3^{ns}
D. conformis	0.78	98	60.6	83	59.2	15	68.2	51.3	9.0^{ns}
Total/mean		879	70.5	693	69.0	186	76.2	21.2	
Modified F value			8.23***		7.69***		2.25***	8.69***	

*** $p < 0.001$ * $p < 0.05$ ns not significant

Table 7.5 Buttrot occurrence in Dryobalanops (Kapur) species

Species	Mean timber s.g.	ALL TREES		SOUND TREES		ROTTEN TREES		% rotten	D.r.h. difference (rotten-sound) (cm)
		Number	Mean d.r.h. (cm)	Number	Mean d.r.h. (cm)	Number	Mean d.r.h. (cm)		
D. lanceolata	0.72	306	84.1	243	82.7	63	89.7	20.6	7.0 ns
D. aromatica	0.88	490	73.8	206	68.3	284	77.8	58.0	9.6 ***
D. beccarii	0.78	312	73.6	130	66.4	182	78.7	58.3	12.3 ***
D. oblongifolia	0.86	335	74.6	119	68.9	216	77.8	64.5	8.9 ***
Total/mean		1443	76.1	698	73.0	745	79.0	51.6	
Modified F value			14.02***		22.05***		4.09**	56.79***	

*** $p < 0.001$ ** $p < 0.01$ ns not significant

TABLE 7.6 Buttrot occurrence in Shorea (Yellow Meranti) species

Species	Mean timber s.g.	ALL TREES		SOUND TREES		ROTTEN TREES		% rotten	D.r.h. difference (rotten-sound) (cm)
		Number	Mean d.r.h. (cm)	Number	Mean d.r.h. (cm)	Number	Mean d.r.h (cm)		
Medium weight species									
S. faguetiana	0.66	113	70.9	59	71.6	54	70.0	47.8	-1.6^{ns}
S. multiflora	0.67	72	86.3	27	81.0	45	89.5	62.5	8.5^{ns}
Heavy species									
S. collaris	0.70	349	62.8	159	56.4	190	68.1	54.4	11.7***
S. dolichocarpa	0.90	80	50.4	28	45.9	52	52.8	65.0	6.9^{ns}
S. faguetioides	0.74	145	60.1	44	49.1	101	64.9	69.7	15.8***
Total/mean		759	54.4	317	59.4	442	67.9	58.2	
Modified F value			19.31***		11.83***		11.55***	4.34**	

*** $p < 0.001$ ** $p < 0.01$ ns not significant

TABLE 7.7 Buttrot occurrence in Shorea (Red Meranti) species

Species	Mean timber s.g.	ALL TREES Number	ALL TREES Mean d.r.h (cm)	SOUND TREES Number	SOUND TREES Mean d.r.h. (cm)	ROTTEN TREES Number	ROTTEN TREES Mean d.r.h. (cm)	% rotten	D.r.h. difference (rotten-sound) (cm)
Light red Merantis									
S. amplexicaulis	0.58	51	53.1	21	49.1	30	55.9	58.8	6.8^{ns}
S. beccariana	0.64	269	71.3	131	67.8	138	74.7	51.3	7.0*
S. ferruginea	0.69	186	70.6	69	61.2	117	76.1	62.9	14.9***
S. leprosula	0.61	76	77.7	51	76.4	25	81.3	32.9	4.1^{ns}
S. leptoclados	0.54	124	87.5	86	82.0	38	100.1	30.6	18.1***
S. macrophylla	n.d.	139	77.1	79	70.2	60	86.2	43.2	15.9***
S. macroptera	0.66	285	58.1	145	52.6	140	63.7	49.1	11.0***
S. mecisopteryx	0.56	57	79.9	39	79.9	18	79.9	31.6	0
S. myrionerva	0.59	180	59.9	88	54.8	92	64.7	51.1	9.9***
S. parvifolia	0.58	837	75.4	500	72.4	337	79.9	40.3	7.5***
S. pilosa	0.53	87	71.2	43	68.8	44	73.6	50.6	4.8^{ns}
S. pinanga	0.53	231	76.2	127	71.3	104	82.3	45.0	11.1^{ns}
S. quadrinervis	0.66	205	60.5	94	55.2	111	65.0	54.2	9.8***
S. rubra	0.62	366	70.7	125	62.6	241	74.9	65.8	12.2***
S. sagittata	0.59	650	75.9	269	65.3	381	83.4	58.6	18.0***
S. scaberrima	0.67	216	66.1	109	63.4	107	68.8	49.5	5.4^{ns}
S. dasyphylla	0.53	132	64.8	77	61.2	55	69.8	41.7	8.6**
Dark Red Merantis									
S. argentifolia	0.69	153	80.2	67	66.7	86	90.8	56.2	24.1***
S. curtisii	0.80	134	94.1	50	84.1	84	100.1	62.7	16.0**
S. pauciflora	0.74	124	77.5	68	73.7	56	82.1	45.2	8.4^{ns}
S. slooteni	0.82	65	65.4	26	59.5	39	69.4	60.0	9.9^{ns}
Total/mean		4567	72.4	2264	67.1	2303	77.6	50.4	
Modified F value			24.03***		13.19***		16.66***	8.31***	

*** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$ ns not significant

TABLE 7.8 Buttrot occurrence in miscellaneous species

Species	Mean timber s.g.	ALL TREES		SOUND TREES		ROTTEN TREES		% rotten	D.r.h. difference (rotten-sound) (cm)
		Number	Mean d.r.h. (cm)	Number	Mean d.r.h. (cm)	Number	Mean d.r.h. (cm)		
Non Dipterocarps									
Elateriospermum tapos	(0.84)	151	46.2	137	45.9	14	49.1	9.3	3.3 ns
Eusideroxylon zwageri	1.09	94	77.3	35	63.8	59	85.4	62.8	21.6 ***
Dipterocarps									
Anisoptera grossivenia	0.78	52	78.1	25	78.0	27	78.2	51.9	0.2 ns
Hopea dyeri	0.85	44	57.2	28	53.0	16	64.6	36.4	11.6 ns
Parashorea smythiesii	0.83	130	74.8	66	71.8	64	77.9	49.2	6.1 ns
Shorea lamellata (W.M.)	0.75	64	93.9	33	87.9	31	100.4	48.4	12.6 ns
Shorea ochracea (W.M.)	0.62	74	87.8	46	80.9	28	99.2	37.8	18.3 **
Shorea laevis (S.B.)	0.99	77	100.3	36	88.5	41	110.6	53.2	22.0 **
Shorea superba (S.B.)	1.02	46	81.1	36	79.8	10	85.7	21.7	5.9 ns

*** $p < 0.001$ ** $p < 0.01$ ns not significant

Figure 7.2

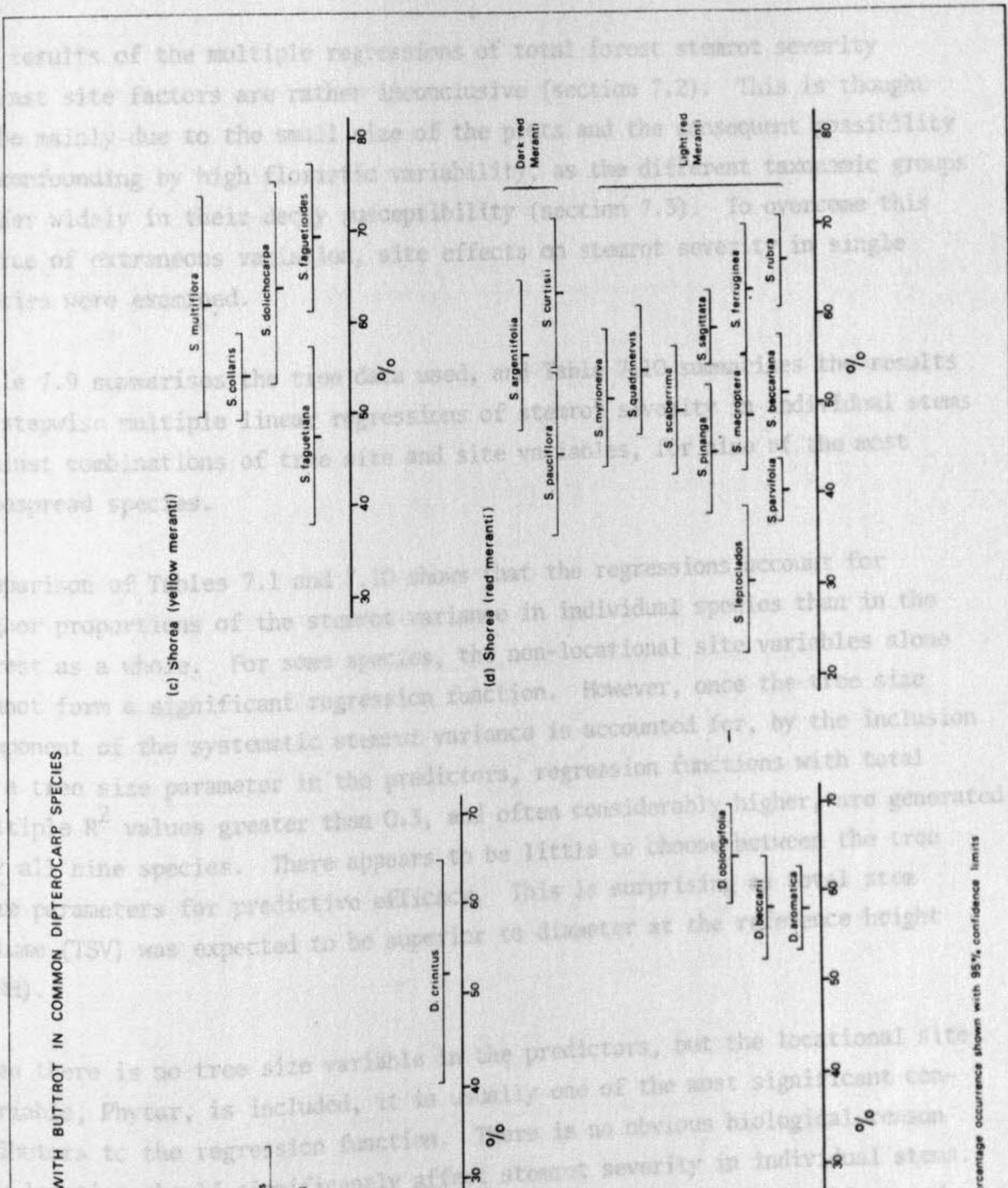

PERCENTAGE OF DRILLED TREES WITH BUTTROT IN COMMON DIPTEROCARP SPECIES
(a) Dipterocarpus
D. pachyphyllus
D. acutangulus
D. conformis
D. verrucosus
D. mundus
D. caudiferus
D. crinitus
(b) Dryobalanops
D. lanceolata
D. beccarii
D. aromatica
D. oblongifolia
(c) Shorea (yellow meranti)
S. faguetiana
S. collaris
S. multiflora
S. dolichocarpa
S. faguetioides
(d) Shorea (red meranti)
S. pauciflora
S. argentifolia
S. curtisii
Dark red Meranti
S. myrionerva
S. quadrinervis
S. scaberrima
S. pinanga
S. sagittata
S. leptocladOS
S. macroptera
S. ferruginea
S. parvifolia
S. beccariana
S. rubra
Light red Meranti
%
Percentage occurrence shown with 95% confidence limits

TABLE 7.9 Tree data used in multiple regression of intraspecific variation of stemrot severity on site variables and tree size

Species	Total number of trees	Mean: Diameter at reference height (cm)	Mean: Total stem volume (m^3)	Decayed Trees: Number	Decayed Trees: % of Total	Mean severity of decay (% volume lost to decay): per tree	Mean severity of decay (% volume lost to decay): per decayed tree
Dipterocarpus caudiferus	18	69.3	6.94	6	33	0.5	1.6
Dryobalanops aromatica	47	64.4	4.90	39	83	12.6	15.1
Dryobalanops oblongifolia	75	63.7	4.16	49	65	8.4	12.8
Shorea collaris (Y.M.)	27	50.0	2.31	22	81	21.7	26.6
Shorea faguetioides (Y.M.)	28	49.8	2.39	22	79	14.9	19.0
Shorea beccariana (R.M.)	20	60.7	5.00	6	30	5.1	17.2
Shorea parvifolia (R.M.)	64	65.0	5.25	31	48	10.5	21.7
Shorea rubra (R.M.)	22	62.1	4.36	17	77	10.8	14.0
Shorea sagittata (R.M.)	31	63.6	4.70	14	45	10.7	23.8
Total	332	61.8	4.44	214	64	10.6	16.7

Table 7.10 Stepwise multiple regression of stemrot severity in common dipterocarp species on site factors and tree size

Species	Number of trees	Predictor variables used	Multiple R^2	Significant predictor variables $p < 0.001$***	$p < 0.01$**	$p < 0.05$*
Dipterocarpus caudiferus	18	Plot scores on Factor 1-10	0			
		Factor scores + Total stem volume	.431			+TSV -Factor 4 (topsoil P)
		Factor scores + Diameter reference height	.328			-Factor 4 (topsoil P) +D.r.h.
Dryobalanops aromatica	47	Plot scores on Factors 1-10	.491	-Factor 4 (topsoil P)	-Factor 9 (exchange Ca)	-Factor 8 (depth)
		Factor scores + Phytar	.516	Phytar		-Factor 4 (topsoil P) -Factor 9 (exchange Ca) + Factor 1 (shale) -Factor 7 (subsoil o.m.)
		Factor scores + total stem volume	.491	-Factor 4 (topsoil P)	-Factor 9 (exchange Ca)	-Factor 8 (depth)
		Factor scores + diameter reference height	.490	+D.r.h.	-Factor 4 (topsoil P) -Factor 9 (exchange Ca)	
		Factor scores + Phytar + D.r.h.	.490	+D.r.h.	-Factor 4 (topsoil P) -Factor 9 (exchange Ca)	
Dryobalanops oblongifolia	75	Plot scores on Factors 1-10	.320	-Factor 9 (exchange Ca)	-Factor 4 (topsoil P)	-Factor 7 (subsoil o.m.) + Factor 6 (exchange Mg)
		Factor scores + Phytar	.385	Phytar	-Factor 9 (exchange Ca) -Factor 7 (subsoil o.m.)	
		Factor scores + total stem volume	.498	+TSV	-Factor 7 (subsoil o.m.)	-Factor 2 (topsoil o.m.) -Factor 10 (reserve Mg) + Factor 5 (slope)
		Factor scores + diameter reference height	.507	+D.r.h.	-Factor 7 (subsoil o.m.)	-Factor 10(reserve Mg) + Factor 5 (slope)
		Factor scores + Phytar + D.r.h.	.531	+D.r.h	-Factor 7 (subsoil o.m.)	-Factor 10 (reserve Mg) -Phytar +Factor 5 (slope)

Table 7.10 (page 2)

Species	Number of trees	Predictor variables used	Multiple R^2	Significant predictor variables		
				$p < 0.001$***	$p < 0.01$**	$p < 0.05$*
Shorea collaris	27	Plot scores on Factors 1-10	.418	+Factor 7 (Subsoil o.m.)		- Factor 8 (depth)
		Factor scores + Phytar	.560	+Factor 7 (subsoil o.m.)	+ Factor 5 (slope)	Phytar
		Factor scores + total stem volume	.418	+Factor 7 (subsoil o.m.)		- Factor 8 (depth)
		Factor scores + diameter reference height	.591	+D.r.h. -Factor 9 (exchange Ca)		
		Factor scores + Phytar + D.r.h.	.591	+D.r.h. -Factor 9 (exchange Ca)		
Shorea faguetioides	28	Plot scores on Factors 1-10	.454		-Factor 6 (exchange Mg)	+ Factor 8 (depth) + Factor 5 (slope)
		Factor scores + Phytar	.524		-Factor 6 (exchange Mg)	+ Factor 8 (depth) + Factor 5 (slope) Phytar
		Factor scores + total stem volume	.687	+TSV		+ Factor 8 (depth) -Factor 7 (subsoil o.m.)
		Factor scores + diameter reference height	.642	+D.r.h.		+ Factor 8 (depth) -Factor 1 (shale)
		Factor scores + Phytar + D.r.h.	.642	+D.r.h.		+ Factor 8 (depth) -Factor 1 (shale)
Shorea beccariana	20	Plot scores on Factors 1-10	0			
		Factor scores + Phytar	0			
		Factor scores + total Stem volume	.450			+TSV -Factor 8 (depth) -Factor 5 (slope)
		Factor scores + diameter reference height	.409			+D.r.h. -Factor 8 (depth) -Factor 5 (slope)
		Factor scores + Phytar + D.r.h.	.409			D.r.h. -Factor 8 (depth) -Factor 5 (slope)

Table 7.10 (page 3)

Species	Number of trees	Predictor variables used	Multiple R^2	Significant predictor variables: $p < 0.001$***	$p < 0.01$**	$p < 0.05$*
Shorea parvifolia	64	Plot scores on Factors 1-10	.116		+Factor 4 (topsoil P)	
		Factor scores + Phytar	.245		+Factor 4 (topsoil)	Phytar -Factor 6 (exchange Mg)
		Factor scores + total stem volume	.338	+TSV		-Factor 6 (exchange Mg) +Factor 4 (Topsoil P)
		Factor scores + diameter reference height	.331	+D.r.h.		-Factor 6 (exchange Mg)
		Factor scores + Phytar + D.r.h.	.382	+D.r.h.		-Factor 6 (exchange Mg) -Factor 7 (subsoil o.m.) Phytar
Shorea rubra	22	Plot scores on Factors 1-10	0			
		Factor scores + Phytar	.326		Phytar	
		Factor scores + total stem volume	.320		+TSV	
		Factor scores + diameter reference height	.440	+D.r.h.		
		Factor scores + Phytar + D.r.h.	.440	+D.r.h.		
Shorea sagittata	31	Plot scores on Factors 1-10	.317		Factor 3 (pH)	-Factor 4 (Topsoil P)
		Factor scores + Phytar	.361		Factor 3 (pH) Phytar	
		Factor scores + total stem volume	.366		+TSV	+Factor 3 (pH)
		Factor scores + diameter reference height	.395	+D.r.h.		+Factor 3 (pH)
		Factor scores + Phytar + D.r.h.	.395	+D.r.h.		+Factor 3 (pH)

same sense for all species, but some general trends are apparent.

The significant chemical factors generally have negative coefficients, and stemrot severity tends to be highest on infertile sites. The positive effects of Factor 4 (topsoil phosphorus) in *Shorea parvifolia* and Factors 6 and 10 (exchangeable and reserve magnesium) in *Dryobalanops oblongifolia* are exceptions to this trend.

The consistently important chemical factors are those loaded by variables with high local topomorphic and probabilistic variability. They are Factors 4 (topsoil phosphorus), 6 (exchangeable magnesium), 7 (subsoil organic matter) and 9 (exchangeable calcium). A notable exception from this list is Factor 2 (topsoil organic matter). The factors with loadings by geological or reserve mineral nutrient variables and reflecting more stable lithomorphic soil characteristics are relatively unimportant.

Compared with their rankings as floristic discriminants, the importance of magnesium has been relatively downgraded, whilst calcium assumes a more significant role. Because of its role in both photosynthesis and respiration, it is easy to see how the tree's internal magnesium status may affect the quantity of photosynthesate, and its partition into respiration, new cell formation and the formation of fungistatic secondary metabolites.

The generally positive coefficients for Factor 5 (slope) and the negative coefficients for Factor 8 (depth) show that stemrot tends to be more severe in shallow soils on steep flank slopes than in the deeper soils of the ridge crests. This appears to contradict the field experience of North Sarawak loggers that decay is worse on ridge crest sites. However, Table 7.11 does not include tree size effects, which far outweigh the combined edaphic factors. The concentration of larger and more easily extractable stems on the ridge crests and upper slopes means that stemrot may be more apparent in these sites.

7.5 Discussion of site effects on hollow decay in the MDF

The results described indicate that there is great interspecific variability in the frequency of buttrot, and that there is apparently a considerable degree of association between site conditions and intraspecific variation in the severity of stem rot, once allowance is made for the predominant effect of tree size. In the previous chapter it has been shown that there appears to

TABLE 7.11 Summary of site effects on the severity of stemrot in common dipterocarp species

Species \ Factor	1	2	3	4	5	6	7	8	9	10
Dipterocarpus caudiferus				-						
Dryobalanops aromatica	+			--				-	--	
Dryobalanops oblongifolia		-		--	+	+	-		-	-
Shorea collaris					+		+++	-	---	
Shorea faguetioides	-				+	--	-	+		
Shorea beccariana					-			-		
Shorea parvifolia				++		-	-			
Shorea rubra										
Shorea sagittata			++	-						

$\pm$ $p < 0.05$

++/-- $p < 0.01$

+++/--- $p < 0.001$

be a high degree of association between site conditions and floristically defined forest types. It has also been shown that there are varying degrees of site influence over the distribution of some of the commoner species in the MDF. However, these various site effects are not synergistic and do not combine to give consistent congregation of rot-susceptible or rot-resistant species on particular site types. The site conditions appear to affect stem-rot variation in the forest as a whole less than in individual species.

In general, the site characteristics most influencing intraspecific variation of stemrot severity are those with high local variability and which vary with topography and chance factors. This contrasts with the importance of the less variable parent material derived properties in the distribution of forest types and of individual species. However, the contrast is not to be overstressed, as the pattern of influences operating in a species can be complex. This is seen in Table 7.12 which summarises the findings on site effects on five commercially important dipterocarps.

Within individual species, stemrot tends to be more severe on infertile sites. In the forest as a whole, however, stemrot appears to be slightly worse on more fertile sites. The apparent contradiction is probably due to site effects on forest floristic composition. These may cause weak concentrations of relatively susceptible species on more fertile sites. This tendency is sufficient to mask the opposite trend in intraspecific stemrot variation. As noted above, however, sampling considerations make total forest regressions suspect, so that this interpretation is speculative.

The various results can be used to support several hypotheses about the causes and adaptive advantages of hollow decay in the MDF and similar forests. The total forest regression results, such as they are, accord with the idea that relatively rapid growth in more fertile sites leads to the formation of less dense and less durable timber, and hence to higher decay levels (e.g. Wyatt-Smith, 1958).

The intraspecific stemrot regression results support the idea that hollow decay is an advantageous adaptation to a nutrient-deficient environment. Stemrot brings the nutrient content of the metabolically inert heartwood back into active circulation. This is achieved at the cost of a marginal decrease in the mechanical strength of the stem. The effectiveness of hollow decay as a non-fatal nutrient cycling process is increased by the higher cation

TABLE 7.12 Summarised comparison of major site effects on distribution and growth characteristics of some common MDF species

Species	FIDP site factors with effect on:		
	Distribution	Basal area	Stemrot severity
Dryobalanops aromatica	Low Reserve magnesium (Factor 6)	None	Topsoil phosphate and exchangeable calcium (Factors 4 and 9)
Dryobalanops oblongifolia	Shale soils with low topsoil organic matter (Factors 1 and 2)	Topsoil organic matter and magnesium (Factors 2, 6 and 10).	Organic matter, Reserve magnesium and slope (Factors 2, 5, 7 and 10)
Shorea collaris (Y.M.)	Inconsistent	Exchangeable calcium and magnesium, and soil pH (Factors 3, 6 and 9)	Subsoil organic matter, depth, exchangeable calcium (Factors 7, 8, and 9)
Shorea faguetioides (Y.M.)	Deep soils of low magnesium status (Factors 6, 8, and 10)	Slope (Factor 5)	Shale, slope, exchangeable magnesium, depth (Factors 1, 5, 6, and 8)
Shorea parvifolia (R.M.)	High phosphate soils (Factors 4 and 7)	Shale, pH, subsoil organic matter and phosphate, Reserve magnesium. (Factors 1, 3, 7 and 10)	Topsoil phosphate, exchangeable magnesium (Factors 4 and 6)

contents of rotten wood than in sound wood, and the apparent migration of nutrients into infected timber (Hare, 1966; Dessureault and Rich, 1973; Salford et al., 1974; Fukuda et al., 1976).

Janzen (1976) has suggested an ingenious variation of this hypothesis. The hollow interior of a rotten stem provides an environment that is close to ideal for microbial and faunal activity. It therefore tends to concentrate litter decomposition and mineralisation processes in the immediate vicinity of the stem, and possibly improve the individual tree's mineral nutrition. This suggestion has had some support from the observation of adventitious root development within hollow stems in temperate forests (Fisher, 1976).

For these suggestions to be valid, trees should be able to survive and continue growth for long periods after infection. This seems to be the case for some MDF species, judging from the buttrot occurrence and tree size data. In the second group of species described (Section 7.3), there are large and significant differences in drh between the sound and rotten stems. This may be viewed purely as a probability effect. The larger stems are, overall, probably older and have therefore had longer periods in which to encounter a viable, infective pathogen-vector combination. However, the existence of green and growing stems with massive hollow decay in these species suggests that they are able to survive infection for long periods.

The strength of the tubular structure of the decayed stems of these species is probably sufficient to withstand the normal mechanical stresses caused by wind pressure and gravity. The timbers of the species of this group are dense and have high mechanical strength properties.

The third group of species is also characterised by very high buttrot frequencies. These species, including many yellow merantis, have lighter and softer timbers. The size differences between sound and rotten stems in species of this group are relatively small and insignificant. This and the relatively modest sizes achieved suggest that trees of these species do not grow for long after infection. The loss in stem strength due to hollowing may be critical. If hollow decay is a significant cause of mortality in these species, it can hardly be regarded as an advantageous nutrient-enhancing adaptation.

The full results of the FIDP inventory showed that stemrot normally occurs in association with buttrot (FIDP, 1974 (c)). This suggests that the root system and the butt of the bole are the main infection courts. Injury to these tissues probably increases the rate of successful infection. Biotic factors, particularly subterranean termites and other insects, are probably important both in causing injury and in transmission of the pathogens (Anderson, 1961 (b)); Thapa, 1968; Panzer, 1975).

Direct root transmission without an insect vector may also occur. This mode of transmission has been described for the spread of *Fomes annosus* in temperate conifers (Hodges, 1970). Mammalian injury is thought to be of minor importance in the MDF. The only significant human activity is the practice of blaze slashing along hunting and transit paths. This minor form of damage is mostly confined to ridge crests, as these are the preferred lines of pedestrian access in the Sarawak MDF.

The intraspecific regression results show that stemrot is more severe in shallow soils on steep slopes. This may be due to the higher probability of root or butt injury by mechanical agents on these sites. Root abrasion by stones is one possible mechanism, caused by the mass movement of a stony regolith or by wind pressure-induced root movement (J.R. Palmer, pers.comm., 1969). This form of injury is regarded as significant in the spread of stem cankers in *Maesopsis eminii* in Uganda (Ofong, 1974). Another possibility is that roots are more likely to be exposed to injury and atmospheric desiccation by surface wash on these slopes.

An alternative explanation for the slope effect on decay levels may be in the increased formation of reaction wood. Tension and compression wood are laid down as a response to mechanical stress, such as imposed by wind pressure, or asymmetric crowns on steep slopes. As noted above, this type of tissue is more susceptible to fungal infection than normal wood (Section 3.2.3).

As noted in Section 2.2.3, landslips are thought to be a significant contributor to landscape evolution and to tree mortality in some areas of the MDF. Dryness (1967) has suggested that highly localised ground loading by the mass of very large trees may predispose the regolith to mass movement. If this factor is important, hollow decay can be seen as an advantageous adaptation to these conditions, as it reduces the mass of the stem by dispensing with the inert pith material. It may be that the reduction in landslip hazard offsets the slight reduction in the mechanical strength of the stem.

CHAPTER 8

GENERAL DISCUSSION AND CONCLUSIONS

Introduction

The results of the two parts of this study have been described and discussed separately in Chapters 6 and 7. The aim of this concluding chapter is to integrate the results as far as possible, to interpret them in a wider ecological context, and to consider their practical implications.

Synopsis of Results

Before proceeding with interpretation, the main general findings are listed below. More details of individual and specific effects, and the methodological reservations are given in the relevant sections of Chapters 6 and 7.

(a) The factor analyses of the site data arrays objectively extract large numbers of factors (Sections 5.2.1.1, 5.3.2.1 and 5.3.3.2). The detailed results of the factor analyses depend on the input variables used and the range of soil types sampled (Tables 6.1, 6.8 and 6.12).

Because of the differences in the input arrays, there are few common factors identifiable in the three sets of factor analyses.

(b) The first and most important factor extracted in all of the analyses has heavy loadings by soil parent material and reserve mineral nutrient variables. In the MDF ecological plots, which include soils from igneous as well as sedimentary rocks, reserve potassium loads on its own separate factor, and not on the first, general reserve nutrient factor (Tables 6.1 and 6.8). In the FIDP plots, which are restricted to sedimentary parent materials, reserve potassium is included in the first factor, but reserve magnesium is separately loaded on to its own factor (Table 6.12). The other factors that are more or less common to all three sets of analyses are those with loadings by topsoil organic matter, topographic, and soil depth variables.

(c) Analyses of variance of the plot factor scores show that there is highly significant spatial clustering of site properties (Tables 6.3, 6.14 and 6.15). The degree of clustering is highest for factors loaded by variables closely related to the soil parent material. These include soil texture and reserve mineral nutrients, as well as actual parent material properties. The factors loaded by topographic, soil organic matter and exchangeable cation variables are less clustered and have greater local variability (Sections 6.2.1.2 and 6.3.2).

(d) Discriminant analyses, starting from objective floristic groupings of the MDF ecological plots, and using the 1963-66 site data, show marked association between the distribution of the floristically defined forest types and site conditions. Site properties related to soil parent material are the most significant discriminants, whether factor scores or the original raw site data are used. However, it is not parent material itself, or the general reserve nutrient factor that are the most important. They are consistently outranked by the variables or factors related to the contents of free iron and aluminium oxides, and also by soil pH. This combination suggests that soil labile aluminium may be important (Section 6.2.2.2, Tables 6.10 and 6.11).

(e) Similar discriminant analyses using the 1971-72 site data from a small but wide-ranging sample of the same plots also show a high degree of association between forest floristic composition and site conditions. Site properties related to soil parent material are again important. In this case, the general reserve nutrient factor is highly significant. Reserve levels of potassium and, less consistently, of phosphorus are also significant (Section 6.2.13, Tables 6.6 and 6.7).

(f) The FIDP plot results show that the distribution of many common tree species can be related to site conditions. The limiting site properties vary widely between species. All of the ten site factors are critical in the distribution of one or more of the 39 species examined. Similarly, most of the species are selective with respect to at least one site factor (Tables 6.19 and 6.21). In general, site properties related to soil parent material are more influential than variable characteristics that are affected by local forest processes (see 8.3.2 below). However, the first, parent material and general reserve nutrient factor is generally less influential than the minor factors loaded with individual nutrients. Factors related to soil magnesium levels are particularly important (Section 6.3.4, Tables 6.19 - 6.24).

(g) Soil depth is the most significant morphological property in species distributions. Topographic position appears to be generally unimportant (Table 6.25).

(h) The plot-wise multiple regressions of total forest basal area parameters against site variables are distorted by a sampling bias. This gives rise to a large and artificial locational effect (Table 6.17). The non-locational site factors appear to be of minor importance. There is a slight tendency for basal areas to be higher on ridge crest sites, with soils of coarse texture and low reserve base levels. Reserve phosphorus has a weak and inconsistent positive effect (Section 6.3.3, Tables 6.16 and 6.17).

(i) Individual species basal areas are generally more affected by site conditions than is total forest basal area. The species basal area regressions and the species distribution results differ in their ranking of species for site sensitivity. For individual species they also differ in the ranking of influential site variables. The significant site factors vary considerably between species. In general, factors related to the more variable site properties such as organic matter and exchangeable cations are more important influences on species basal areas than on distributions (Section 6.3.5, Tables 6.25 and 6.26).

(j) The buttrot frequency results show that there are considerable differences between genera, timber groups and species (Section 7.3, Tables 7.3 - 7.8 and Figures 7.1 and 7.2).

(k) Within individual species, considerable site effects on stemrot severity are apparent, once the tree size effect is allowed for (Table 7.10). In general, the variable site properties, such as soil organic matter, exchangeable cations and depth are more significant than those more directly related to soil parent material. In most of the species examined stemrot tends to be more severe on shallow and infertile soils (Section 7.3 and Table 7.11).

(l) The stemrot severity data for the forest as a whole are suspect because of the very small sampling unit. Stemrot severity in the forest as a whole appears to be less affected by site conditions than in individual species. The more variable site properties are the most significant, although less so than in the regressions for some individual species. Total forest stemrot severity is slightly higher on more fertile soils (Sections 7.2 and 7.5, Tables 7.1 - 2).

8.3 Ecological Interpretation of Results

8.3.1 Niche Considerations in the MDF

Before proposing a general model of MDF site relationships, some general points need to be considered.

The first is the validity of the concept of multiple separate niches in the MDF. In the literature there appear to be some doubts about the existence of large numbers of separate niches in the tropical rainforest. These doubts may be partly due to oversimplification of the rainforest environment. This is a problem that has been discussed in general terms by Pianka (1976). He showed that if the environmental hyperspace is of few dimensions, the high linear overlap of species ranges on any single environmental axis that is inevitable in a species-rich community must imply considerable niche overlap. However, in a complex, multi-dimensional environment, there can be considerable linear overlap between species ranges on each axis taken separately, without precluding a high degree of niche separation in environmental hyperspace (Parrish and Bazzaz, 1976).

There are also reservations about multiple niches because the many different species in diverse plant communities appear to have broadly similar trophic requirements. Grubb (1977) suggests that, during most of the vegetative parts of their lives, many species do have very similar environmental needs, so that there is considerable niche overlap. However, niches may shift with ageing or phenological change. Grubb suggests that for part of their lives, particularly during reproduction, otherwise overlapping species may have distinct environmental demands, so that their whole-life niches are quite separate. The environment will have its greatest effect on interspecific competition during these phases of niche divergence.

These theoretical considerations suggest that multiple distinct niches are feasible in species-rich plant communities. The project results show that numerous niches exist in the MDF environment, and that many of them are filled.

An important feature of the MDF site data factor analyses is the large number of factors objectively extracted (8.2 (a)). This shows the multidimensional complexity of the MDF edaphic environment and its potential to contain many niches. The individual species distribution results show that many of these are exploited by edaphically restricted and adapted species (8.2 (f)). The results of the discriminant analyses confirm this, as they show that recurrent associations of species are consistently restricted to limited parts of the range of site conditions sampled (8.2 (d) and (e)).

Although useful, the idea of multiple separate niches cannot be too rigidly applied in the MDF. It is not thought that all of the 2,000 odd tree species have separate niches. There are undoubtedly cases of complete or partial niche overlap. The project results show that there are also species which are edaphically more or less indiscriminate (8.2 (f)).

Even for adapted species, the niche is not visualised in terms of rigidly exclusive limits on distribution. As discussed in Section 2.1.2, the recruitment of an individual stem into the upper canopy of the MDF is the end result of a complex process, at several stages of which probability plays a major part. For a highly adapted species, the niche is seen as a zone in environmental hyperspace, in which site conditions significantly increase the probability of eventual recruitment. Non-adapted species are those in which probabilities are more or less equal throughout environmental space. This view of the niche means that even highly adapted species are able to occur beyond their normal niche limits, although the probabilities of such occurrences are low.

The important role of chance in recruitment also means that any delineation of a niche type may lack some of its potential complement of adapted species. This may be due to the lack of a nearby source of seed, or because of chance destruction of regeneration.

Spatial exclusion may also cause some floristic deficiencies in niche delineations. Individual niche areas may be limited in broken terrain, such as in much of upland Sarawak. Given the large size of the mature trees, such delineations may be able to accommodate only a few stems. Lack of space may exclude the other site-compatible species.

Because of the poor dispersal of the dipterocarps, floristic deficiencies of individual niche delineations in the MDF tend to be self-perpetuating, unless there is a nearby seed source to take advantage of recruitment opportunities that arise.

8.3.2 Time Scales in the MDF

Soil depth is the topographical/morphological site property that has most influence on species distributions (8.2 (g) and Table 6.23). It also has important effects on intraspecific variation in stemrot severity (8.2 (b)). Soil depth partly determines the soil's total available moisture capacity, and therefore the frequency and severity of moisture stress (Baillie, 1976 (a)). However, in these results, and in the MDF in general, soil depth is interpreted mainly as an indicator of relative erosion rates and site stability.

Theoretically, site stability is a factor in the dynamics of all terrestial plant communities. In many, however, the biological processes proceed much more rapidly than geomorphological change, so that site changes are negligible in the lifespans of individual plants, and probably only of minor importance for the community (Birkeland, 1974). This may not be true for high forest communities, particularly those in unstable landscapes.

In the Sarawak MDF, many individual trees grow for more than a century, and a few may live for more than 500 years (Cousens, 1965; Poore, 1968). These trees are growing in an environment in which pedological and geomorphological processes are proceeding rapidly.

If Haile's (1968 (b)) estimate of 0.5 mm for the mean annual attrition rate of the upland Sarawak landscape is of the right order, the preponderance of sola less than one metre deep implies that profiles may be completely truncated every 1,000 - 5,000 years. Thus the edaphic environment of a mature tree may change significantly within its lifetime. Even the local geomorphology of a site may change perceptibly within the span of a few generations of trees. Thus the biological, pedological and geomorphological time scales of the MDF are more compressed together and of more equal magnitudes than in most other ecosystems.

The rapid rate of profile truncation and renewal means that some site characteristics vary considerably with time. Properties related to the underlying parent material will be relatively unaffected, and are likely to be fairly constant. Properties related to forest processes and pedogenetic maturity are likely to be more ephemeral. The project results show that the soil organic matter, exchangeable cation and depth characteristics have high local spatial variability (8.2 (c)). This is probably paralleled by rapid variation in time.

Rapid profile truncation means that fresh parent material is constantly being exposed to weathering. Continuous and rapid weathering in shallow soils leads to a constant release of mineral nutrients within the rooting depth of the forest. Some of the parent materials are nutrient-poor polycylic sediments. Together with the probably large losses of the released nutrients to leaching or mass movement, this suggests that the amounts of nutrients entering the soil may not be large. It is clear from the analytical data for these soils (Table 2.4), that these nutrients do not remain for long in available and vulnerable forms. It is probable that some, at least, are taken up by the vegetation, so intensity between forest types and species. Individual trees can have perceptible effects on the chemical properties of the soils in their immediate vicinity. This has been shown in temperate forests (Zinke, 1962; Gersper and Holowaychuk, 1971) and in tropical plantations (Kang, 1977). No similar detailed studies in tropical rainforests are known, although Ashton (1964 (a)) noted localised bleaching of albic horizons in assocation with the litter of *Dryobalanops aromatica* in Brunei.

Interspecific differences in the chemical effects so far described are of degree, rather than type. There is also the possibility of highly specific chemical modification of the environment by individual trees, through the secretion of phytoalexins. These are compounds that are released in minute quantities by some higher plants. They have marked antibiotic effects on other nearby plants, of the same or different species (Deverall, 1971; Ingham, 1972). Phytoalexis has not yet been confirmed in the MDF, but is probably of some importance. Phytoalexic effects against regeneration of the same species have been noted in *Grevillea robusta*, a subtropical rainforest tree in Australia (Webb et al., 1967). These and similar compounds may also affect the microbial population responsible for litter decomposition, and thus indirectly affect soil organic matter and available nutrient levels.

In addition to these chemical effects, forest processes affect soil morphological and physical properties and site topography.

In the results soil depth is generally the morphological site property with most effect on the forest (8.2 (g) and (k)). It is thought this effect is reciprocated, and that MDF forest processes considerably influence variation in erosion rates, site stability and, hence, soil depth. Similar effects probably operate in many terrestial plant communities, but are much intensified in high forests, particularly those in unstable landscapes such as upland Sarawak.

This is partly due to the large size of the individual plants. Unlike herbaceous plants, the death of individual trees can cause considerable local disturbance of the soil, by uprooting and the subsequent infilling of the rootstock cavities (Furley, 1975). In the MDF and other tropical rainforests this effect is magnified by the tendency of large treefalls to drag down neighbouring, non-moribund stems, because of the intermeshing of their crowns by climbers (Strong, 1977).

As discussed in Section 7.4, the large size of individual trees can influence erosion rates, by increasing the landslip hazard on some sites.

The forest may also increase local erosion rates by concentrating precipitation and surface wash by stemflow. However, intensification of surface wash downslope of large trees is not conspicuous in the MDF.

As noted above (8.3.2), the site properties most affected by forest processes tend to be variable in space and time. This is because the processes described vary mostly at single tree scale, and are therefore highly localised and of relatively short duration.

8.3.4 A Model of MDF-Site Relationships

By combination of the project results (8.2) and the general considerations above (8.3.1 - 3), it is possible to propose a provisional model for MDF-site relationships.

The MDF and its edaphic environment are visualised as a nest of envelopes of diminishing variation. The image of an envelope is used to convey the impression of wide amplitudes of variation on some axes and narrow ranges on others.

The constraining axes of the outer, major envelopes are related to the soil parent materials. Site properties that vary relatively little within the geologically-determined envelopes include texture, reserve nutrients and free iron and aluminium oxide levels (8.2 (c)). The forest characteristics more or less constrained by the site's geology are those related to floristics. These include the overall floristic composition of the forest, and the distribution of many of the common and important species (8.2 (d) - (f)). Because of the role of chance in determining floristic composition (8.3.1), these forest characteristics vary more than the lithomorphic site properties.

Other site and forest characteristics can vary widely within the main geological/floristic envelopes. The variable site properties include soil organic matter, exchangeable cations and some profile morphological variables, particularly soil depth (8.2 (c)). The forest characteristics include some finer floristic variation, physiognomic and growth parameters, and hollow decay.

Because of the wide variation possible for these characteristics within the main envelopes, there can be considerable overlap between envelopes. However, the overlap is not complete, because the site geology does impose some limits. The weathering of the soil parent material is the ultimate source of the cycling mineral nutrients. The parent material content of these nutrients and their rate of release by weathering therefore somewhat constrict the range of variation of soil exchangeable cation, available phosphorus and organic matter levels. Similarly, the wide local variation in the physiognomy and hollow decay of the forest is more or less constrained by local floristics, which are in turn influenced by site geology.

There is considerable covariation of these variable and ephemeral site and forest characteristics within the main geological/floristic envelopes. For instance, stemrot severity, within species and in the forest as a whole, is related to the more variable site characteristics (8.2 (m) and (l)). Basal area variation within species is also partly related to these site properties (8.2 (i)). This covariation is visualised as a series of subordinate envelopes with each major envelope. The site and forest axes of most restricted variation in these minor envelopes may differ from those of the main ones, so that the nested envelopes analogy is not completely apposite. The major envelopes are probably fairly fixed in space because of their relationship to the local geology. The minor envelopes are thought to be nomadic and able to move around, over long time spans, within the confines of the major envelopes.

The role of topography in limiting this movement is problematical. The factor analysis of the 1971-72 MDF ecological plot site data shows moderate catenary trends in soil pH and organic matter characteristics (Table 6.1). No such trends are apparent in the factor analysis of the 1963-66 site data from these plots (Table 6.8). There are no marked catenary trends apparent in the factor analysis of the FIDP plot site data, even for the exchangeable cation variables (Table 6.12).

Topographic position does not appear to have much influence on forest characteristics either. The MDF ecological plot discriminant analyses show that topography is unimportant in determining the distribution of floristically defined forest types (Tables 6.6 and 6.10). The topographic position factor influences the distribution of only 7 of the 39 species examined individually in the FIDP plot analyses (Table 6.19). Taking all species together, topography is among the least important site characteristics in the determination of distributions (Table 6.23).

Topography is a little more influential on forest physiognomic and growth characteristics, but it is still not a major factor. The topographically loaded factor makes significant contributions to the total forest basal area regression functions, but these are small and account for less than 2% of the total variance (Table 6.16). For the individual species basal areas, the topographic factor contributes in a significant but inconsistent and minor way to the regression functions of two of nine species tested (Tables 6.25 and 6.26). The topographic factor makes no significant contribution to the regression of total forest stemrot severity (Tables 7.1 and 7.2). The forest characteristic apparently showing the most marked topographic effect is the variation of stemrot within individual species. The topographic factor contributes significantly to the regression function of four of the nine species examined (Tables 7.10 and 7.11). However, it is thought that it is the slope angle loading on the same factor, rather than topographic position itself, that is important in these results.

This apparent lack of topographic effects on forest variation contradicts earlier work and subjective impressions in the field. This disagreement may be more apparent than real. In upland Sarawak topography shows a high degree of lithological control (Section 2.2.2). This means that topographic change is often an indication of geological change. The project results indicate that it is the underlying geological variation rather than the superficial topographic change which is the main influence on forest variation. For example, in the ridge and vale landscape of upland Central Sarawak, the ridge crest soils are often derived mainly from greywacke, whilst the mid- and lower slope parent materials have substantial shale components. In this case the systematic forest variation from crest to lower slope is attributed to geological variation rather than topography *per se*. In terms of the proposed model, this landscape contains two or more major geological/floristic envelopes, rather than a single envelope in which topography is a major influence on forest variation.

The covariance of topography and geology in upland Sarawak accounts for some of the marked forest effects previously attributed mainly to topography, (e.g. Brunig, 1969 (b)). It may also account for the apparent importance of topography in some of Ashton's (1964 (a) and 1973) single-site studies. In much of Sarawak the distinction between direct and indirect topographic effects is academic. It may, however, be significant in lithologically homogeneous areas, such as the outcrops of some of the Baram Group shales of North Sarawak or the Mesozoic shales of West Sarawak.

Because of its effects on soil moisture and aeration, topography is still thought to be of some ecological importance in the MDF, despite the lack of consistent and convincing evidence in the results. This contention gets support from some of Ashton's (1973) single-site studies, where confounding with geological variation cannot always account for the apparent importance of topography. There are also some results from dipterocarp forests in West Malaysia in which topography appears to have an effect on forest independently of geology (e.g. Burgess, 1972; Whitmore, 1973; Ashton, 1976 (a)).

It is clear from the results and the derived model that a single value for the relative proportions of the forest variance that can be attributed to edaphic and non-edaphic sources is meaningless. Not only will the figure vary with the forest parameter considered and the site data available, but also with the range of site and forest types sampled. Because some of the non-edaphic sources of variation are scale-neutral, their relative contributions will tend to increase as the sample range is narrowed. Even within specified ranges, the present results are too incomplete and inconsistent to permit useful estimates. It is clear, however, that the edaphic contribution remains substantial, even for very restricted sampling ranges.

8.4 Practical Implications of Results

8.4.1 Silviculture

These studies were conducted in unexploited virgin forests, which have very uneven age structures and high floristic diversity. After exploitation, the second and subsequent rotation forests will be of simpler age structure and lower floristic diversity. There will be higher proportions of the light-tolerant and faster growing species that are characteristic of the building stages of forest development (Whitmore, 1975. Medium density timber species such as keruings *(Dipterocarpus spp.)*, kapurs *(Dryobalanops spp.)*, and yellow and light red merantis *(Shorea spp.)* will be more frequent than in virgin forests. The project results of most direct silvicultural interest are therefore those relating to likely performance of these species. However, site relationships in virgin forests can give only rough indications of site effects on potential productivity in post-exploitation stands.

Current MDF silviculture is basically a uniform system, and relies entirely on natural regeneration for the stocking of the post-exploitation stands (Wyatt-Smith, 1961 (a); Whitmore, 1975). The protection and encouragement of the existing regeneration is the aim of the silvicultural operations. At present no account is taken of site conditions.

The present results show that many of the commercial species have edaphically restricted ranges in the virgin forests (8.2 (f)). It seems a reasonable assumption that these species will be at their most productive in similar edaphic ranges in the post-exploitation stands. It will therefore be beneficial to concentrate the regeneration of these species onto suitable sites, as far as is possible.

For many species the ranges are determined mostly by lithomorphic site properties (8.2 (f)). These tend to be of low local variability (8.2 (c)). Combined with the generally poor dispersal of the dipterocarps, this suggests that the regeneration of these species, such as *Dipterocarpus acutangulus*, *D. caudiferus*, *Dryobalanops aromatica*, *D. beccarii*, *Shorea macroptera* and *S. superba*, is likely to be naturally concentrated mainly on suitable sites. The species basal area regression results suggest that there may be some local variation in the productivity of these species within these lithomorphically determined ranges (8.2 (i)). The important site characteristics tend to vary over short distances (8.2 (c)). It is probably impracticable to take silvicultural account of these differences. For these species, therefore, the current silvicultural procedures appear quite adequate in geologically homogeneous areas.

There are other species, including the commercially important *Dryobalanops oblongifolia* and *Shorea parvifolia*, that have ranges largely determined by site characteristics such as soil depth and organic matter levels (Table 6.24). These properties have greater local variability than those related to soil parent material (8.2 (c)). The regeneration of these species is therefore quite likely to occur on unsuitable sites. Theoretically it is desirable to treat these species as weeds on the unsuitable sites, as long as there is ample regeneration of more site-compatible species present. In practice, the short range variation of the critical site characteristics will make site assessment laborious and probably impracticable.

Discussion has so far been concerned with geologically homogeneous areas. In landscapes of rapid geological change, regeneration is more likely to be naturally dispersed to unsuitable sites. In this case, the results in Table 6.24 may prove useful. For example, species such as *Dipterocarpus acutangulus*, *Dryobalanops aromatica*, *Shorea faguetioides* and *S. superba* are species apparently adapted to sites of low mineral nutrient status. In the ridge and vale landscape of Central Sarawak, they appear to be more or less restricted to the deep and infertile sandstone soils. They therefore tend to be concentrated on ridge crests. Their fruits may easily be dispersed downslope to unsuitable sites. If there is ample and mixed regeneration on the more fertile shale soils of the lower slopes, the ridge crest species should be silviculturally treated as weed species.

The stipulations about ample and mixed regeneration are important. Without it, there is no possibility of edaphically refining a uniform silvicultural system. In fact, preliminary results cast doubts on the suitability of uniform system silviculture in the Sarawak MDF. Post-exploitation regeneration appears to be sparse and uneven. In part, this can be attributed to logging damage (Lau, 1975; Lee, 1972 (c)). This form of damage can be reduced by more controlled logging operations, particularly as the intensity of extraction is less than in some other dipterocarp forests (e.g. Nicholson, 1965). However, logging damage is likely to increase as operations are extended into the MDF of the more rugged terrain of the interior.

If poor regeneration proves to be a widespread problem, it may be necessary to consider augmenting it with some form of planting. If indigenous MDF species are considered, the individual species site restrictions summarised in Tables 6.19, 6.21 and 6.24 should provide useful indications of the best species/site combinations to try.

However, plantation with indigenous species may be hazardous. The planted material will generally be out of synchronisation with the natural, irregular fruiting pattern. It will receive the full attentions of the local pest and disease populations (Janzen, 1970). If well-grown seedlings are planted, some of these hazards will be much reduced. The introduction of suitable exotic species might also be considered and tested.

The possibility of adjusting site conditions to forest requirements rather than *vice versa* is also a possibility. It is thought to be rather far-fetched at present. If it should ever be considered seriously, the present results indicate that many species are most responsive to variation in lithomorphic site characteristics. These properties tend to be less amenable to alteration by management, so that the possibilities for these species are limited. However, some species do respond to manageable soil properties. For example, the productivity of *Shorea parvifolia*, the most important red meranti species of Central Sarawak, may well increase with phosphatic fertilising. Similarly, *Dipterocarpus caudiferus*, an important keruing species, may respond positively to dolomitic lime.

Before discussing the practical implications of the site conditions-hollow decay results, it should be re-emphasised that they were obtained from virgin forest data. Decay relations in the younger and less diverse post-exploitation stands will probably be considerably different. Because of the absence of old, over-mature stems, the probability factor in infection will be reduced. However, the higher densities of the commercial species may increase the infection hazard. Massive infections in artificially simplified populations of tropical rainforest species have been noted in Brazilian rubber (Sioli, 1973), and in *Acacia catechu* in India (Bakshi et al., 1976).

If hollow decay does prove serious in the post-exploitation stands, the present results suggest that the best way of controlling it is by adjustment of the forest floristic composition. If possible, the proportion of non-susceptible species, such as most keruings (*Dipterocarpus spp.*) and *Dryobalanops lanceolata*, should be increased (Tables 7.3 - 7.8).

This is possible only in the early stages of the rotation, and as long as there is regeneration of the desired species present. For a stand in which such floristic alterations are not possible, the results suggest that site management may possibly reduce the severity of stemrot. If *Dipterocarpus caudiferus*, *Dryobalanops aromatica*, *D. oblongifolia* and *Shorea sagittata* are important, phosphatic fertiliser might reduce the decay hazard (Table 7.11). However, if *Shorea parvifolia* is present, such fertiliser application may actually increase the decay risk. If *Dryobalanops aromatica*, *D. oblongifolia* and *Shorea collaris* are present, calcitic liming might be beneficial.

.4.2 Natural Resources Assessment

The possible use of ascertained soil-forest relationships to increase the precision of MDF forest inventory and soil survey is among the project objectives listed in Section 1.2.

The current MDF inventory procedure involves stratified ground sampling of photogrammetrically determined terrain and forest classes (Brunig, 1969 (b); FIDP, 1974 (b)). The terrain classes are topographically defined and delineated. As topography and geology are closely related in upland Sarawak, the terrain classification more or less distinguishes between the main soil parent material types.

The project results show that lithomorphic site characteristics predominate as determinants of gross floristic variation (8.2 (d) - (f)). The results therefore generally vindicate the current procedures. The air photograph interpretation should perhaps have a more consciously photogeological basis (Brunig, 1969 (b)). As much attention should be given to variation in the forms of landscape dis-section as to its intensity (FIDP, 1974 (b)).

The results show that there is some edaphic covariation with the finer floristic and physiognomic variation in the main geological/floristic delineations (8.2 (f), (h), (i), (k) and (1)).

At present it does not appear that this covariation can be practically applied to increasing the precision of routine MDF inventory. The proportion of non-edaphic forest variation is unknown, but is certainly substantial. The covariation tends to operate at highly localised scales. Finally, many of the important site characteristics are chemical, e.g. the role of exchangeable magnesium in distribution of many species (Tables 6.19, 6.21 and 6.24). At present variations in these site characteristics cannot generally be detected photogrammetrically or in the field, and laboratory analyses are required. It will usually be more economical to increase the intensity of ground enumeration in the inventory than to get involved in the gathering of soil chemical data for inferential purposes.

The exception to this is where forest inventory happens to be preceded by a soil survey. The project results indicate that it should then be possible to increase inventory precision using soil analytical data. For example, data on exchangeable magnesium levels will indicate which of *Dipterocarpus acutangulus* or *D. caudiferus* is likely to be more important amongst the keruings. Similarly, data on topsoil reserve phosphorus levels should indicate the likely proportions of *Shorea parvifolia* and *S. quadrinervis* in the light red merantis (Table 6.24).

There is probably some scope for the use of MDF variation as an aid to soil survey and land assessment. The main floristic divisons are related to soil parent materials. These are obviously very important in soil survey. In general though, they are likely to be inferred directly from field observation, photogeological interpretation and previous geological survey data, rather than indirectly from forest characteristics.

There are three main problems in using the finer site-forest covariation within the main geological/floristic delineations for the prediction of soil and land characteristics.

Firstly, the present state of the art does not enable finer floristic variations in the MDF to be distinguished by aerial photographic interpretation. This is shown by the results from the MDF experimental inventory blocks in the Bck-Tisam P.F. (Ashton, 1973). This means that, at present, much of the floristic variation can only be ascertained from ground enumeration data.

The second problem is the unknown, but substantial, proportion of independent site variance. This lessens the precision of prediction of site characteristics from forest data, and makes ground checking essential.

The final problem is the nature of the site information that can be inferred from forest characteristics. The project results show that many forest characteristics are more or less related to soil chemical properties, particularly magnesium and phosphorus levels (8.2 (d) - (i), (k) - (l)). The relationship with some site physical and morphological characteristics such as finer textural variation, drainage and slope angle is less close. These site characteristics can therefore be less precisely predicted from forest data. However, these characteristics are very important in the determination of agricultural land capability, because they are less amenable to alteration by management than chemical deficiencies or imbalances (Montgomery and Klingebiel, 1960; Riquier, 1974). This is true even for land evaluation systems devised particularly for the generally physically favourable and chemically deficient soils of the humid tropics (Smyth, 1966; Sys and Frankart, 1971).

For these reasons it is unlikely that inference of site characteristics from forest data can be more than a useful supplement to conventional soil survey. The long term economic and social consequences of poor land evaluation in the planning of agricultural development can be very serious. For this reason alone direct observation of site characteristics is unlikely to be greatly reduced.

If a soil survey is preceded by a forest inventory, the project results show that detailed data about the distributions of some species can yield useful supplementary information on the chemical nature of the soils. Inspection of Table 6.24 suggests that congregations of *Dipterocarpus acutangulus, Dryobalanops aromatica, Shorea faguetioides* and *S. macroptera* indicate soils of low magnesium status. An abundance of *Dipterocarpus caudiferus* is indicative of relatively high magnesium status. *Elateriospermum tapos* and *Dryobalanops oblongifolia* are characteristic of sites with low topsoil organic matter contents. *Elateriospermum tapos* again, and *Shorea parvifolia* show that reserve phosphorus levels in the topsoils are quite high. *Shorea quadrinervis*, on the other hand, is indicative of poor reserve phosphorus status.

Although the results do not indicate major changes in current forest inventory or soil survey procedures, they do show the value of a free exchange of detailed information. At present natural resource assessment tends to be compartmentalised. Closer cooperation, both in the field and in interpretation, will be mutually beneficial.

8.4.3 Land allocation

The results show that individual species respond more to site variation than does the forest as a whole. This is true for basal area and for stemrot severity (8.2 (h) and (i), 8.2 (k) and (l)). Individual species also show considerable site influence on their distributions (8.2 (f)). If there was a wide price differential between various MDF timbers, the results would indicate considerable site variation in economic forestry potential. At present, however, the emphasis is on maximum outturn of mixed timber. The project results suggest that the intersite differences for this kind of forestry are not large. At present there does not seem to be any need to allow for major differences in forestry potential in intersectorial land allocation. However, Ashton's (1973) preliminary results did show significant site differences in overall forest productivity. The negative conclusion must therefore remain tentative at present. If market conditions alter in the direction of marked preferences for individual species, the situation will change considerably.

8.5 General Conclusions

The project was conceived in an opportunistic way, particularly with respect to sampling design and the collection of forest data. It has produced many interesting results, interpretation of which is by no means complete. The results contain inconsistencies and contradictions. Many of these are due to methodological shortcomings, but some are due to the inherent complexity of the MDF ecosystem.

The practical implications of the results are discussed in the previous section (8.3). In general, the results do not point to immediate major alterations of the current procedures in MDF silviculture, forest inventory or soil survey. However, the results do generate many ideas for further research.

From an economic viewpoint, the priority for completely new studies should be in the post-exploitation forests. These are going to be the long term productive MDF resource. The influence of site conditions on their management and performance is going to be of major practical importance. Possible lines of investigation include the influence of site conditions on regrowth under uniform silvicultural management, possibilities of differential silvicultural management according to site conditions, and the effects of site modifications such as liming or phosphatic fertilisers on timber yield and quality. Other possibilities include the effect of species density and stand age on infection by timber rot pathogens, and the differential effect of site conditions.

Investigations should also continue in undisturbed natural forest. As well as its intrinsic scientific value, research in natural forest will help to clarify some of the influences and processes operating in post-exploitation stands. Some of the work in natural forest will be the continued analysis of existing data. An example of this is the further analysis of the 1963-66 MDF ecological plot data, carried out by Mr. C. Legg in 1978. This is reported separately. However, there is also a need for new studies to be initiated and new plots established, particularly in areas where security of tenure permits long term dynamic studies to be carried out.

Despite its shortcomings, it is hoped that the present project will provide a coherent continuation of earlier work, and a useful starting point for future studies.

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APPENDIX I

LABORATORY ANALYSES

A.1.1 Methods

The chemical and physical analyses, except for the measurements of stone content and the coefficient of linear expansion (COLE), for all of the soil samples collected during the project were carried out in the Chemistry Laboratory of the Sarawak Department of Agriculture's Research Centre at Semongok. The methods currently employed in this laboratory are as described in detail by Sim (1965), except that the sodium, potassium, calcium and magnesium contents of soil extracts are now determined by atomic absorption, rather than by flame emission photometery or EDTA titration.

The following is a brief summary of the methods used.

Soil pH is measured with a Pye pH meter in a 1:2.5 soil: water suspension that has been standing overnight.

Moisture content is measured gravimetrically by overnight drying at 105^{o}C.

Organic carbon is measured by the Walkley and Black method, in which the soil organic matter is oxidised by acidified potassium dichromate, followed by titration against acid ferrous sulphate to determine the unused dichromate.

Total nitrogen is measured by a semi-micro Kjeldahl method of acid digestion, steam distillation after the addition of caustic soda, and titration of the evolved ammonia against hydrochloric acid.

The reserve nutrients are extracted with boiling concentrated hydrochloric acid after 30 minutes dry ignition at 800^{o}C.

Reserve phosphorus is determined by the method of Fogg and Wilkinson, which involves the colorimetric measurement of the blue complex formed with acid ammonium molybdate, with ascorbic acid as the reductant.

The Group III oxides (mainly iron and aluminium) are determined by precipitation from the reserve nutrients soil extract by the addition of ammonium hydroxide.

After the removal of the Group III oxides, the reserve bases are determined by atomic absorption on the diluted filtrate.

The exchangeable ions are extracted by leaching the soil with approximately normal ammonium acetate, buffered to pH7. The bases in the extract are determined by atomic absorption.

Cation exchange capacity is determined by removal of the exchangeable ammonium from the leached soil, by the addition of caustic soda and distillation. The distilled ammonia is titrated against hydrochloric acid.

Granulometric composition is determined by the pipette method, after soil pre-treatment with hydrogen peroxide and dilute hydrochloric acid. Dispersion is achieved by stirring and overnight shaking with soxium hexametaphosphate. The pipetting intervals used give upper and lower size limits for the silt fraction of 0.05 and 0.002 mm.

Particle density is determined by the pycnometer method, using locally available commercial kerosene as the non-polar liquid.

These are the routine analyses that were performed on soil samples collected during the present project. Mention has also been made of other determinations, particularly in Chapter 2. These include:

Available phosphorus was extracted by the method of Bray and Kurtz, using hydrochloric acid and ammonium fluoride. The phosphate content of the extract was determined colorimetrically, using ammonium molybdate, with stannous chloride as reductant.

There have been several sets of clay mineralogical studies of Sarawak soils, mostly carried out in Britain and Holland. X-ray diffraction and differential thermal analysis were the main methods used.

Thin section studies of the micromorphology of Sarawak soils have been carried out in Holland, Britain and Malaysia.

A.1.2 Discussion of Analytical Methods

The extraction of 'reserve' nutrients with hot concentrated hydrochloric acid is not a common practice nowadays. It is thought to be unduly disruptive of the exchange complex and to fall between the more commonly used extraction methods that are aimed at either the total or the readily available forms of the nutrients (Allen, 1974; Hesse, 1971). However, the reserve extraction has been found to be very useful in Sarawak, and its results agree better with plant uptake and crop yield studies than do the more conventional available or exchangeable levels (Bailey, 1966 and 1967). Other authors have also suggested that there is a place for this type of extraction in the analysis of the highly weathered and leached soils of the humid tropics (e.g. Young, 1976).

There has been considerable discussion about the methods of dispersion of these soils, prior to granulometric analysis. Because of the effective cementing action of pedogenic iron and aluminium oxides, the soils of the humid tropics are notoriously difficult to disperse. It may be that, in some cases, silt fractions are exaggerated because of poor clay dispersion. However, it has been argued that very severe dispersion procedures produce completely artificial results, that bear little relation to the aggregation, and therefore the physical behaviour, of the soil particles in field conditions (Andriesse, 1975). Andriesse suggests that minimal dispersion is more appropriate for most purposes and that complete dispersion is only necessary for mineralogical studies.

The determination of cation exchange capacity by distillation of the ammonium saturated soil with caustic soda may lead to inflated values if the soil contains substantial amounts of organic matter. This is due to the hydrolysis of nitrogenous organic compounds and the evolution of additional ammonia.

The results of the analyses must be interpreted in the light of what is known of tropical rainforest ecology and nutrition. The soil compartment of the rapid turnover biopedological nutrient cycle is probably better characterised by the available or exchangeable forms of the nutrients. The reserve extractions include nutrients that are only marginally and slowly participating in the nutrient cycle.

However, as discussed above (Chapters 6 and 8), the available forms of the nutrients are thought to vary rapidly in time and space, within parent material determined limits. This variability renders the determinations less useful unless very exhaustive sampling is undertaken. Therefore, for many agricultural and other edaphic purposes, the reserve forms are more informative. They do not indicate the instantaneous available nutrient status of the soil. However, they do show the size of the pool from which the available nutrients will be drawn, and hence the approximate level about which the available nutrient status will oscillate. Because of their relationship to soil parent materials, the levels of reserve forms vary less in time and space, and can therefore be satisfactorily characterised at lower sampling intensities.

Because of this, they were the preferred analyses, and were retained when it was necessary to economise on laboratory requirements in requesting soil analyses for the MDF ecological plot soil samples in 1971-72. It was unfortunate that Group III oxides were not included with the reserve nutrients in this request, as the pedogenic iron and aluminium oxides were later revealed to be of some importance as floristic determinants.

Considerations of lower variability also led to the specification of reserve nutrient determinations for the Brunei studies (Austin et al., 1972) and for the original 1963-66 site data for the Sarawak MDF ecological plots (Ashton, 1973).

APPENDIX II

SCIENTIFIC AND COMMON NAMES

The lists below include the species mentioned in the text and tables of this report. Species mentioned only in titles in the bibliography are not included. Common names are given only where they have been used in the text.

Scientific nomenclature is after Ashton (1964 (b) and 1968), Whitmore (1975), the Index Kewensis and supplements, and information supplied by the Commonwealth Mycological Institude.

A.2.1 PLANTS

A.2.1.1 Dipterocarps

Anisoptera grossivenia V. Sloot.	
Dipterocarpus acutangulus Vesque	Keruing
D. caudiferus Merr	"
D. conformis V. Sloot.	"
D. crinitus Dyer	"
D. globosus Vesque	"
D. mundus V. Sloot.	"
D. pachyphyllus Meijer	"
D. verrucosus Foxw. et V. Sloot.	"
Dryobalanops aromatica Gaertn. f.	Kapur
D. beccarii Dyer	"
D. lanceolata Burck	"
D. oblongifolia Dyer	"
Hopea dyeri Heim.	
Parashorea smythiesii Wyatt-Smith ex Ashton	
Shorea lamellata Foxw.	White meranti
S. ochracea Sym.	" "

Shorea collaris V. Sloot.	Yellow meranti
S. dolichocarpa V. Sloot.	" "
S. faguetiana Heim.	" "
S. faguetioides Ashton	" "
S. multiflora (Burck) Sym.	" "
Shorea albida Sym.	Red meranti Alan
S. amplexicaulis Ashton	Red meranti
S. argentifolia Sym.	" "
S. beccariana Burck	" "
S. curtissii Dyer ex King	Seraya (W. Malaysia) Red meranti (Sarawak)
S. ferruginea Dyer ex Brandis	Red meranti
S. leprosula Miq.	" "
S. leptoclados (= *S. johorensis* Foxw.)	" "
S. macrophylla (De Vriese) Ashton	Red meranti Engkabang
S. macroptera Dyer	Red meranti
S. mecisopteryx Ridl.	" "
S. myrionerva Wood ex Ashton	" "
S. parvifolia Dyer	" "
S. pauciflora King	" "
S. pilosa Ashton	" "
S. pinanga Scheff.	" "
S. quadrinervis V. Slcot.	" "
S. rubra Ashton	" "
S. sagittata Ashton	" "
S. scaberrima Burck	" "
S. slooteni Wood ex Ashton	" "
Shorea atrinervosa Sym.	Selangan batu
S. havilandii Brandis	" "
S. laevis Ridl.	" "
S. superba Sym. ex Wood	" "

A.2.1.2 Non-dipterocarps

Acacia catechu Willd.

Artocarpus anisophyllus Miq.	
Bertholletia excelsa Berg	Brazil nut tree
Casuarina equisetifolia J.R. and G. Forst	
Cryptomeria japonica L.	
Dacryodes excelsa Vahl	Tabonuco
D. incurvata (Engl.) H.J. Lam	
Elaeis guineensis Jacq.	Oil palm
Elateriospermum tapos Bl.	
Eperua spp.	Wallaba
Eucalyptus marginata Sm.	Jarrah
Eusideroxylon zwageri T. and B.	Belian
Gonostylus bancanus (Miq.) Kurz	Ramin
Grevillea robusta A. Cunn.	
Hevea brasiliensis (Willd. ex A.juss.) M.A.	Rubber
Imperata cylindra (L.) P. Beauv.	Lallang
Koompassia malaccensis Maing. ex Benth.	
Maesopsis emini Engl.	
Manilkara huberi (Ducke) Standley	Macaranduba
Milletia vasta Kosterm.	
More excelsa Benth	Mora
M. gonggrijpii Kleinhoonte	Morabukea
Ocotea radiaei (Schomb.) Mez.	Greenheart
Picea mariana Mill.	Black spruce

Pinus caribaea Mor.
P. elliottii Engelm.
P. taeda L. — Loblolly pine

Piper nigrum L. — Black pepper

Populus tremuloides Michx. — Trembling Aspen

Qualea rosea Aub. pl.Guin.

Santiria grandiflora Kalkman.

A.2.2 FUNGI

Botrydiploida theobromae Pat.

Fomes annosus (= Heterobasidion annosum, q.v.)

Heterobasidion annosum (Fr.) Bref.

Phytophtora cinnamomi Rands