SECONDARY PLANT SUCCESSION IN TROPICAL MONTANE MINDANAO

M.C. KELLMAN

**RESEARCH SCHOOL OF PACIFIC STUDIES
DEPARTMENT OF BIOGEOGRAPHY & GEOMORPHOLOGY**

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PREFACE

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Voucher specimens of plants named are housed in the Herbarium Australiense, CSIRO, Canberra, and the Department of Biogeography and Geomorphology, Australian National University, Canberra.

Simon Fraser University
Burnaby 2, B.C.,
Canada

M.C. Kellman

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INTRODUCTION

Secondary vegetation is today a prominent feature of humid tropical landscapes, and is rapidly replacing much primary, or at least "high", rain forest. Most of this vegetation until recently was probably exclusively the product of man's primitive agricultural activities, as the moist habitat makes the use of fire difficult without prior forest clearance. While today various systems of shifting cultivation are still responsible for the production of vast new areas of secondary vegetation, and the maintenance of these in an "early" secondary state, European man has done much to extend them. The abandonment of unproductive plantations has created extensive areas of this vegetation and, more recently, large scale logging operations have introduced a new type of secondary community to the landscape.

Despite its widespread occurrence, secondary tropical vegetation has received little attention in the literature. A concern among ecologists to concentrate upon the shrinking areas of primary forest together with the difficult working conditions in secondary tropical vegetation probably both contribute to this omission. Most mention of secondary vegetation in the tropics is in passing reference in publications mainly concerned with primary forest or with practical problems (e.g. Asprey and Robbins 1953, Beard 1945, Brown 1919, Brown and Mathews 1914, Wardlaw 1931, Whitford 1906). Even when observations have been more intensive (e.g. Burkill 1919, Clayton 1958, Greig-Smith 1952, Kennoyer 1929), the lack of micro-environmental measurements and an insufficiency of sites to enable the accurate interpretation of spatial variation in terms of a time sequence, have restricted the usefulness of the results. Unfortunately, the long-term observations of Symington (1933) in Malaya were prematurely terminated: it is to be hoped that those started by Anderson (1960) in Sarawak will not meet a similar fate. The work of Ross (1954) in Nigeria is the only published attempt to make micro-environmental measurements in secondary vegetation and to relate these to observed differences (and inferred changes) in the vegetation. These results, too, are restricted by an insufficiency of sites. With this paucity of detailed information, it is not surprising that accounts of this vegetation type (Richards 1952, Fosberg 1960, Kostermans 1960) have been very general.

Figure 1. Southeast Mindanao showing the location of the study area. Altitudes in feet.

This study attempts to provide more concrete information on secondary tropical vegetation. A research design at a level between the broad general survey of a large geographic area and an intensive examination of a single stand was selected, with the successional aspects included by sampling stands of a variety of ages in which other possibly influencing factors could be held constant or measured. The three major factors, other than age, that may possibly affect secondary vegetation are the source population of species, the environment and the type of human disturbance before site abandonment. Under field conditions it was found most practicable to hold the first two of these constant, by selecting stands that were in close proximity to each other, while assessing the disturbance variable by selecting stands sufficiently young to permit verbal reports of their histories to be used with some assurance. While this resulted in stands of no more than 27 years' age being sampled, the complex differences that existed in even such youthful vegetation provided ample scope for research.

The study area sought, therefore, was one in which environmental variation was minimal, which contained stands of a variety of secondary vegetation sufficiently small to permit adequate sampling in the time available, the site histories of which could be determined with some accuracy and which were, preferably, recovering from human disturbance only for the first time. Mindanao, the large southern island of the Philippine archipelago, was selected as a suitable region in which to locate such an area: pre-war reports indicated the existence there of large areas of primary forest, some native shifting cultivators and many new roads extending into unsettled areas. When the island was first visited by the author in early 1964, it was clear that extensive, and undocumented, changes had taken place in the post-war period. Most notable was a vast immigration of settlers to the lowlands and the consequent disappearance of much natural vegetation. Despite these changes a suitable area was found on the eastern slopes of the Mount Apo mountain massif on the western side of Davao Gulf in southeastern Mindanao (Fig. 1); further travel about the Philippines revealed that secondary vegetation was being increasingly restricted to such upland habitats.

Figure 2. Planimetric map of the study area derived from Plate 1.

GUMATE, THE STUDY AREA

The study area was situated in the Mount Apo massif which lies some 20 km west of Davao City ($7^{\circ}5' \text{ N}$, $125^{\circ}30' \text{ E}$) in southeast Mindanao (Fig. 1). The massif includes three distinct peaks: Mount Apo itself, the highest (2938 m a.s.l.) and most westerly, Mount Talomo (2674 m) 8 km to the northeast, and Mount Sibulan (1322 m) 18 km to the southeast of the main peak. The three peaks are separated by plateaux about 1000 m in altitude and the rugged upper slopes change to a broad (8-13 km) semi-circular fan of uniform slope stretching eastwards to the western shore of Davao Gulf (Plate 1, Fig. 2).

Gumate was not a recognised administrative unit but a term, probably recently, applied to the area surrounding a creek of this name. For present purposes it is used to describe the area covering the sampled vegetation stands. These extended roughly 2.6 km in an east-west direction and 1.3 km in a north-south direction, with altitudes varying from 870 m in the east to 1235 m in the west (Fig. 2, Table 1). There was considerable topographic variation within the area itself; the lower and more easterly portion consisted of broad interfluvies separated by deep gullies, while in the upper half topography became more rugged and many small streams flowed in deep valleys separated by steep-sided ridges. As a main reason for selecting an area of such limited extent was the hope that its environment would be uniform, an attempt is made below to assess this uniformity, especially in the light of the area's topographic diversity.

Geology

The whole mountain massif is thought to be composed of post-Tertiary volcanics, predominantly andesites (Smith 1908, 1911; Willis 1937) and in the study area this was the only type of bedrock seen. While Mount Apo itself shows signs of recent volcanic activity (fumaroles still exist at its summit), the two lower peaks seem to be of greater antiquity, both showing signs of advanced erosion. Most recent ejecta from Mount Apo appear to have been deposited westwards in the Kidapawan district (Pendleton 1942) and no convincing evidence of any eastward deposition was found in any soil pit at Gumate. The latter area thus seems to have experienced geologic stability for a relatively long period.

Table 1. Average altitudes, slopes and aspects of sampled sites

<u>Site (Stand)</u>	<u>Altitude (m)</u>	<u>Slope (%)</u>	<u>Aspect</u>
1	980	40-50	S
2	1000	10-50	S
3	970	30-35	SE
4	965	15	E
5	1085	35	E
6	1075	40	S
7	940	10	SE
8	980	45	SE
9	1030	30	SE
10	950	25	NE
11	925	45	S
12	1235	40	S
13	1185	30	S
14	950	12	E
15	870	14	E
16	885	17	E
17	1055	15	E
18	1030	35	SW

Climate

Southeast Mindanao experiences the high temperatures and lack of seasonal variation that are typical of the humid tropics. Although influenced by several air mass types, the region's rainfall régime also lacks seasonality (Fig. 3). According to Manalo (1965), eastern Mindanao experiences a northeasterly monsoonal air flow from November until March. This air mass is typically shallow and although producing abundant rainfall on the east coast at this time, does not have a comparable effect to the west of the low eastern mountain range. During the latter half of March or early April this northeasterly monsoonal circulation gives way to the northeast Trades which predominate during May and June and whose effects on rainfall extend westward over much of the island. A slight rainfall maximum is experienced at Davao City during this period. During the remaining summer months southeastern Mindanao experiences weak southeast Trades, the summer monsoon being effective only farther west. Rainfall at Davao City during this period is moderate and the slight peak in October is probably associated with the passage south of inter-tropical convergence zone. The region is comparatively free of cyclones and only 1% of those experienced in the Philippines before World War II affected Davao (Allied Geographical Section, Southwest Pacific, 1942).

At an elevation of 900-1200 m, Gumate lay slightly below a cloud cover which developed on most mornings and persisted until nightfall. Frequent slight falls of the cloud base resulted in periods of envelopment, a phenomenon that was a dominant feature of the day-to-day weather, reducing isolation and producing rainfall that was abundant and constant. A complete year's records of daily incoming short-wave radiation, maximum and minimum temperatures and rainfall were made at Gumate during the course of field work; monthly totals are shown in Fig. 4. Daily maximum temperatures were several degrees below those experienced in the lowlands but showed the same lack of seasonal variation; rainfall was nearly double the average for Davao City but likewise did not show distinct seasonal trends.

Monthly totals in incoming short-wave radiation are shown in Fig. 4; total energy income for the year was 127.8 kg cal/sq. cm. Despite

Figure 3. Monthly means of daily maximum and minimum temperatures and rainfall at Davao City during the post-World War II period, and during the period of field observations.

Figure 4. Meteorological records made in the study area during the year November 17, 1964 - November 16, 1965. Monthly totals of incoming short-wave radiation, monthly means of daily maximum and minimum air temperatures and monthly rainfall totals are shown.

the persistence of a dense cloud over the area, this figure differed little from the estimates made by Budyko (1958) and Landsberg (1961) for lowland Mindanao generally, namely 120-140 kg cal/sq. cm per year. This phenomenon is attributed to the combined effects of the altitude of the area and reflection from clouds when the sun shines through gaps in them; under partially cloudy conditions, radiation well above that experienced under clear-sky conditions was often experienced for short periods. Consequently, despite the heavy cloud cover, plants in the area received a similar energy input and faced the same heat transfer problems as plants at sea level. Because of the limited number of instruments available, no measurements of radiation variations within the area were made; some decrease doubtless existed from the lowest to the highest stands as a result of differing cloud thicknesses and frequencies but, as the eastern edge of the cloud blanket usually lay well beyond the lowest stand, this variation was probably small. The effect of differing aspects on radiation receipts was likewise probably slight as a high proportion of the total was all-directional diffuse radiation, equally available to all stands sampled.

Monthly averages of daily maximum and minimum temperatures are shown in Fig. 4. Daily maximum temperatures averaged 28.3°C and daily minimum temperatures 17.0°C , the absolute maximum and minimum recordings being 32.5°C (90.5°F) and 12.5°C (54.5°F). No temperature measurements could be made throughout the study area and free air lapse rates are of little use for estimating these. Actual maximum temperature differences are most closely related to differences in surface radiation balance, especially receipts if the albedo is constant, and the limited albedo data available from other areas (Budyko 1958; Davies 1962) suggests that this is fairly constant for surfaces with a complete cover of healthy vegetation such as existed in the study area. As radiation receipts in the area probably declined with altitude, it must be concluded that maximum temperature lapse rates there were somewhat higher than those found over the greater altitudinal range between Davao City and Gumate, namely 3.2°C per 1000 m. Daily minimum air temperature variation, on the other hand, is largely a reflection of nocturnal surface radiation and local topographic effects on air drainage. As cloud cover and wind speed tended to be uniform over the area on most nights, and no marked

depressions existed, it is concluded that minimum temperature variations throughout the area were not great and probably were very localised on an intra-stand rather than inter-stand scale. The mean monthly temperatures recorded at Davao City during the post-war period were closely similar to those measured during the year's field work (Fig. 3) and it is assumed that a similar relationship held at Gumate, making the year's records there representative of the longer period when most of the stands studied were developing.

A total of 422.1 cm (166 in) of precipitation was recorded in the study area during the year's observations, with a seasonal distribution as shown in Fig. 4. Rainfall over 0.1 mm was recorded on 272 days of the year, the longest dry spell being six days. Although considerable month-to-month rainfall variation occurred this was erratic rather than regularly seasonal suggesting that localized weather conditions, and not seasonal air-mass movements, were responsible for the annual distribution.

Rainfall variation was measured with a number of widely distributed rain gauges (Fig. 2); readings were made at ten day or longer intervals over a nine month period, and the total rainfall received compared with the total recorded at the meteorological installation for the same period. The percentage differences calculated from these comparisons and the total annual rainfall that would have resulted from these differences are shown in Table 2. Clearly, rainfall increased with altitude and, at the highest site sampled (1235 m), was probably well above that recorded at the meteorological installation. This effect may have been exaggerated by evaporation losses from the gauges for, although precautions were taken to minimise this, those at lower altitude, which were exposed to greater insolation, may have lost proportionately more than those at higher altitudes. These rainfall differences throughout the area probably had little effect on the vegetation. Rainfall at the lowest site was sufficient to keep the soil surface layers close to field capacity throughout most of the year and the excess moisture received at higher sites was superfluous. Indeed, the only influence which this excess could have had on plants would have been the adverse effects of soil waterlogging which was unlikely on the steep slopes and well drained soils of the area.

Table 2. Rainfall variation within the study area

<u>Site</u> (see Fig 2)	<u>Altitude</u> (m)	<u>Days of comparison</u> <u>with meteorological</u> <u>installation</u>	<u>% difference from</u> <u>meteorological</u> <u>installation</u>	<u>Approx.annual</u> <u>total at site</u> (cm)
c	875	261	-13.28	364
j	1006	261	- 1.25	427
i	1036	299	+ 2.59	433
d	1067	269	+ 5.32	445

Figure 5. Variations in the annual totals of rainfall at Davao City during the post-World War II period.

Because of the possible significance of past droughts on the regeneration of the stands studied, an attempt was made to assess the likelihood of this having occurred by comparing rainfall at Gumate with that at Davao City. A correlation of monthly rainfall totals for the year at these two stations yields a coefficient of only 0.56 ($P > 0.05$). This low spatial correlation suggests rather different rainfall mechanisms operating in the two areas, although only 25 km apart, and indicates that the records from Davao City were only crudely indicative of past conditions at Gumate, although the best available. The year's rainfall total at Davao City was above the post-war mean (208 cm : 184 cm), and the régime was very different from the average (Fig. 3,5). However, variability in régime is characteristic of the station, as seasonal variability for the average year (s.d. 3.87 cm) is well below the variability for any given month throughout the post-war period. The driest continuous month of the year at Davao City was December, with 8.42 cm. During the post-war period, this station experienced 36 months with rainfall less than this figure, including 14 one-month, 4 two-month, 3 three-month, and 1 five-month dry spells. Because of these relative droughts in the past, it is conceivable that some features of the secondary vegetation may have had their origin in an exceptional dry spell during the post-war period, although the large annual rainfall and the high storage capacity of the clayey soil would militate against this. Indeed, when the area was first visited by the author in February and March of 1964, it was enduring a dry spell of greater severity than was ever experienced during the subsequent year of observations there.

Soil moisture and temperature

If the year's climatological records are representative, Gumate is characterized by surface soil moisture conditions that are near ideal for plant growth under all cover types throughout most of the year. A total of 1094 soil moisture tension measurements were made in the upper 5 cm of the soil throughout the year in connection with sampling stand micro-environments. These were made at 10-day intervals at a number of fixed sites, and a number of daily measurements made for sample periods at 10 points within each stand. Moisture conditions fluctuated about field capacity with individual readings varying from saturation immediately

after a shower of rain to several hundreds of centimetres of tension during dry spells. Of the 1904 measurements, only nine were over 500 cm tension; four were over 1000 cm, three of these at a site thoroughly permeated by tree fern roots at which the only tensions greater than wilting point (approx. 12,500 cm) were measured.

Soil surface temperatures were recorded at similar times and sites as moisture tensions. The accuracy of these figures is questionable, however, as they showed a steady drift toward higher temperatures throughout the year, suggesting some progressive faults in the measuring device (probably rapid aging of the thermistors). For what the measurements are worth, they indicate temperatures in the upper twenties ($^{\circ}\text{C}$) that tended to be steady at a given site under a stable vegetation cover. Most short-term fluctuations were related to heavy rain showers which in many cases produced slight temperature rises of several days' duration. Diurnal fluctuations under a closed vegetation cover were negligible and it is probable that significant fluctuations only occurred in the soil of well weeded fields. Only at two sites in cultivated fields were severe fluctuations recorded in the drift toward higher temperatures. However, the highest recorded soil surface temperature was only 37°C .

Soils

The soils of the lower eastern slopes of Mount Apo massif are mapped by Mariano, Lopez and Romero (1953) as a single series, Tugbok Clay, which they describe as follows:

The surface soil of Tugbok Clay consists of brown to weak reddish-brown, prismatic and slightly compact clay 30 to 35 cm deep. It is hard and brittle when dry, but plastic when moist. The sub-soil is reddish brown yellowish-red, slightly compact clay loam that goes to a depth of 100 cm from the surface. The boundary between the two layers is very gradual as to be almost imperceptible. The substratum is a light brown clay with weathering rocks and boulders. The surface soil contains a fair amount of organic matter and is of slightly acid reaction. Roots penetrate the solum readily in spite of the somewhat heavy nature of the soil... Surface drainage is good and internal drainage fair to good... The soil is slightly susceptible to erosion. (p. 38).

This soil seems to fit into the Acid Brown Forest Soil great soil group of Dudal and Moorman's (1964) classification of southeast Asian soils.

The rugged upper slopes of the region are classed by these authors as undifferentiated mountain soils, but an examination of the soils in the study area revealed a close resemblance to Tugbok Clay, despite a tendency to thinner and more stony solums, coarser textures and slightly higher acidities. After examining many soils in the area, two series were distinguished on the basis of colour differences, Tagurano Clay Loam being somewhat redder than Gumate Clay Loam. Soil bodies of the two series seemed to occur as a complex mosaic throughout the area which, at the level of detail examined, showed no regular patterning. Field descriptions of two representative profiles are given below.

Tagurano Clay Loam

Elevation 910 m 10% SE facing slope. Andesite parent material.

Vegetation: mixed herbs of early regrowth. Good drainage. No apparent erosion.

0			Some leaf litter
A1	0-10	cm	5 YR 3/4 dark reddish brown clay loam. Medium crumb structure. pH 5.5-6.0. Many roots. Soil very friable. Clear irregular boundary.
A3	10-22	cm	5 YR 4/4 reddish brown clay loam. Weak prismatic structure. pH 5.5-6.0. Many roots. Diffuse boundary.
B1	22-57	cm	5 YR 3/4 dark reddish brown clay. Massive structure. pH 6.0. Some roots. Diffuse boundary.
B2	57-135	cm	5 YR 3/4 dark reddish brown clay. Massive structure. pH 6.0. No roots. Diffuse boundary.
B3	135-172	cm	5 YR 3/4 dark reddish brown clay. Massive structure. pH 5.5-6.0. No roots. Diffuse boundary.
C	172 cm +		5 YR 3/4 dark reddish brown clay loam. Massive structure. pH 5.5-6.0. Many black (5 YR 2/1) cobbles weathering to strong brown (7.5 YR 5/8) colours.

Gumate Clay Loam

Elevation 810 m 70% N facing slope. Rugged topography. Andesite parent material. Drainage apparently good. Recently logged-over primary dipterocarp forest, despite which the profile appears to be undisturbed.

Table 3. Textural and chemical analyses of two representative soils

Horizon	2mm	2-.05 mm	.05-.002 mm	.002mm	pH (H ₂ O)	pH (KCl)	%C	%N	C/N	CEC (meq %/100gm)	Base sat.	P ₂ O ₅ (ppm)	Exch. cations (meq/100 gm)			
													Ca	Mg	K	Na
Gumate profile																
0-5 cm	6.7	48.1	43.7	8.2	4.6	3.9	3.22	1.29	2.5	62.08	2.71	40	1.23	Tr	0.40	0.05
5-20 cm	<1.0	50.9	43.7	5.4	4.5	4.4	3.14	0.68	4.6	54.57	1.72	140	0.67	Tr	0.23	0.04
20-50 cm	<1.0	52.9	39.2	7.9	5.1	4.8	1.91	0.20	9.6	26.06	2.23	90	0.43	Tr	0.05	0.10
50-80 cm	<1.0	49.5	33.9	16.6	5.2	4.9	0.62	0.13	4.8	30.34	1.75	44	0.44	Tr	0.09	Tr
80-110 cm	<1.0	50.6	36.9	12.5	5.2	4.8	0.97	0.26	3.7	37.42	1.50	40	0.45	Tr	0.06	0.05
110-140 cm	<1.0	40.9	39.7	19.4	5.3	5.0	0.66	0.10	6.6	37.53	2.03	30	0.66	Tr	0.06	0.04
Tagurano profile																
0-5 cm	3.4	50.4	45.6	4.0	5.4	4.6	8.48	1.20	7.1	44.55	14.99	50	4.89	1.22	0.47	0.10
5-20 cm	<1.0	29.8	64.8	5.4	4.9	4.1	2.56	0.47	5.5	44.58	3.30	Tr	1.11	0.08	0.23	0.05
20-50 cm	<1.0	11.9	73.1	15.0	5.0	3.8	1.11	0.16	6.9	36.65	2.81	Tr	0.88	Tr	0.11	0.04
50-80 cm	<1.0	17.5	67.2	15.3	5.2	3.8	0.39	0.06	6.5	33.92	4.33	Tr	1.23	0.03	0.11	0.10
80-110 cm	7.1	36.0	57.2	6.8	5.8	3.9	0.20	0.02	10.0	30.56	13.02	80	2.90	0.66	0.23	0.19

O	1	cm	Clear boundary. Contains both recognisable and decomposed organic matter.
A1	0-8	cm	10 YR 3/3 dark brown clay loam. No structure. pH 5.5. Many roots of forest species. Diffuse boundary.
A3	8-36	cm	10 YR 3/4 dark yellowish brown clay loam. No structure. pH 5.5. Many roots. Diffuse boundary.
B2	36-70	cm	7.5 YR 3/2 dark brown clay. Massive structure. pH 5.5. Some small roots and yellowish brown weathered andesite pebbles. Diffuse boundary.
B3	70-110	cm	10 YR 3/4 dark yellowish brown sandy clay loam. Massive structure. pH 5.5. No roots. Many partly weathered andesite pebbles. Diffuse boundary.
C	110	cm +	10 YR 4/3 brown sandy clay loam. Massive structure. pH 5.0. No roots. The horizon consists of partly weathered andesite cobbles in a clay loam matrix.

The predominant colours in both profiles were dark browns and dark reddish browns; diffuse boundaries were usual and pH was somewhat acid becoming more so at depth.

The results of textural and chemical analyses performed on samples taken from two representative profiles are given in Table 3. The Tagurano profile was located in undisturbed dipterocarp forest near stand 5 on a slope of some 45%, and the Gumate profile in an undisturbed portion of logged-over forest above stand 9 on a slope of about 30%.

Textures were all somewhat coarser than those estimated in the field, and the textural morphology of the two profiles was distinctly different. In the Gumate profile, the sand and silt fractions were relatively constant but clay showed some increase below 50 cm indicating eluviation of this fraction. The Tagurano profile, by contrast, was apparently a two-layered structure; clay and silt fractions increased in the subsoil, apparently a result of eluviation, but fell again below 1 m in what was a lithologically distinct horizon. Both the coarse fractions and chemical composition suggest that this was a buried surface soil.

Per cent nitrogen and carbon showed the same pattern of distribution in both profiles; the relatively low carbon content in the Gumate surface horizon may have reflected the effects of recent logging. Cation

Plate 1. Oblique aerial photograph of the study area.

Plate 2. Aerial photograph of stand 12. The probable corners of the originally cleared site are bracketed. The lowest portion of the site, where Musa is still prominent, was occupied by Japanese troops in the closing stages of World War II. Sampling was restricted to the upper (right hand) half of the stand.

exchange capacities of the two profiles were roughly similar. The Gumate profile was markedly deficient in exchangeable magnesium while other elements had an irregular distribution throughout the profile, phosphorous being remarkably high in the subsoil. The abundance of exchangeable cations and phosphorous in the lowest horizon of the Tagurano profile, where absence of organic matter indicates burial for a lengthy period, is remarkable in view of the abundant percolation that must have taken place there; it contradicts the often repeated assertion that nutrient leaching is always rapid under humid tropical conditions. Soil pH's (mean of the H_2O and KCl methods) varied from 4.3 to 5.2 in the Gumate profile and between 4.4 and 5.0 in the Tagurano profile, the Gumate surface soil being somewhat more acid.

In summary, the two profiles may be said to be relatively fertile by world standards and are certainly not "typical" latosols. Carbon and nitrogen levels were exceptionally high and, although base saturations were low, exchangeable cations, with the exception of magnesium in one profile, were appreciable. Phosphorous content was variable, but only in the Tagurano profile did it fall below 20 ppm. It is difficult to draw any firm conclusions about the soils of the whole area from only two profiles which appeared so similar in the field yet proved different on detailed analysis. Further evidence suggesting considerable local soil variation, and lack of any correlation between it and vegetation, will be cited below.

Primary forest

Gumate lay in the upper fringes of the lowland dipterocarp rain forest, a type which, before man's appearance in large numbers, had covered most well drained sites below 1000 m in the Philippines (Brown 1919; Brown and Mathews 1914; Merrill 1923; Whitford 1906, 1909). Only small undisturbed patches of this forest type persist in the study area today, but these are sufficiently widespread to indicate that the sites of all regrowth stands studied (with the possible exception of stand 12, see below) originally supported primary lowland dipterocarp rain forest. One of these remnants was sampled as a control (stand 13) and these data, together with more extensive observations about other remnants, form the basis of the description that follows.

Height of the main forest canopy varied greatly, and is most appropriately described as the zone of maximum crown density. In stand 13 the main density occurred at about 20 m while emergent trees protruded to about 40 m. In nearby logged-over forest, the measurement of 33 haphazardly selected trees gave heights ranging from 19-45 m with a modal grouping in the 25-30 m height class. The scattered emergents were mainly species of Dipterocarpaceae which, at lower altitudes, are more frequent forming the main canopy layer and, at altitudes slightly above the study area, disappear altogether, the forest assuming a "mid-mountain" aspect (Brown 1919). The density of trees over 3 m in height averaged one tree every 0.68 sq. m with a distribution skewed markedly to the smaller size classes. While some species present in the lower classes did not occur in higher classes, suggesting maturity at this size, others also occurred as large individuals and must, therefore, have been juvenile forms of eventual canopy trees. Only two emergents were counted in the 450 sq. m sample of stand 13, and both were in the same 25 sq. m quadrat. Consequently although they together comprised the vast bulk of the vegetation mass present, their physiological control over the community was far less than sheer size would suggest. Throughout the forest, large individuals such as these were widely scattered and only in the few places where several congregated into a grove could their control over the community have been commensurate with their size. It thus seems that, in the sampled stand, control over the community was exercised by the medium sized, canopy-forming, trees rather than the large emergents. It seems improbable, however, that such control by a single class is a permanent feature of so small a forest area for, while some of these trees (e.g. Astryocalyx calcyina) had attained their maximum size, others (e.g. cf. Shorea almon) were not yet fully developed and may have eventually formed an "emergent-dominated" stand. The size class of current physiological controllers (or dominants in the loose sense) at any small site, therefore, depended upon the combined effects of the tree species present, their relative abundances, and maturities.

Despite an overall sparseness of undergrowth (plants under 3 m high), it was markedly patchy in distribution. Although not sampled, large climbers and tree epiphytes were a prominent feature of the forest; among the climbers, rattans (Daemonorops spp.) and Freycinetia spp. were

most common. Epiphytic ferns and mosses were abundant and showed considerable host preferences.

The forests at Gumate exhibited the floristic complexity characteristic of tropical vegetation. Eighteen different tree species over 3 m tall were counted in stand 13 where there were also 81 undergrowth species in only 18 sq. m. The largest tree, and most common emergent in these forests, was the commercially valuable "white lauaan" (cf. Shorea almon). Other smaller emergents were "red lauaan" (Shorea sp.) and "tangile" (Shorea cf. polysperma) both of which were also logged. Some oaks (Lithocarpus spp.) also attained emergent status when mature. A greater variety of species was found among the smaller trees that composed most of the forest canopy. Species of Lithocarpus were common, two being distinguished although more probably existed. The melastome Astryocalyx calycina was also a prominent member of this class, its many small trunk shoots being distinctive amongst the clean boles of the other trees. Other common tree species of this size were Lasianthus sp., Clethra cf. canescens, Ficus sp. and a species of Loganiaceae. In stand 13, of the 14 trees included in the 100-10,000 kg class that approximates the canopy trees, five were Astryocalyx calycina, three of a species of Loganiaceae and two of cf. Shorea almon. The smallest forest trees (those over 3 m in height but weighing less than 100 kg) were floristically more diverse. Prominent among these were tree ferns (Cyathea contaminans and C. elmeri) and Saurauia sp. whose special ecological role is considered below. Palms (other than rattans) and pandans were numerically insignificant although visually prominent. Of the 50 trees counted in this smallest size class, 11 were immature individuals of larger trees, 16 were Saurauia sp., nine were tree ferns and two were softwood secondary regrowth species.

The forest undergrowth was extremely complex floristically. In stand 13, herbs made up 35% of fresh weight of this layer, ferns (other than tree ferns) 22% and vines 16%. Of the remainder, 26% was tree or tree fern seedlings and 2% small woody plants. The most prominent herb was Elatostema sp. which, although congregating into dense thickets at intervals, was also of high frequency. In stand 13 it occurred in 16 of the 18 quadrats and made up a greater proportion of the undergrowth (33%)

than any other species. Selaginella sp. was a second frequent species that locally formed dense thickets. Ferns, notably Athyrium sp. and Indet. (1780), were widespread. Daemonorops spp. and Freycinetia sp. were both frequent and of large mass in the undergrowth. Daemonorops spp. occurred in 6 of the 18 quadrats and made up 8.5% of undergrowth weight while Freycinetia sp. occurred in 8 quadrats and made up 2.4% of the undergrowth weight.

Sixteen per cent (by fresh weight) of the forest undergrowth in stand 13 was made up of tree seedlings and 10% of juvenile tree ferns. Eight of the eighteen tree species counted in this stand were also found in juvenile form in the undergrowth and it therefore seemed that the forest was reproducing itself satisfactorily. Among these eight species there were seven co-occurrences of juvenile with mature individuals in the same quadrat and, although the sample was too small from which to draw firm conclusions, it seems that many of the tree species were regenerating in situ.

Because of the absence of cyclones in this area, windthrow, either of individuals or groups of trees, is infrequent. When individual trees died they seemed to remain upright until most branches had fallen and the trunk was well decomposed after which they broke several feet above the ground and, in falling, did not greatly disturb the soil or the surrounding vegetation. Unless destroyed by the falling trunk, seedlings of the dead tree or some other canopy tree were present to mature in the gap formed. Whether this did in fact occur will be discussed in a later section and it is sufficient to note here that only an occasional second growth species, typical of large abandoned areas, was found in these openings. In a tree-fall opening of stand 13 only one such tree had appeared. There were also some species typical of forest openings, amongst them Saurauia sp. However, the overwhelming proportion of plants that filled these openings were tree ferns, the abundant parent plants in the forest understorey apparently providing plentiful sources of colonists. Long after the opening had been closed and the dead trunk decomposed, its site could be detected by a distinct line of tree ferns. Whether the crown gap was normally closed by a juvenile tree elongating

rapidly or whether this was accomplished merely by an in-branching of the adjacent trees is unclear; observation led me to believe that the latter was the more common process.

Human occupance

The eastern flank of the Mount Apo massif was the pristine home of the Bagobo tribe. At the time of the Spanish founding of Davao City in 1849, these pagan shifting cultivators were occupying an area extending from the Digos valley, south of Mount Apo, to the eastern slopes of Mount Talomo (Fig. 1). Although tribal mythology indicates a long residence in this region (Benedict 1916; Cole 1911, 1913), and although they were certainly responsible for extensive alteration of the local vegetation (Cole 1913; Montano 1886), it seems likely that Gumate remained undisturbed during this period. The main population centre was at Sibulan, well to the south of the study area, (Benedict 1916; Cole 1911, 1913; Montano 1886) and agricultural activities seem to have been concentrated on the gentler lower slopes of the volcanic fan. Moreover, Sawyer (1900) classes Gumate as in an inter-tribal zone between Bagobos and Guiangas, which further suggests minimal pre-historic disturbance of the area. Local informants denied the presence of any Bagobos there when the study area was first settled by aliens before the second world war, and no charcoal was seen in any soil profile examined. Following the establishment of Davao City, the Bagobos were encouraged to move to the coast by the Spanish administration where they could be more easily controlled and proselytized. The forests at Gumate, therefore, remained relatively undisturbed until recently.

Severe human disturbance at Gumate did not begin until the 1930's when Japanese-operated plantations were extended into the area. These plantations, using immigrant Visayan and native Bagobo labour, had been established in Davao after the turn of the century and were slowly extended up the fertile eastern slopes of Mount Talomo until, at the outbreak of World War II in this theatre, forest land in the area was being cleared and new abaca (Musa textilis, "manila hemp") fields established. Accounts of the nature and extent of this clearance were obtained from local farmers who, as young men, had worked as labourers on these

plantations. Unfortunately, these accounts, although agreeing in general outline, contained conflicting details and the history of the highest cleared land, which included stand 12, is particularly obscure.

All evidence indicates that this initial forest clearance and abaca field establishment did not differ markedly from that presently carried out in the area. Forest trees, with the exception of a few large individuals, are cut and, when a sufficiently long dry period occurs, burnt; the remnant trees succumb a few years later for unknown reasons. The soil is not tilled, and abaca suckers are merely planted among the scattered debris in small holes. Subsequent weeding of the abaca fields is usually carried out twice annually by groups of men with sickles; this also entails little disturbance. Abaca normally requires 3 years to mature and thus fields in the area would have been harvested for only two years before the outbreak of war. This latter process involves cutting of the mature stalks and preliminary stripping of the fibre from the leaf sheaths in the field, followed by final machine-stripping of the fibre at the central processing plant; again, disturbance to the soil is minimal and removal of material from the field small. To conclude, this initial disturbance in the area, although drastic insofar as it involved forest removal, did not produce serious site deterioration.

The oldest stands sampled dated from this pre-war clearance. Stands 11 and 12 had been reportedly cleared in 1938 but abandoned without cultivation. Stand 12 posed a special problem for, while all other stands that were reported as secondary by local informants were clearly not virgin, this stand was indistinguishable from the surrounding forest. A second-hand report claimed that the site had been cleared prior to the war and one informant said that when he first visited the site in 1954 it had been covered by many small forest trees. While some evidence supported past clearance of the site other evidence contradicted this. In the first place the lower edge of the stand, albeit indistinct, was a rough continuation of a farm boundary on the opposite valley side (Fig. 2). Secondly, Japanese soldiers had lived for some time below this site where rusted pieces of equipment could still be found, suggesting that it may have been a clearing. Thirdly, there was some evidence from aerial photographs

(Plate 2) of a sudden reduction in tree height above the lower edge of the stand and sampling revealed that tree girth there was considerably lower than in the forest. However, the stand was the highest sampled and may merely have been mid-mountain forest from which large dipterocarps were naturally absent; although forest with large dipterocarps occurred immediately below it, none was present above and the common species cf. Shorea almon was not counted in any layer although Shorea cf. polysperma occurred in the tree layer. Micro-environmental conditions were generally more similar to those in regrowth than in high forest but these may have been still more similar to those of virgin mid-mountain forest. Despite this conflicting evidence, it was decided to sample and treat the stand as re-growth, interpreting the results with caution.

Stand 14 occupied the site of a former plantation house and abaca processing shed established in 1938 and maintained for approximately three years. A number of other sites were also first cleared at this time although later re-cleared after the war. Sites 14 and 16 had probably been first cleared in 1936 and undergone five years of abaca cropping before the outbreak of war while sites 4, 7 and 10 had probably been cleared in 1938 and cultivated to abaca for a few years (Table 4).

No clear picture of war-time occupancy of the area could be obtained and, while disruption of the abaca plantations certainly occurred at its close, their status during the four war years is uncertain. In the absence of definite evidence it has been assumed that abaca cultivation was suspended at the outbreak of war in 1941. Towards the close of the war, during Allied re-occupation of Mindanao, Gumate became a refuge for Japanese soldiers and scattered pieces of equipment could still be found as evidence of this occupation. These soldiers reportedly grew some food crops but the location of their fields was inexact and their size probably small. Two informants said that site 5 had been used in this way, one claiming that it had been cleared from forest at this time and the other, more convincingly, that it had been part of a pre-war plantation.

At the close of the war, the abaca plantations were sub-divided into smaller, mainly peasant, farms. The old fields, which were probably

Table 4. Approximate histories of disturbance of sampled sites. C, cleared; B, burned; CpB, cleared and probably burned; L, selectively logged; r, upland rice; c, corn; d, coffee; a, abaca; h, house site; f, other food crops.

<u>Site</u>	<u>1935</u>	<u>1940</u>	<u>1945</u>	<u>1950</u>	<u>1955</u>	<u>1960</u>	<u>1965</u>	<u>Age of secondary stand (years)</u>
1			CpB.....				CB,rca.....	1.0
2			CpB				C	2.5
3						CpB.....		7.0
4	CpB a a		C a.....					19.0
5	C?.....	CpB f	f					21.0
6						CBd+a.....		6.5
7	CpB.....			CpB a a a a a a a a a a a a a a a a				7.0
8			CpB.....					19.0
9			CpB.....					19.0
10		CpB a a	C.....					19.0
11	CpB.....							27.0
12	CpB.....							27.0
13								
14	C h h h h.....							23.0
15	CpB a a a a a a			CpB a rc.....		B.....		3.0
16	CpB a a a a a a					CpB.....		7.0
17							L...	1.0
18							C...	1.0

covered with young secondary vegetation, were cleared to establish ownership rights and the remaining abaca harvested. Most were then relinquished to regrowth and only the flatter sites used intensively for subsistence (hill rice, maize) and cash (abaca, coffee) crops. Sites on steeper slopes, where a buffalo and plough could not be used to control the cogon grass (Imperata cylindrica), were used at irregular intervals to raise emergency food crops by shifting cultivation methods of "slash and burn" and dibble planting. Some further clearance of primary forest (followed by partial abandonment) took place in the mid-1950's. Most of the regrowth stands sampled occupied sites abandoned after agricultural activities in the post-war period. Sites 3, 8 and 9 were cleared from forest and abandoned after only a brief period of cash cropping. Sites 4, 7, 10, 15 and 16 were cleared from regrowth after the war and abandoned after varied degrees of use (Table 4).

The area had been logged twice since the war and, although of brief duration, this had left a significant imprint upon the vegetation. In the mid-1950's portions of forest both north and south of Gumate Creek were logged, while in 1963 and 1964 more extensive logging was undertaken around the house site, the extent of which can be seen in Fig. 2. Only large individuals of the three common dipterocarp species (Shorea sp., S. polysperma and cf. S. almon) were extracted. Selected trees were felled without topping and the bole dragged to a trucking site, methods which seriously damaged the immature trees and the surface soil.

The severity of disturbance was thus very irregular, being greatest around spar poles and least where few commercially valuable trees had stood. The two stands selected were not, therefore, representative of overall conditions. The first, stand 17, was taken as representative of forest that had undergone a moderate degree of logging. Several large trees had been removed but a greater number of smaller individuals remained standing. Stand 18 was located at an old spar pole site that represented areas stripped of forest but abandoned without burning or cultivation. Both sites were abandoned about one year before sampling.

METHODS

AUTECOLOGICAL DATA

The only practicable way of gaining insight into the autecologies of the species in the area was to observe their performances in the field in coincidence with environmental measures taken at the same places. The method involves two possible sources of gross error. Firstly, the accessibility factor is not controlled; sufficient time may not have elapsed for a species to fill all its potential positions within a study area. Secondly, the response of a species may be altered by inter-specific competition. It will be demonstrated that the accessibility factor was not a major source of floristic variability, while the second source of error was circumvented by assessing plant responses only at the immature stages when inter-specific competition is minimal. Nevertheless, the autecological conclusions are only tentative.

SAMPLING THE VEGETATION

A sampling design was sought which would provide data on the performance of all species in the regrowth stands, to permit an examination of the plant succession process. Interest in succession required that a distinction be made between supposedly influenced and supposedly influencing plants in each stand. As the performance of the "influenced" plants was to be related to their micro-environments, as the effects of inter-specific competition were to be avoided, and as the facilities for environmental measurements were limited, the low limit of 70 cm was set on the maximum height of these plants; the exact figure was determined by the height of radiation sensors used (see below). The performance of these plants, hereafter termed the ground layer, was measured by presence and frequency. Plants over this height were treated as "influencing".

Fresh weight of above-ground material was adopted as a suitable (although clearly not ideal) general measure of an "influencing" plant's ability to interfere with the atmospheric and soil micro-environment beneath it. It was a value that could be applied to all growth forms, could be added to permit consideration of plants in various combinations, and was readily measurable in the field by direct weighing or estimation

from trunk dimensions. "Influencing" plants were further classified into those under 300 cm in height and those over it, to enable an assessment of the separate effects of smaller plants which occasionally formed dense thickets 1-3 m tall. The two groups are hereafter termed the "intermediate" layer and the "overstorey" respectively. Individual plants in one or both layers were allotted to their species which, in turn, could be grouped into particular species combinations or, in total, into structural units.

The sampling of climbers and epiphytes posed a special problem. In the ground and intermediate layers, where cover was the sampling criterion and in which all plant material could be reached easily, these life forms were sampled. However, no appropriate method could be devised to sample large climbers and epiphytes, whose foliage occurred in the overstorey. Although epiphytes were common in the forest, large vines, with the exception of rattans, were locally less prominent than most accounts of rain forest would lead one to suspect. In the regrowth as well, also contrary to most accounts and, indeed, to the author's observations in low-altitude vegetation in Mindanao, neither life form was common. Because of this, the errors introduced by such an omission are not so great as they might have been in many other areas. Furthermore, Ogawa et al. (1965) report that, in Thai rain forests, total leaf weight of a stand (albeit on an oven-dry basis) per unit area is largely independent of large climbers, the leaf weight of a given tree being inversely proportional to the number and size of lianas supported by it. As tree weights in the present work were being estimated on the basis of liana-free sample trees, it follows that the estimates made probably gave a reasonably accurate measure of total leaf weight over unit area, although omitting the weight contributed by liana stems.

The total contribution of each species to the stand was determined as the sum of the fresh weights of all individuals of that species from the three layers recognised. Overall stand mass was estimated as the sum of total above-ground fresh weights for all plants in the stand.

Quadrats

Because plants in the influencing layers were usually much bigger than those in the ground layer, the size of plot appropriate to sampling the latter was unsuitable for sampling the former. Consequently, at least two sample plot sizes were necessary, each subdivided into equal numbers of quadrats that could be located in pairs throughout the stand to ensure that the influencing : influenced relationship was always assessed.

A 1 sq. m quadrat was selected as suitable for sampling the ground layer. Plants of the intermediate and overstorey layers which influence the micro-environment of such a quadrat should, theoretically, be arranged in and around it, the threshold proximity for effective influence increasing as the plants increase in size. For plants of the intermediate layer, the identical 1 sq. m sample quadrat was used, while for the overstorey a 25 sq. m quadrat, arranged concentrically about this, was adopted. This latter size was thought adequate to sample the influencing overstorey in most stands where trees were small and of high density. Although a larger overstorey quadrat would have better sampled the four stands in which trees were large (11, 12, 13, 17), such variation would have made sample comparisons difficult.

In sampling, a "rooted-in" criterion was used for counting overstorey plants, while in the ground and intermediate layers cover was adopted as the counting criterion. Fig. 6 illustrates the application of these criteria.

The stands, which were selected on the bases of their internally uniform histories of disturbance and their small size, had boundaries which were usually readily recognizable by structural discontinuities. A quadrat arrangement within these boundaries was sought which would give an accurate and usable representation of the vegetation there, obtained with minimal effort.

Logistic problems prohibited a dispersed random or regular grid arrangement of quadrats. Contiguous placement of quadrats in a belt transect overcame these difficulties, was unlikely to coincide with any vegetation patterning, and provided an efficient sampling shape (Bauer 1943; Bormann 1953; Clapham 1932; Pechanec and Stewart 1940). The belts

Figure 6. Dimensions of the sample quadrats used and the criteria employed for counting plants within these.

were located so as to cross any observed or likely heterogeneity in the stands (e.g. concentric patterning, in response to differing migration rates from the stand margins, and patterning associated with slope-related environmental gradients). Most transects, then, traversed stands in the direction of slope and, where a stand was crossed before an adequate (see below) sample was obtained, further short transects were placed across otherwise un-sampled portions usually at right angles to the original orientation.

While this sampling design lacked randomization it was enforced by the extraordinarily difficult working conditions encountered; bias in the siting of individual quadrats was absent insofar as once a traverse starting point and direction had been selected, the location of all subsequent quadrats was fixed.

Sample size

Because sample results were to be used, in part, for comparative purposes, a design ensuring standard sampling intensity in all stands was sought. Fixed sample sizes and fixed stand area percentages were inappropriate; variable stand sizes invalidated the first, while stand areas were not accurately known. Instead, the species : area curve of each stand was employed to determine an arbitrarily fixed, but uniformly applicable, sample size at which returns ceased to be commensurate with the effort expended.

Tests were periodically made as the sample was enlarged to assess whether a predetermined increase in species numbers had been maintained. This involved selecting, in the light of time restrictions and field conditions, the following:

- a) the sampling efficiency required to be maintained,
- b) the size of the interval between tests, and
- c) the minimum area to be sampled before starting to make these tests.

Inter-test intervals had to be larger than any clones or individuals encountered yet be practicable, while the "minimal area" had to be of sufficient size to satisfactorily embrace all types of heterogeneity

encountered. After extensive initial samples in several stands (2, 9, a corn field, an abaca plantation and early woody regrowth), a 15-quadrat minimal area, a 3-quadrat interval between tests, and a 1:2 ratio of percentage species increase to percentage area increase, was adopted. The procedure followed, therefore, was to sample an initial 15 quadrats, count the number of species encountered, then sample a further 3 quadrats. If the percentage species increase provided by this increase was less than half the percentage area increase (in this case 20%), sampling was terminated. If, on the other hand, the percentage species increase was more than half the percentage area increase, then a further 3 quadrats were sampled and the test repeated.

In practice, all save four stands were adequately sampled by 18 quadrats, these four requiring 21 quadrats. The species : area curves used are shown in Fig. 7, and in Table 5 the percentage species increase that each 3-quadrat area increase produced throughout the sample, are shown. Clearly, most stands showed an irregular pattern of termination point positions (had the test been applied throughout sampling) which justifies the use of minimal areas encompassing such heterogeneities. While the uniformity in sample areas that this method yielded may suggest that the results of the attempted sampling intensity standardization were not commensurate with the effort expended, this was apparently a result of an unknown uniformity in stand floristic characteristics.

Estimating tree weights

Because of the practical impossibility of cutting and weighing all trees encountered while sampling, some approximation of an individual tree's weight was sought from a measurable characteristic of the accessible lower trunk. Basal area was used; measurements were made at approximately 140 cm above the ground, and any marked swelling on the trunk was avoided by measuring slightly above or below this level. Where trees were of coppicing or low-branching growth form, separate pole or branch measurements were made and each, with its canopy, treated as an individual tree. The abundant aerial roots on many tree ferns gave some difficulty; where possible these were cut away, or measurements were made higher on the trunk which was usually very uniform throughout most of its length.

Figure 7. Species : area curves of the sampled stands.

Table 5. Percentage increases in species numbers for sample area increases of three quadrats. AF, abaca field; CF, corn field; YR, young woody regrowth in its second cycle or regeneration.

* indicates point at which sampling would have stopped if an initial minimum of 15 quadrats had not been sampled in all stands.

<u>Stand</u>	<u>Quadrat intervals and % area increases</u>					
	<u>3-6</u> <u>100%</u>	<u>6-9</u> <u>50%</u>	<u>9-12</u> <u>33.3%</u>	<u>12-15</u> <u>25%</u>	<u>15-18</u> <u>20%</u>	<u>18-21</u> <u>16.7%</u>
1	25*	13*	24	10*	4*	-
2	7*	6*	13*	21	9*	-
3	48*	21*	14*	12*	5*	-
4	24*	11*	8*	21	4*	-
5	28*	24*	18*	19	16	3*
6	48*	50	16*	3*	8*	-
7	35*	19*	23	19	5*	-
8	43*	8*	21	15	8*	-
9	76*	17*	17	17	11	6*
10	92	39	26	13	14	4*
11	72	38	17	10*	5*	-
12	31*	26	13*	18	11	3*
13	52	37	20	22	2*	-
14	22*	25*	47	5*	0*	-
15	9*	25*	27	5*	5*	-
16	33*	0*	10*	14	4	-
17	27*	14*	16*	5*	8*	-
18	84	33	16*	13	6*	-
AF	25*	6*	24	14	13	4*
CF	35*	26	0*	0*	3*	-
YR	43*	12*	8	13	0*	-

The accuracy of basal area as an estimate of individual plant weight depends upon the constancy of gross morphology, as expressed by the basal area : total volume ratios of the plants concerned, and the specific gravity of their constituent material. Because all plants are not similar in these respects, the data were collected in three groups on the basis of gross morphology: woody trees, tree ferns, and musaceous herbs. Woody trees were further separated into hardwooded and softwooded trees on the basis of wood specific gravity, as measured by the difficulty of cutting it.

The basal area : weight relationships of these four groups were sampled by measuring the basal areas of individuals, cutting them as close to the ground as possible, and weighing them. The smaller individuals were weighed with pocket spring balances while the larger, which required sawing into many segments, were weighed with a steel-yard. Within each group, sampling aimed at including the maximum possible morphological and floristic variety. The samples taken are summarized in Table 6.

Linear regressions of weight on basal area predicted zero weight at basal areas of 35 sq. cm or more in all groups except tree ferns. Logarithmic regression lines and freehand curves did not, on the other hand, have this disadvantage. Simple extrapolation of regression lines beyond the range of the sample data is statistically suspect but, given a reasonably low error of estimate about a curve with a simple equation and assuming stability of the implied relationship in the unknown range, one can make tentative estimates of the dependent variable. In the hardwooded (forest) tree group, therefore, where canopy individuals were included in the sample, extrapolations using a mathematically derived curve were, to some degree, justified because the most likely change in growth characteristics, and hence basal area : weight ratio, was likely to be past once the tree had reached the canopy.

These considerations led to the selection of the following regression lines. For hardwooded tree weight estimates the logarithmic curve was selected because although its total accuracy of estimate was lower than the linear regression, it was apparently more accurate in the critical lower range (Fig. 8). The freehand curve was rejected because

Table 6. Details of sample taken to determine basal area : weight relationships of trees

Tree group	Sample			Encountered in vegetation		
	Individuals	Species	Range of basal areas (cm ²)	Species	Range of basal areas (cm ²)	No. of extrapolations necessary
Hardwood trees	20	12	12-1480	54	10-50000	11
Softwood trees	37	8	10-520	20	10-1150	2
Tree ferns	11	3	35-290	3	32-400	20
<u>Musa</u> spp.	9	2	43-400	2	22-240	-

Figure 8. Regression lines used to estimate hardwood tree and tree fern weights from measured basal areas.

Table 7. Adjusted standard errors of the estimate of tree weights (kg) using three types of predicting curve

<u>Group</u>	<u>Linear</u> <u>regression</u>	<u>Logarithmic</u> <u>regression</u>	<u>Freehand</u> <u>curve</u>
Hardwood trees	386.4	427.2	528.2
Softwood trees	58.8	89.6	38.9
Tree ferns	29.8	21.1	22.8
<u>Musa</u> spp.	5.1	7.0	3.6

Figure 9. Freehand curve used to estimate softwood tree weights from measured basal areas.

Figure 10. Freehand curve used to estimate weights of Musa plants from measured basal areas.

its estimates were inaccurate and it did not permit extrapolations. For softwooded trees the freehand curve was accurate throughout its range, including low values, and as only two extrapolations were necessary it was adopted (Fig. 9). For similar reasons the freehand curve was selected for weight estimates of Musa spp. (Fig. 10). Among tree ferns, logarithmic and freehand curves gave near-identical accuracies of estimates; the logarithmic curve was selected as it permitted extrapolation (Fig. 8).

SAMPLING STAND MICRO-ENVIRONMENTS

The assumption of a uniform "macro" or "un-influenced" environment in the study area had already been made, and, consequently, sampling was concentrated on the micro-environment of stands which, in theory, is influenced by the vegetation there and intimately involved in the process of plant succession. The vertical limits of this micro-environment were set by technical restrictions to be mentioned below. The assumption of minimal inter-specific competition within the influenced or ground layer has also been made, and the environmental phenomena measured were those likely to have some directly restrictive effect upon the ability of plants to establish themselves in the stands under study and to grow to a height of 70 cm there. However, it is recognized that all competitive effects cannot be eliminated and, consequently, apparent tolerance ranges of plants may have been more restricted than their true ranges. "Environment" is used here to refer only to those phenomena which may in some way affect a plant in situ. Any phenomena or events responsible for the immigration of the plant are termed "accessibility" factors and considered elsewhere.

The following five factors were selected for study:

- a) radiation,
- b) soil moisture,
- c) soil macro-nutrients,
- d) air temperature, and
- e) soil pH.

Further subdivision within each factor resulted in a total of 20 variables being measured (see below and Table 14).

Radiation

Measurement was restricted to incoming short wave radiation or insolation. Because of possible variability in spectral quality of shade insolation among stands, spectrally selective photoelectric and photochemical techniques were rejected in favour of some nonselective instrument measuring in absolute energy units. Bimetallic actinographs, which were both robust and transportable, were used for, although of relatively low absolute precision, these were thought to measure sufficiently accurately for the purpose of the study. The possible variability in spectral quality of shade insolation during the revegetation of sites also made it desirable to measure this in separate wavebands, particularly distinguishing the physiologically less active green and yellow band from the more active shorter and longer wavebands. Kodak Wratten filters No.12 and 29 provided relatively sharp cut-offs at suitable wavelengths (approx. 0.52 and 0.62 microns) and were fitted above the actinograph bimetals. By utilizing three instruments, one unfiltered and two filtered, it was possible to measure total incoming radiation and, by subtraction, radiation in the 0.52, 0.52-0.62, and 0.62 wavebands. These three bands are hereafter termed "blue", "green" and "red" respectively, for convenience. All measurements were made on a daily basis, totals being integrated by making spot readings on the actinograph charts at intervals representing 15 minutes, throughout the day.

Insolation measurement beneath a vegetation canopy, unless made continuously, must be related to some external standard by appropriate sampling and comparison, and expressed as a percentage thereof. The accuracy of such sample percentages depends, of course, upon their constancy at a given point over long periods, and Anderson (1964) justifiably criticizes the use of such "daylight factors" (at least when applied to total insolation) in temperate areas where a changing solar altitude and the deciduous tree habit produce serious errors. In the study area, where solar altitude oscillated seasonally about the zenith and all stands were evergreen, these objections to the method lose force. Percentage variations on a day-to-day basis may give rise to more serious error, however, for much of the radiation received beneath canopies is in the form of sun flecks, and the coincidence of cloudy or clear conditions with the appropriate solar position on any day may produce considerable day-to-

day differences in percentage of external radiation received at a point on the stand floor. To test how serious a sampling error was introduced by this variation, three actinographs were left at identical positions beneath a canopy throughout a 14-day sample period, and the measured results related to external conditions as percentages thereof. These percentages are listed in Table 8, together with those of a number of shorter trials conducted in several regrowth stands before sampling was begun. While it is clear that considerable day-to-day variation occurred, most percentages at a given position maintained the same daily order of magnitude which, in some measure, validates their use in comparisons.

Insufficient instruments were available to permit of two complete sets being used for external and shaded measurements making it necessary to estimate daily blue, green and red external radiation from the measured total daily radiation receipt. This was achieved by measuring the spectral composition of external radiation over a 29-day sample period using three instruments and fitting regression lines of inputs in these spectral bands on total daily inputs (Fig. 11). Energy receipts in each band could be predicted with some accuracy; adjusted standard errors of the estimate for red, green and blue were 10.8, 11.8 and 8.4 cal, respectively.

With external conditions predictable, the three actinographs were then used for sampling shade radiation on the stand floors. The height of the actinograph receiving surfaces (25 cm) necessarily determined, in large part, the definition of the upper limit of the sampled ground layer. Each instrument was mounted on three pegs driven into the ground, this serving to raise the receiving surfaces a further 10-20 cm depending on the slope of the ground surface. As a certain degree of disturbance of the ground vegetation was necessary around each instrument, the upper limit of the ground layer was defined as 70 cm, at which height it was assumed that the measured amounts of radiation were those actually received by the plants of the ground layer.

The actinograph sensors, each measuring only 50 sq. cm, provided an extremely small sample area, and it was therefore necessary to make measurements at as many points as possible in a given stand. Initially, measurements were attempted by placing three actinographs close together

Figure 11. Regression lines used to estimate daily blue, green and red radiation receipts from the total daily receipts.

Table 8. Day-to-day variations in the shade insolation receipts at fixed points expressed as percentages of that received externally

Location	<u>% of total radiation</u>	<u>% of green + red radiation</u>	<u>% of red radiation</u>
Logged forest	15.06	15.59	15.40
	17.37	15.34	15.25
	17.69	14.69	13.22
	15.86	13.66	14.75
	18.40	24.01	19.76
	16.58	21.27	21.08
	14.45	17.59	13.81
	11.31	14.29	14.07
	13.81	17.08	13.59
	11.45	11.65	13.65
	16.86	17.34	20.51
	11.40	13.93	15.72
	14.04	19.53	17.31
	17.99	14.97	16.87
Stand 1	16.04	10.56	9.79
	28.99	10.66	10.85
	27.89	14.55	11.37
Stand 2	2.63	7.80	Trace
	2.91	4.80	Trace
	4.23	7.69	Trace
Stand 2	34.56	27.81	22.67
	36.00	35.52	20.18
	36.37	27.85	18.40
Stand 7	46.80	60.97	-
	48.64	62.83	-
Stand 8	6.11	4.50	Trace
	2.97	3.73	Trace
	6.04	8.42	0.97
Stand 9	14.27	22.07	25.78
	17.91	15.05	11.93
	14.86	14.76	21.13

in the same 1 sq. m quadrat, but this resulted in unacceptable disturbance of the vegetation and, moreover, gave results indicating great spatial variation in receipts even within so small an area. As the computations of radiation in separate spectral bands required subtractions between the three instrument records, this method could not be employed and an alternative technique was devised whereby the three instruments were "rotated" through three quadrats on three consecutive days. Measurements made at each site were then reduced to percentages of external radiation and from these the spectral band percentages received at each site were calculated. The daily variations of radiation percentages received at a given point (Table 8) indicated that considerable error was introduced by this "rotation" method, and the computed green and blue radiation percentages were probably too inaccurate to be of great use. On the other hand, both total and red radiation were measured directly and were thus of greater reliability.

The rotation method of measurement restricted sampling to groups of three quadrats at a time. Initially it was hoped to sample nine quadrats in each stand but time limitations required this to be reduced to six. Because vegetation sampling involved clear felling, all environmental sampling was carried out prior to this. At the start of field-work, therefore, 12 "permanent" quadrats were laid out in each stand to be used as sites for micro-environmental measurements and later to form part of the vegetation sample. The six radiation measurements were taken in alternate quadrats of these 12 permanent quadrats. Ideally, actinograph charts should have been changed only before sunrise or after sunset but, as this proved impossible under field conditions, changes were carried out $1\frac{1}{2}$ hours after dawn or $1\frac{1}{2}$ hours before darkness fell. When integrating the daily totals from each chart, the extra $1\frac{1}{2}$ hours radiation from a previous day was added to the current day's record. The absolute amount of radiation received in this extra $1\frac{1}{2}$ hours was always only a small proportion of the daily total, making any errors introduced by this technique comparatively slight.

Soil moisture

Soil moisture was measured directly in centimetres of tension; a measure thought to be ecologically more significant than per cent moisture content,

and one permitting a single set of calibration curves to be used for all solids encountered. Tension was measured by the electrical conductivity method using fibreglass blocks (Colman 1946; Colman and Hendrix 1949). Possible error due to the conductivity of salts in solution was thought to be minor in the perhumid conditions of the study area. Cells were calibrated from saturation to "wilting point" on a pressure membrane apparatus.

The limited numbers of cells available restricted measurements to the soil surface layer where it was found that a cell could be adequately embedded in 5 cm of soil; this served to define the lower limit of the stand micro-environment considered. To assess temporal variations, a single cell was installed in each stand and read at 10-day intervals throughout a period of 10 months. These measurements indicated, however, that there was far greater day-to-day variation, in response to regular rain showers, than there was seasonal variation and, consequently, more frequent readings would have been desirable. An added source of error in the measurements was the frequent occurrence of afternoon rain; as visiting all cells was a full day's task, those visited latest were often read in the rain and their results thus biased toward wetness. Unfortunately, it proved impossible to circumvent either of these difficulties. To assess spatial variation of soil moisture within each stand, cells were placed in the surface soil of 9 of the permanent quadrats and these, as well as the permanent cell, were read daily over a one week period during which time at least one drying cycle could usually be covered. Using these data, a regression line of mean soil moisture tension upon soil moisture tension measured by the permanent cell, was constructed for each stand, a straight line regression giving an adequate fit in all save one instance. Using these regressions, each permanent cell measurement made could be altered to provide a more realistic "mean soil moisture condition" for the stand at that time. From the data collected in this way three measures of stand surface soil moisture condition were obtained:

- a) a mean annual soil moisture figure was calculated from the corrected permanent block readings;
- b) the mean deviation of the same readings was used as a measure of soil moisture temporal instability;
- c) finally, a mean figure for soil moisture spatial instability was derived from the daily mean deviation measurements made at the 10 points in each stand throughout the week of readings.

A major drawback of this sampling design was that during the week of sample measurements an adequate range of soil moisture conditions was not always experienced. In most cases, the extension of the period by several days overcame this limitation, but in a few instances the regressions had to be based on data from a restricted range. A second drawback was that values reflecting the poor initial siting of a permanent cell could not always be corrected by the regression line. In stand 8, for example, the placing of the permanent cell at an excessively wet point was not recognised until after the sampling had been concluded, by which time movement of the cell would have interrupted the sequence of measurements. Because of these inaccuracies, the soil moisture figures collected should not be regarded as comparable with those measured in a laboratory or under ideal field conditions. They do, however, represent the first attempt to measure soil moisture conditions under tropical regrowth vegetation and to test the common assumption that this variable is of great importance to the succession.

Soil nutrients and pH

Because of the inherent arbitrariness of all soil nutrient analyses, and the impossibility of carrying out field trials in the time available, the currently most widely used chemical analysis techniques were employed in measuring soil nutrients which, at least, permitted crude comparisons with work in other areas. Exchangeable cations (Ca, Mg, K, Na) were leached with ammonium acetate in alcohol; phosphorous (as ppm of P_2O_5) was extracted by the Truog method; total nitrogen was determined by the Kjeldahl method. In addition, percentage carbon was determined by the Walkley and Black method and cation exchange capacity by saturation with sodium acetate, the absorbed sodium subsequently being leached with ammonium acetate. All analyses were performed by the Soil Science Laboratory of the Royal Tropical Institute, Amsterdam. As costs restricted the number of analyses to one per stand, composite samples were taken from the upper 5 cm of the surface soil in the 12 permanent quadrats of each stand. Sub-samples in each quadrat were taken with a probe after removing recognisable plant litter from the soil surface; they were then air dried and thoroughly mixed before shipment. It was assumed that temporal variation of soil nutrients was minimal and that the samples were representative of conditions in the stands over some period of time.

Surface soil pH was assumed to vary negligibly over short periods of time and measurements made on the soil samples collected for nutrient analysis were assumed to be representative of stand conditions. The soil was shaken with pure water, or a 1 N solution of potassium chloride, in a soil : solution ratio of 1:2.5, and the pH determined with a glass electrode.

Air temperature

In the time available, only daily maximum and minimum air temperature could be measured. The thermometer was placed in a small screen, mounted on a stout peg which could be driven into the ground, leaving the thermometer in a horizontal position approximately 20 cm above the soil surface. Sampling in each stand was restricted to approximately one week and temperatures related to those measured at the meteorological installation and expressed as differences (positive or negative) from them. To test whether a constant difference was maintained at a given site, a ten day trial was carried out with the thermometer in a fixed position (Table 9). Some day-to-day variation did exist, but all measured differences tended to be of the same order of magnitude and the method was adopted as the best available. To obtain a space-average of temperature differences, measurements were made in 6 of the 12 permanent quadrats, the thermometer being moved daily in conjunction with the "rotation" of actinographs.

Mean values of all micro-environmental conditions measured in each stand are summarised in Table 14; comments on these values and tests of the significance of their differences belong to a following section. In summary, the greatest deficiency of all measurements was the small sample size that each represented, the area or volume sampled being minute in comparison with the dimensions of the vegetation sample. However, the sole alternative was to have restricted measurement to a small number of variables, and it was thought that, in an exploratory study, the measurement of a wide range of variables, albeit with low accuracy, offered greater promise of useful results.

Table 9. Day-to-day variations in maximum and minimum air temperature differences at a fixed position on a stand floor. Expressed as differences ($^{\circ}\text{C}$) from temperatures measured at the meteorological installation.

<u>Daily maximum temperature</u> <u>differences</u>	<u>Daily minimum temperature</u> <u>differences</u>
- 6.0	+ 0.2
- 6.5	+ 0.5
- 6.2	- 0.1
- 3.2	+ 0.9
- 3.8	+ 0.7
- 8.6	+ 0.7
- 7.6	- 0.2
- 8.2	0.0
- 6.0	- 1.0
- 6.2	+ 0.9

Sampling litter fall

Litter fall, including dead leaves and small twigs, was sampled in the regrowth stands using 12 aluminium foil trays, each of 625 sq. cm area. This foil, although cheap and non-corrodible, proved not to be the ideal material as it was easily torn and, if the fixing weights rolled off, tended to curl under the impact of raindrops. To allow for errors introduced by this curling a 20% loss factor was added in computing the results. Records from badly torn or curled trays were discarded. Trays were initially placed in the 12 permanent quadrats but were later transferred to new positions in the stands when vegetation sampling was carried out. In most cases trays were cleared twice during the sampling period, which varied from 43 to 92 days depending on the condition of the trays. Although this sample period may seem unrealistically short, the evergreen nature of all stands is thought to have prevented serious error. When collected, the litter was dried in tins on a plant specimen drier, weighed, thoroughly pulverized and a sub-sample taken for chemical analysis. Litter fall data for the sample periods were reduced to dry litter fall / sq. m/ day and this converted to an annual figure. The results are listed in Table 20 and will be further discussed below. Although these results were of low absolute accuracy because of the poor techniques used and the small sample area (0.6 sq. m in most stands), they agree in general with those from other tropical rain forest areas, including regrowth, quoted by Nye and Greenland (1960).

In the three grassland stands (14, 15, 16), litter collection trays could not be used and as an alternative a 50 x 400 cm plot was pegged out in each stand, and from this all dead material, both standing and lying on the ground, was removed. This was repeated after 100 days and all the new dead material removed was collected, dried and weighed. The results, however, (Table 20) showed litter production in these stands to be far in excess of that under woody vegetation. The reason for these high figures seems to have been stimulated production caused by removal of the dead material, and the inclusion of standing dead matter, most of which would normally have decomposed before falling to the ground. Micro-environmental conditions were not greatly different from those in

other stands, suggesting no great difference in decomposition rates, yet there was no marked accumulation of litter on the soil surface. For these reasons, the litter production figures from grasslands were discarded as gross over-estimates.

THE SECONDARY VEGETATION

In this description of the sampled stands of secondary vegetation, upon which initial hypotheses about the course of succession are based, emphasis is placed on structural characteristics, the stability of each stand as evidenced by the occurrence together of mature and juvenile plants of the same species, and the relationship between stand morphology and age. The term "prominence" is used to describe the relative importance of a species or other plant group in a stand, and is measured in two ways. (1) "Mass" or "plant mass" refers to fresh weight of above-ground plant material. Both absolute mass (measured in kg per sq. m) and relative mass (as a percentage of the total stand mass) are used. (2) "Summed frequency" is used as an approximate measure of the numbers of individual plants of a life form type in a stand. Sampling did not distinguish between individual plants in the intermediate and ground layers and, as a result, no absolute individual count could be made. As an alternative, the separate frequencies of species of the type, or the "summed frequency", was used. All species frequencies were reduced to an 18 quadrat sample, the value 18 representing the maximum frequency that could be attained by any species in a stand. The adjective "predominant" (and its associated noun and verb) is applied to species or to life forms that make up a greater proportion of the mass of a stand than any other group of the same rank. The term "juvenile" is applied to plants under 300 cm in height which, when mature, exceeded this height, and to plants under 70 cm in height which, when mature, reached a height of 70-300 cm.

LIFE FORMS

Superficial observations in the study area suggested that most stands could be classified into a limited number of categories on the basis of the overwhelming prominence of a single, distinct, life form. Gross morphological differences of local plants were sufficient to enable the ready recognition of the following types:

- a) small herbs,
- b) large zingiberaceous herbs,
- c) large musaceous herbs,
- d) tree ferns,
- e) softwooded (second growth) trees, and
- f) hardwooded (forest) trees.

The first three groups may be defined as "plants with no woody parts above ground" (Willis 1960), while the second and third groups were distinguished from the first on the basis of size and peculiarities of shape. The term "large" as used here refers to the ability of a plant to attain a height of 3 m or more when mature. Zingiberaceous herbs comprised two species, Costus speciosus and Hornstedtia sp., both of which possessed elongate bracted stems with sessile elliptical leaves arranged alternately along most of their lengths. The musaceous herb group included two species, Musa textilis (including both cultivated and wild varieties) and a wild banana, Musa sp.; both were treelike in appearance with their stems un-branched and sheathed by the petioles of large leaves.

The fourth group, tree ferns, comprised two distinguishable species, Cyathea contaminans and C. elmeri, both of which had stout, erect, dictyostelic, unbranched "trunks" with large leaves arranged spirally in terminal crowns. The last two groups were distinguished from all others by being woody trees with branched stems. The distinction between the two was less easily defined, however; it was based on relative softness of wood, size at maturity and certain leaf characters. Species placed in group (e) seldom attained a height greater than 20 m and often possessed leaves which were large, pale green and non-leathery. In addition, most had relatively soft wood that was easily cut with a machete. In contrast, species placed in group (f) attained a variety of heights at maturity but many exceeded 20 m and some reached 40 m. Their leaves tended to be small, dark green and leathery. Small woody shrubs and vines were an anomolous group which, for convenience, were placed with small herbs. They did not constitute more than a very small proportion of the total vegetation mass in any one stand.

In Fig. 12 histograms of the percentage mass contributed by each of these six groups to each stand have been plotted. Clearly, much of the mass in most stands belonged to a single life form; in 8 of the 18 stands one group contributed more than 80% of the total stand mass, whilst in 4 other stands one group contributed between 60 and 80%. In no stand did the predominant life form contribute less than 30% to the

stand mass. While the overall picture, therefore, was one of overwhelming predominance of a single life form, a number of stands did not conform to this pattern; in stands 2, 7, 8, 11 and 18 the predominant life form contributed less than 50% to the stand mass. The occurrence of these transitional stands is not unexpected in view of the certain instability of the vegetation being studied. What is notable, however, is that, despite this instability, so few transitional stands occurred.

STAND DESCRIPTIONS

The main structural characteristics and floristic richness of each stand are summarised in Table 10, and the floras encountered are tabulated in the appendix.

Stands in which small herbs predominated (1,14,15,16)

These were characterized by low total plant mass, most of which was concentrated in the intermediate layer (Table 10) and species otherwise common as weeds in cultivated fields. Each stand had undergone differing degrees of disturbance, however, and their floristic compositions appeared to reflect this. In stand 1, where past disturbance had been light, 48 species were sampled and several herb species were prominent. Notable among these was Paspalum conjugatum which contributed 38% to the total stand mass, Microglossa pyrifolia (12%), Pteridium aquilinum (9%), and Imperata cylindrica var. major (6%). The last two species appeared to be mutually exclusive and were never seen together; in stand 1 each was prominent in a separate portion of the stand (Plate 3), a feature repeatedly observed in other herbaceous vegetation of the area. The other, more intensely disturbed, stands were floristically poorer and a single species tended to be overwhelmingly prominent. Most species present in these other stands also occurred in stand 1. In stand 15, where only 21 species were counted, 16 were common to stand 1 and two species, Imperata cylindrica var. major and Elephantopus mollis were overwhelmingly prominent, contributing 69% and 21% to the stand mass respectively (Plates 4,5). Twenty-three species were sampled in stand 14, sixteen of these also occurring in stand 1. In this stand, the tall bunch grass Panicum maximum made up 75% of the total stand mass. In stand 16, twenty-six species were sampled, 17 of which also occurred in stand 1, and a

Figure 12. Structure of the sampled stands. Histograms of the % mass contributed to each stand by the six life forms distinguished are shown.

Table 10. Structure and floristic richness of sampled stands

<u>Stand</u>	<u>Mass (kg/m²)</u>				<u>No. of species</u>
	<u>Ground Layer</u>	<u>Intermediate layer</u>	<u>Overstorey</u>	<u>Total</u>	
	<u>0-70 cm</u>	<u>70-300 cm</u>	<u>300 cm +</u>		
1	1.05	1.85	0.21	3.11	48
2	0.61	1.81	1.50	3.92	45
3	0.41	0.99	10.22	11.68	77
4	0.25	1.78	6.10	8.13	55
5	0.18	0.40	12.77	13.36	93
6	0.51	1.10	10.25	11.86	66
7	0.57	1.51	6.22	8.31	46
8	0.23	1.14	10.21	11.57	61
9	0.29	0.39	9.63	10.31	61
10	0.25	0.72	12.58	13.56	50
11	0.13	1.00	35.92	37.05	78
12	0.27	0.52	41.13	41.92	81
13	0.14	0.74	1119.58	1120.46	85
14	0.17	6.72	1.34	8.24	23
15	0.12	1.46	—	1.58	21
16	0.25	2.14	0.32	2.71	26
17	0.36	1.84	53.17	55.38	91
18	0.31	1.73	0.22	2.25	104

greater number were prominent; Imperata cylindrica var. major made up 17% of the stand mass, Setaria palmifolia 10%, Paspalum conjugatum 10%, and a fern, Nephrolepis sp., 9%.

The prominent herbaceous layer in each stand appeared to be maintaining itself adequately. The percentage of intermediate layer herb species also sampled in the ground layer were as follows: stand 1, 78%; stand 14, 70%; stand 15, 89%; stand 16, 56%. It cannot be inferred from this, however, that micro-environmental conditions beneath the herb layers were adequate for the sexual reproduction of component species. Many species were reproducing vegetatively and under such conditions only the creation of an environment unsuitable to the parent plant (such as overtopping by trees) could lead to elimination of these species.

The prominence of life forms other than herbs is given in Table 11. Hardwood tree species were absent from all stands while the musaceous herbs were all remnants of cultivated Musa textilis. All stands contained both large zingiberaceous herbs but only in stand 16 did they seem to be assuming a prominence. All stands contained some softwood tree species (mainly seedlings) but only in stand 16 were there large numbers of these (Plate 7). In stand 14, almost the total softwood tree weight was composed of two senescent individuals, one of Ficus sp. and the other of Mallovus paniculatus. Only in stand 1 were juvenile tree ferns prominent.

To conclude, therefore, it appeared that in stand 1 either zingiberaceous herbs, softwood trees or tree ferns may eventually have assumed a predominant position in the stand. Stand 16 appeared to be well on the way to a predominance shared between zingiberaceous herbs and softwood trees with no sign that tree ferns may have eventually achieved a predominant position in the stand. The future of stand 14 was uncertain; although it possessed some juvenile plants of larger life form types, its 23 year age suggested that it had been in a relatively stable state and that few of these juvenile plants would eventually reach maturity. Stand 15 was in all respects depauperate of plants of taller life form and it seemed likely that any change would be, at best, a lengthy process.

Table 11. The prominence of minor life forms in stands 1, 14, 15, 16. SF, summed frequency; %M, % of total plant mass contributed by this type.

Stand	Large musaceous herbs			Large zingiberaceous herbs			Softwood trees			Tree ferns			Hardwood trees		
	Spp.	SF	%M	Spp.	SF	%M	Spp.	SF	%M	Spp.	SF	%M	Spp.	SF	%M
1	1	4	4.75	2	8	0.63	6	17	2.54	1	21	5.92	-	-	-
14	1	8	2.80	2	10	0.25	5	11	11.79	1	5	1.96	-	-	-
15	-	-	-	2	2	Tr	4	5	1.21	1	1	Tr	-	-	-
16	1	3	3.54	2	24	23.25	5	30	11.53	-	-	-	-	-	-

Plate 3. External view of stand 1. Pteridium aquilinum predominates on the right-hand side of the photograph and Imperata cylindrica var. major on the left-hand side. Remnants of Musa textilis, planted before site abandonment, are scattered throughout the stand.

Plate 4. Stand 15. Imperata cylindrica var. major predominates. An isolated patch of Miscanthus floridulus (not sampled) can be seen in the background.

Plate 5. A section of stand 15. The dense mat of Imperata cylindrica var. major is interspersed with scattered Nephrolepis sp. and Elephantopus mollis.

Plate 6. An external view of stand 9. Cyathea spp. are almost exclusively predominant. Only occasional mature softwood trees emerge through the low (6-7 m) canopy.

Plate 7. A section of stand 16. Young softwood trees emerging from the dense mat of Imperata cylindrica var. major and other grassland herbs.

Plate 8. The interior of stand 3. The trees are small and densely distributed; undergrowth is a mixture of regrowth, forest herbs and hardwood tree seedlings.

Plate 9. Stand 4. The Canopy of softwood trees is breaking up and a layer of small herbs and Hornstedtia sp. is appearing.

Plate 10. An external view of stand 7. The stand is composed of a dense thicket of Hornstedtia sp. among which are scattered isolated individuals and clumps of tree ferns and softwood trees.

Plate 11. A section of stand 10. Cyathea spp. form a thin, but continuous, canopy. The presence of smaller tree ferns of all sizes beneath the canopy indicates successful reproduction in situ.

Stands in which softwood trees predominated (3,4,5,6)

These stands were characterized by a moderate plant mass (8-14 kg/sq. m) and an overstorey largely made up of softwood trees. In most stands a single softwood species predominated. Intermediate layer mass in these stands approximated 1 kg/sq. m and ground layer mass 0.5 kg/sq. m.

Despite these gross similarities, these stands differed markedly in detail. While stands 3 and 6 were of similar age, stands 4 and 5 were far older. Total plant mass in these first two stands was similar (11.7 and 11.9 kg/sq. m, respectively), while between stand 4 and 5 a greater difference existed (8.1 and 13.4 kg/sq. m, respectively). The floristic richness of these stands also varied (Table 10) but all were richer in this respect than the stands in which small herbs predominated.

In stand 3 the softwood Omalanthus cf. surigaoense predominated, making up 72% of the stand mass and forming an even canopy at approximately 12 m height (Plate 8). The only other overstorey plants of significant size were Musa sp. (7% of total weight), the wild variety of Musa textilis (6%) and the softwood Alphitonia incana (3.6%). All trees were small and densely distributed; none exceeded 200 sq. cm in basal area and density averaged one tree every 2.2 sq. m. Despite a similar age, history and location, stand 6 was markedly different. Trema orientalis was the marginally predominant tree making up 25% of the total plant mass. Omalanthus cf. surigaoense contributed 24% to the stand mass and Cyathea spp. a similar proportion. Wild abaca and wild banana were also present, however, making up 2.2 and 3.8% of the stand mass respectively. The canopy formed by this mixture of species was far less uniform than that of stand 3 and, indeed, could hardly be termed continuous. Most trees attained a height of 15-20 m but tree density averaged only one tree every 6.4 sq. m and large openings occurred throughout the stand. Thus, despite a total mass similar to that of stand 3, its arrangement was very different.

In stand 5, Mallotus paniculatus was the predominant species making up 65% of the plant mass. Other prominent species in the overstorey were Indet. 1958 (14%) and Cyathea spp. (3.2%). A uniform canopy at 10-12 m was similar to that of stand 3, as was the tree density of 1

tree every 1.9 sq. m. In contrast to the still vigorous growth of softwood trees in the above three stands, those in stand 4 were moribund and many had already died at the time of sampling. As a result, the overstorey mass only contributed 75% of the total stand mass (Table 10). The large number of dead and dying Omalanthus cf. surigaoense in the stand suggested that this was formerly the predominant species. At the time of sampling, however, it contributed only 9.3% of the total plant mass and predominance had passed to the small softwood Ficus sp. (27%) which in most other stands seldom attained canopy height. Other prominent trees in the overstorey were Mallotus paniculatus (9.2%), Clerodendrum sp. (8.4%) and Melastoma cf. polyanthum (3.9%), and a cultigen remnant, Musa textilis (10.6%).

In none of the four stands were the predominant softwood trees maintaining themselves adequately and in stand 4 the death of old trees had left gaps in the canopy (Plate 9). The summed frequencies of juvenile softwood trees was as follows: stand 3, 11; stand 4, 6; stand 5, 6; stand 6, 5. It seemed probable that, unless some other large life form emerged to replace the softwood trees in these stands, their eventual fate would be a return to herb predominance as the canopies degenerated.

The prominence of life forms other than softwood trees is given in Table 12. Considerable variation in the prominence of these types existed in these stands. Only in stand 4 were herbs of any importance; they possibly represented the re-emergence of a herb layer as the canopy degenerated. Also prominent in stand 4 was Hornstedtia sp. which suggested that this species may have eventually shared predominance with smaller herbs. Stand 6 possessed many juvenile tree ferns; whether these eventually predominated depended upon the longevity of the currently predominating softwood trees and as many of these were Trema orientalis, a large-growing and long-lived species, the likelihood of this event occurring seemed remote. A distinction must be made between the longer-lived and often larger-growing softwood trees of the area, such as Trema orientalis and Mallotus paniculatus, which may have lived for some 30 years and attained heights comparable to those of many forest canopy trees, and the shorter-lived and smaller species, typified by Omalanthus spp., which appeared to

Table 12. The prominence of minor life forms in stands 3, 4, 5, 6. SF, summed frequency; %M, % of total plant mass contributed by this type

Stand	Small herbs		Large musaceous herbs			Large zingiberaceous herbs			Softwood trees			Hardwood trees		
	Spp.	%M	Spp.	SF	%M	Spp.	SF	%M	Spp.	SF	%M	Spp.	SF	%M
3	45	7.3	2	13	8.7	2	8	2.1	1	10	1.9	15	21	0.8
4	36	15.9	2	4	1.0	1	12	5.5	1	6	5.5	4	5	0.6
5	42	2.9	2	4	0.9	1	12	0.9	1	11	3.3	37	94	20.0
6	35	8.0	2	6	8.9	1	5	0.8	1	15	25.6	16	18	3.0

reach maturity at about 10 years and to die after 15 years of age. Where the former group was present in a stand, predominance may have passed directly from softwood to hardwood forest trees, tree ferns, if present, remaining suppressed. Where the latter group occurred in a stand their early death allowed tree ferns, if present in sufficient numbers, eventually to predominate there. Stand 5 contained the richest variety of hardwood tree species while stands 3 and 6 both possessed appreciable numbers. Only in stand 4 were they few.

Stands in which tree ferns predominated (9,10)

Both stands were characterized by a predominance of tree ferns, the foliage of which formed a thin, but continuous, canopy at 6-7 m (Plates 6, 11). In stand 9 these constituted 91% of the plant mass and in stand 10, 85%. Despite the greater age of these stands, their total plant mass was similar to that of stands with softwood trees predominant (Table 10). Beneath the canopy, undergrowth was light with little mass in either intermediate or ground layers. Around the base of each fern a dense mat of roots had developed, often covered by a cone of fallen fronds, which appeared efficiently to suppress undergrowth. The tree densities of the two stands were of similar magnitudes, stand 9 having one tree every 4.4 sq. m. Neither stand was floristically rich; the stand 9 sample contained 61 species and the stand 10 sample 51 species. The predominant tree ferns in both stands appeared to be reproducing themselves satisfactorily in situ; in stand 9, sixteen, and in stand 10, thirteen, of the twenty-one quadrats sampled in each, contained juvenile Cyathea spp.

The prominence of other life forms is given in Table 13. Both stands were markedly similar in respect of these. The content of small herbs, zingiberaceous herbs and Musa spp. was low in both stands and only small numbers of softwood trees were establishing themselves. Most of this last group was the structurally small Melastoma cf. polyanthum and Ficus sp. neither of which was capable of attaining a stature sufficiently large to overtop the tree fern canopy. Hardwood trees were establishing only sporadically and it seemed probable that considerable time would elapse before these replaced the tree ferns as the predominant life forms of the stands. To conclude, therefore, the two stands were remarkably similar. Casual observations in other unsampled stands confirmed the general similarity of all regrowth vegetation in which tree ferns predominated.

Table 13. The prominence of minor life forms in stands 9, 10. SF, summed frequency; %M, % of total mass contributed by this type

Stand	Small herbs		Large musaceous herbs			Large zingiberaceous herbs			Softwood trees			Hardwood trees		
	Spp.	%M	Spp.	SF	%M	Spp.	SF	%M	Spp.	SF	%M	Spp.	SF	%M
9	45	5.13	2	4	0.83	2	9	0.30	6	27	2.54	6	7	0.04
10	32	6.48	2	4	2.49	2	17	1.51	3	11	2.58	10	16	2.24

Stand with hardwood trees predominant (12)

The history of this stand has been discussed in some detail above. Hardwood trees made up 9% of the stand mass and formed an irregular, but closed, canopy at 20-30 m height (Plate 2). Tree density (1 tree every 5.8 sq. m) was low in comparison with other regrowth stands although slightly higher than that of the primary forest stand (1 tree every 6.9 sq. m). The hardwood trees appeared to be reproducing themselves satisfactorily in situ; twenty juvenile tree species were counted with a summed frequency of 44. Other life forms were not prominent; zingiberaceous herbs and Musa spp. were absent, while herbs, none of which were typical field weeds, made up less than 1% of the stand mass. Only a single softwood tree seedling was recorded. Tree ferns were the only other prominent group, contributing 3.7% of the stand mass. Juvenile tree ferns were recorded in half of the quadrats and they therefore appeared to be maintaining themselves, if only as a subordinate stratum.

Stands with mixed life form predominance (2,7,8,12,17,18)

These stands appeared to be either in a transitional phase between predominance of one of the several life form types given above or, as in stands 7 and 8, were aberrations from an apparent successional trend from herb predominance to hardwood tree predominance through intermediate stages of softwood and/or tree fern predominance.

Stand 18 was a relatively young stand of low total plant mass (2.3 kg/sq. m) most of which was concentrated in the intermediate layer. While casual inspection suggested that young softwoods of 2-3 m height were predominant in the stand, sampling revealed that these made up only 22% of the total mass, while wild banana contributed 46% to it. Probably, softwood tree species were in process of overtopping a stand composed of juvenile forms of Musa sp.. Omalanthus cf. surigaoense was the most common softwood tree; it occurred in 13 of the 18 quadrats counted and constituted 8.7% of the stand mass. Other common softwoods were Mallotus paniculatus (3.1%), Omalanthus cf. populneus (4.8%) and Trema orientalis (3.5%).

At the time of sampling it was impossible to determine the degree to which the prominent trees might regenerate as all individuals

were still juvenile. Although, when first seen in early 1964, the site was covered by small herbs (mainly composites), a year later these constituted only 19% of the stand. Zingiberaceous herbs made up only 0.6% of the stand and appeared destined for extinction, while tree ferns made up 2.4% of the mass but were counted in only 5 quadrats. Of greatest interest was the number of hardwood tree seedlings present in the ground layer (21 species with a summed frequency of 42), which was comparable with the numbers sampled in primary forest. This large number of forest species, together with a full complement of regrowth species, made this floristically the richest stand sampled with 105 species recorded (Table 10). Clearly this stand possessed the potential seedling population to ensure eventual re-establishment of the forest.

Stand 2 was analagous to stand 18 in that young softwood trees were beginning to predominate. Here, however, they were overtopping an established herb layer instead of young Musa sp., and were of more patchy distribution than in stand 18, an apparent reflection of less successful germination. Floristic richness was less than half that of stand 18 and only 45 species were recorded. The commonest softwood tree was again Omalanthus cf. surigaoense which contributed 13% to the stand mass, while Omalanthus cf. populneus made up 11%, Mallotus paniculatus, 4.1% and Ficus sp., 3% of the total stand mass. The herb layer was still prominent and constituted 35% of the stand mass. Two species, Pteridium aquilinum and Paspalum conjugatum made up most of this group, each contributing 14% to the total. The two zingiberaceous herbs constituted 10% and Musa spp. remnants 18%, of the total. Juvenile tree ferns were counted in 5 quadrats but constituted less than 1% of the total mass at the time of sampling. Only one hardwood tree seedling was counted. The immediate future of the stand, therefore, appeared to be predominance by softwood trees but, because these were mainly shorter-lived species, they may eventually have been replaced by tree ferns. It seemed that re-establishment of forest on the site would be an extremely slow process.

Stand 7 was selected as representative of regrowth in which the large zingiberaceous herb Hornstedtia sp. appeared to predominate (Plate 10). Sampling revealed, however, that although it occurred in all quadrats, it constituted less than 22% of the total stand mass, and

patchily distributed softwoods and tree ferns each made up a greater percentage of the total (31% and 27%, respectively). Total stand mass was comparable to that of stand 4 (Table 10). The most prominent tree was Mallotus paniculatus (16% of total weight) but this species was restricted to a single clump. Clerodendrum sp. made up 6.9% of the total while other softwood species contributed less than 2%. Only 47 species were counted. Hornstedtia sp., reproducing vegetatively by rhizomes, seemed to be maintaining its visually prominent position. Only 5 juvenile softwood tree species were recorded with a summed frequency of 13, while juvenile Cyathea spp. were counted in only 3 quadrats. Small herbs made up 4.9% of the stand mass, a surprisingly low proportion in view of the light shade cast by Hornstedtia sp. Only a single hardwood sapling was counted. There did not appear to be any prospect for drastic change in this stand in the near future. Because of the poor establishment of softwood species and tree ferns, it seemed that these would continue to be patchily distributed if they did not yield completely to competition from the spreading Hornstedtia sp.

Although tree ferns were the predominant group in stand 8, they only made up 31% of the total mass, while softwood trees made up 24% and Musa textilis 22%. These features served to distinguish the stand from numbers 9 and 10. Total plant mass and floristic variety were similar to those of these stands, however (11.6 kg/sq. m and 61 species). The prominent position of Musa textilis was probably the result of periodic harvesting of the mature stalks by local farmers, a continual disturbance that may also have accounted for the high proportion of softwood trees. Several species of this life form were present, the most prominent being Clerodendrum sp. (14%), Macaranga aleuritoides (5.9%), Ficus sp. (4.4%), and Omalanthus cf. surigaoense (2.5%). All groups in the overstorey seemed to be maintaining themselves; juvenile Cyathea spp. occurred in 12 quadrats while 6 species of softwood trees, with a summed frequency of 16, were recorded. Musa textilis appeared to be reproducing vegetatively. Small herbs made up 13% of the stand mass although no single species contributed more than 0.5%; zingiberaceous herbs made up 3.9% of total stand mass. Seven species of hardwood trees, with a summed frequency of 9, were recorded but only one had attained a height of over 3 m. As the structurally prominent species in the stand were maintaining themselves, it seemed likely that the stand would change little in appearance until the hardwood trees matured.

Although of similar age and history to stand 12, stand 11 had a somewhat different composition, softwood trees being prominent there at the time of sampling. Average total stand mass was comparable (37.1 against 41.9 kg/sq. m), however, as was floristic richness (78 against 81 species). Tree density at one tree every 6.4 sq. m, and canopy height at 15-30 m, were also similar, although the latter feature had greater range in stand 11. Softwood trees made up 47% of the stand mass, most of this being contributed by Mallotus paniculatus (35%) and Trema orientalis (6.8%). Hardwood trees made up 43% of the stand mass, the commonest species being more numerous. Lauraceae sp. comprised 12%, Lithocarpus sp. 7.3%, Lithocarpus sp. 8.4%, cf. Syzygium sp. 7.7%, and cf. Geunsia sp. 4.8% of the total stand mass. These hardwood trees appeared to be reproducing themselves more successfully than the softwoods; while only 4 softwood species with a summed frequency of 5 were counted, 9 hardwood species with a summed frequency of 10 were recorded. Tree ferns made up 8% of the stand mass and juvenile forms were counted in 11 quadrats. Neither Musa spp. nor any large zingiberaceous herbs were present, and small herbs contributed only 1.7% to the stand mass, a figure comparable with that of primary forest. It seemed certain that this stand would proceed steadily toward complete predominance of hardwood trees and the re-establishment of the forest ecosystem.

Stand 17 was unique among the sampled stands in not having undergone complete clearance. Logging had removed the larger trees and, at the time of sampling, medium-sized and small hardwood trees were predominant, making up 97% of the stand. Plant mass had been severely reduced from the levels of primary forest and only amounted to 55.4 kg/sq. m. An abundance of regrowth species had entered the stand but these constituted only a minor portion of the total mass. Of great interest were the numbers of juvenile hardwood trees; 26 species were counted with a summed frequency of 63. Most were relatively large and appeared to have germinated prior to logging. Moreover, none of them were dying in the changed micro-environment. At the time of sampling most were soon to be overtopped by regrowth species and returned to a less hostile micro-environment, and it seemed likely, therefore, that these seedlings would survive and eventually fill the canopy gaps. Whether the trees that were left standing survived is uncertain; many had been damaged but none showed signs of impending

death at the time of sampling. However, observations from older remnants of hardwood forest suggest that they might eventually succumb. While the abundant hardwood seedlings ensured an eventual return to forest, the speed with which the structure was to be restored depended upon the survival of advanced growth left standing.

STAND MORPHOLOGY, STABILITY AND THE EFFECTS OF AGE

A high proportion of the stands sampled could be relegated to distinct classes on the basis of the overwhelming predominance of a single life-form in each. As stands were selected (with as little bias as possible) to represent the secondary vegetation of the area, the same applies to the whole. The main life form types were small herbs, softwood trees, tree ferns and hardwood trees, each of which made up more than 50% of the mass in at least one stand. Although stands within each class differed in detail, all were grossly similar in vertical arrangement of mass and in tree density.

A more detailed examination of the stands revealed that only stand 12, in which hardwood trees predominated, was in a stable self-perpetuating state. Both the hardwood trees and the subordinate tree ferns were reproducing themselves in numbers comparable to those in primary forest and other life forms were virtually excluded from the stand. In all other stands, even where the predominant life form was reproducing itself, some juvenile plants of other, larger, life forms were established, indicating an inherent instability.

Attempts to relate stand structure to time inevitably involve using variation observed in space to hypothesise a sequence in time. The justification for this, although circumstantial, is none the less strong. In the first place, stands could be dated with some accuracy and were not, therefore, merely elements of a spatial mosaic of unknown history. Secondly, they occupied an area of generally similar macro-environment, which would be expected to reduce selective effects un-related to time. Thirdly, the stands were sufficiently close to each other to permit the assumption that they were drawing from roughly the same source population of species. Fourthly, the instability of all stands (save stand 12) illustrated the likelihood that none was going to maintain the structure observed at

the time of sampling over an extended period. Finally, my own observations over a 20-month period confirmed this instability in the youngest stands, while local informants could attest to the changes that had taken place in the older stands.

If the main structural elements (life forms) occurring in the vegetation are related to age of the stands, several salient points emerge.

- a) It was only in the younger stands that small herbs predominated; stand 14 was the single exception to this.
- b) Conversely, hardwood trees were only prominent in the two oldest stands, numbers 11 and 12.
- c) Stands of intermediate ages had either softwood trees or tree ferns as their predominant life form.

These points have been illustrated in Fig. 13, where the percentages of total stand mass contributed by the four groups (plus the two morphological groups of large herbs) are plotted against time. For clarity, the means of stands in 5-year age periods have been used. It is inferred from this evidence that structure of secondary vegetation occupying a given site in the study area changed progressively (although not necessarily at a uniform rate) from being composed predominantly of small herbs to being composed predominantly of hardwood trees through a number of intermediate structures, also with a single life form predominant which was commonly either softwood trees or tree ferns or both. The section which follows is a critical examination of this staged succession of life forms. It attempts to determine whether it was a product of the parallel staging of species populations and if this is not the case, the exact cause to which it must be attributed.

Figure 13. The change since time of abandonment in the prominence of the six life forms distinguished in the secondary vegetation of the study area.

PLANT SUCCESSION

Clements (1928), to whom the first clear enunciation of the concept of plant succession must be attributed, recognised successional stages on floristic, structural and even habitat characteristics. Subsequent discussion of the concept, however, has tended to emphasize the floristic aspect of plant succession (e.g. Whittaker 1953). The term succession is used here to refer to an elimination of any attribute followed, in most cases, by its replacement with another, different, attribute. As applied to vegetation, therefore, the term implies elimination and replacement of a species or distinct structural element and does not include a generalized attribute, such as plant mass, which is additive. In contrast to Clements' use of the term, "plant succession", as used here, does not imply a specific direction of change but only vegetation change itself, of the type outlined above.

The analysis assumes that the macro-environment of sites was similar and that, consequently, micro-environmental differences between stands were due to differing vegetation covers. The analysis also assumes that all sites were drawing on roughly the same species population; this requires all sites to have begun re-vegetation with similar viable propagule populations in or on the soil and, since abandonment, to have received a rain of viable propagules of similar composition from external sources. The validity of these two assumptions is tested later.

The structural changes that were taking place in the study area, by the definition of succession given above, can be regarded as successional; they involved the successive elimination of distinct life form types from each stand followed by their replacement with other, equally distinct, types. Two possible explanations can be advanced for this structural succession. Firstly, it may have reflected the differing growth rates of an established population of species, each group of species of similar life form maturing and dying successively. If this were the case, however, the succession would have become cyclical, and there was no evidence of this occurring except in stand 4 where a herb layer seemed to be re-emerging after the death of the predominant softwoods. The comparison of species lists, moreover, revealed that many stands' floras were almost totally different from those of other stands,

the greatest differences tending to be between the youngest and oldest stands. It seemed more likely, therefore, that the successive changes of structural types were the products of successive waves of invading species, a successional process appropriately termed "relay floristics" by Egler (1954). Both casual observations in the field and classical theories of plant succession support this second hypothesis which, in the sections that follow, is examined first.

FLORISTIC SUCCESSION

The successive elimination and replacement of species in a stand of vegetation may be accounted for in either of two ways. Firstly, it may represent the summed effects of chance entrants into and discards from the stand. Chance discards from a stand are theoretically unlikely to occur, however, as conditions are optimal in terms of the accessibility factor for self-maintenance of the flora; the overwhelming proportion of propagules reaching the soil surface of a stand will be produced by the mature individuals of that stand leading to a strong tendency toward floristic stability. Chance entrants into a stand cannot be discounted as a reason for change but, if the external propagule rain on a stand has been constant throughout its re-vegetation, the total received will be small in comparison with that produced locally, and the plants so represented will have a correspondingly small chance of establishment. Chance entrants into, and discards from, the stand, therefore, cannot in themselves provide a satisfactory explanation for floristic succession.

The sole alternative explanation is a change in the stand micro-environment, induced by the current vegetation, which inhibits the regeneration of its constituent species but permits that of other species. Such an inhibition may be absolute, precluding the establishment of any offspring, or relative, involving the production of a micro-environment in which offspring cannot compete successfully with new entrants. If this process occurs, the succeeding species will be representatives of the external propagule rain or of the propagules lying dormant in the soil. This hypothesis of self-induced succession, although basic to Clements' concept of the process designated as "autogenic" succession by Tansley (1935), has been subjected to few experimental examinations (Crocker and Major 1955; Olson 1958).

To examine whether this process was occurring in the vegetation of the study area, two series of tests were conducted. The first examined micro-environmental conditions of stands to determine whether changes were taking place and, if they were, the causes for them. The second series examined the environmental conditions required for the establishment of various species.

In both series of analyses all computations have been made using stand mean values for both micro-environmental phenomena and vegetation characteristics. Although a number of the phenomena were measured at several points within each stand, permitting correlations on a quadrat basis, such a procedure would have necessitated two systems of analysis and would have restricted the number of species available for treatment as few occurred with sufficient frequency. Consequently, all data have been treated on the basis of stand means, with certain within-stand frequency requirements for inclusion of a species in an analysis. Because of this use of means, it is necessary to demonstrate, wherever possible, that the micro-environments of stands were significantly different. In Table 14, stand means of all phenomena measured are summarized and, where sub-samples were taken, the levels of significance of their differences, based on analyses of variance, are given.

Stands' percentage radiation receipts, daily maximum and minimum air temperature differences and mean annual soil moisture tensions were significantly different at the 0.001 level of probability. Percentage receipts of blue and red radiation in stands were significantly different at the 0.01 and 0.1 levels of probability, respectively. Soil moisture spatial instability was significantly different only at the 0.2 probability level, and receipts of green radiation not significantly different even at this level, suggesting that within-stand variation in these two phenomena were too great to permit much reliance to be placed on correlations using stand means. However, other phenomena appeared to be sufficiently different between stands to justify an investigation into causes of these and the response of establishing plants to them.

Table 14. Mean micro-environmental conditions of sampled stands and the probability levels of their differences (where applicable)

Phenomena	Stand																		Prob- ability levels
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
% total radiation	17.16	20.72	11.99	10.54	4.84	10.94	24.81	5.82	14.84	15.17	5.63	3.94	2.49	8.34	11.78	11.30	18.95	10.03	P < .001
% blue radiation	15.35	79.93	13.62	11.91	0.67	7.98	76.46	6.52	65.23	18.08	8.27	3.53	1.70	18.20	32.96	10.35	19.50	3.29	P < .01
% green radiation	15.84	8.40	8.20	9.71	9.35	11.20	16.50	11.75	9.20	10.46	3.46	4.95	8.43	11.62	9.13	17.56	18.54	9.75	P > .2
% red radiation	19.26	22.17	14.99	12.39	5.55	14.04	26.90	7.57	13.33	15.92	6.20	4.97	2.43	7.66	9.07	12.76	19.07	11.57	P < .1
Daily max. temp. depressions (°C)	1.92	2.40	5.70	4.60	5.35	6.08	4.64	4.87	5.22	6.72	5.10	6.57	7.45	6.50	4.35	2.57	3.55	4.30	P < .001
Daily min. temp. differences (°C)	+0.06	-0.68	+0.68	-0.13	-0.70	-0.08	+0.96	+0.34	+0.22	+0.50	+0.70	-1.47	-1.30	+0.24	+0.42	-0.23	-0.22	+0.04	P < .001
Soil moist. spatial instability (cm)	47.14	50.35	48.62	47.14	62.69	34.35	356.91	48.57	50.87	40.38	53.88	56.92	35.72	56.01	40.68	32.79	27.27	62.02	P > .2
Soil moist temporal instability (cm)	88.2	57.5	77.7	38.8	51.2	53.4	27.0	177.3	45.8	23.7	49.8	22.8	40.7	29.1	129.6	47.1	33.5	39.3	
Mean annual soil moist. condition (cm)	139.1	169.3	116.7	61.4	208.7	63.2	94.4	243.6	125.0	82.8	104.5	155.9	124.8	76.1	150.1	51.9	96.0	154.2	P < .001
Soil pH (H ₂ O)	5.7	5.3	5.2	5.5	5.2	4.9	5.5	5.4	5.3	5.8	5.7	4.7	4.7	5.7	6.0	5.7	4.6	4.7	
Soil pH (KCl)	4.8	4.3	4.3	4.5	4.3	4.3	4.4	4.4	4.1	4.3	4.8	3.8	4.2	4.5	4.8	4.8	3.8	4.0	
% carbon in surface soil	3.23	2.90	9.05	6.15	9.71	10.23	4.05	3.86	7.48	4.46	4.16	7.10	8.50	4.04	2.66	3.41	8.81	7.12	
% nitrogen in surface soil	0.47	0.41	0.57	0.46	0.46	0.95	0.43	0.45	0.58	0.24	0.55	0.89	1.09	0.42	0.30	0.36	0.73	0.53	
CEC of surface soil (meq/100 gm)	46.90	42.17	46.46	45.26	42.03	58.93	43.26	38.76	41.37	37.33	39.58	73.53	76.63	33.04	21.20	28.99	63.74	44.84	
P ₂ O ₅ in surface soil (ppm)	24	24	48	24	20	110	24	14	Tr.	30	24	50	40	20	30	60	48	20	
Exch. Ca in surface soil (meq/100 gm)	4.41	2.29	3.30	6.02	4.39	6.66	3.89	4.18	2.30	3.91	6.80	2.34	2.64	5.32	4.66	6.34	1.78	2.28	
Exch. Mg in surface soil (meq/100 gm)	0.83	0.31	0.82	0.95	0.67	1.99	1.02	0.75	Tr.	0.89	1.60	0.97	1.04	0.74	0.68	0.94	0.19	0.05	
Exch. K in surface soil (meq/100 gm)	0.78	0.45	0.45	1.35	0.56	0.35	0.44	0.40	0.14	0.45	0.40	0.46	0.45	0.45	0.54	0.77	0.40	0.45	
Exch. Na in surface soil (meq/100 gm)	0.04	0.04	0.04	0.14	0.10	0.19	0.10	0.29	0.10	0.10	0.14	0.29	0.10	0.04	0.04	0.04	0.10	0.14	
C/N ratio of surface soil	6.9	7.1	15.9	13.4	21.1	10.8	9.4	8.6	12.9	18.6	7.6	8.0	7.8	9.6	8.6	9.5	12.1	13.4	

Stand micro-environmental changes

A number of distinct models of micro-environmental changes taking place in an autogenic succession may be envisaged. Some changes may take place as a stand ages regardless of vegetation type, while others may be produced by certain gross characteristics of the vegetation itself such as its total mass or the mass occupying a given layer. Others may be related to some more detailed characteristic of the vegetation such as the prominence of a particular species or life form. In instances where time, or changes in vegetation mass, are inducing a micro-environmental change, attempts to correlate the prominence of a plant species or life form with the changing phenomenon may produce misleading results. Fig. 14 represents a hypothetical succession in which plant groups (species or life forms) rise and fall, together with a progressive change in an un-related variable. If either intermediate group (B,C) is correlated with the variable, a low coefficient will result (Fig. 15a). If, however, stands sampled include terminal groups, in which only an increase or decrease in prominence is sampled (A,D), then a high, but spurious, correlation coefficient may be calculated (Fig. 15 b, c). As the stands sampled included a progressive decline in prominence of small herbs in the younger stands, and a progressive rise in hardwood trees in the older stands, this feature must be borne in mind when interpreting the results that follow.

Where some plant group does, in fact, produce a change in some micro-environmental factor, two extremes and any number of intermediate conditions may occur. The change produced may be unique, with values changing as the group rises and returning to "normal" as it declines, or the change induced by the group may be maintained in a steady state thereafter despite the decline of the group. In the first instance a high, and valid, correlation coefficient will be recorded, while in the second, a relatively low apparent coefficient will result which will not reveal the true nature of the relationship. While the models postulated are hypothetical, an appreciation of the possibilities that exist enables a realistic interpretation of the field results to be made.

Figure 14. The change of plant groups (A,B,C,D) in a hypothetical succession, accompanied by a change in an un-related environmental variable.

Figure 15. Scatter diagrams of the relationship between the prominence of certain plant groups in Fig.14 and the un-related environmental variable. (a) The relationship for an intermediate plant group (B) which shows the lack of any correlation: (b) and (c) the relationships for the terminal plant groups in the succession, (A),(D), where a high, but spurious, correlation is indicated.

To detect the possible causes of micro-environmental change, a matrix of linear correlation coefficients between 20 micro-environmental variables and 47 vegetation variables as well as time was computed. The 47 vegetation variables, each assumed to be independent, included certain structural characteristics, life forms and individual species (Tables 15, 16, 17, 18). For exploratory purposes linear regressions are assumed; the calculated coefficients provide crude indications of possible relationships and, possessing equal numbers of degrees of freedom, are comparable. Where significant correlations are indicated, the relationship is critically examined and coefficients are, in some instances, rejected as spurious.

The effects of stand age

Correlation coefficients significant at the 0.05 probability level were recorded between stand age and the percentage total, green and red radiation and daily maximum temperature depressions (Table 15). These coefficients were higher than all those between these variables and vegetation characteristics (Tables 16, 17, 18), suggesting that stand age, irrespective of cover type, was producing radiation and daily maximum temperature changes on the ground. Correlations with the logarithms of stand age were not significantly higher. However, considerable changes in both radiation and daily maximum temperatures had already taken place during the brief, unsampled, period between bare ground conditions and a complete herb cover. During this period, lasting no more than a few months, radiation had fallen from 100% to under 25%, and daily maximum temperature differences had changed from zero or positive values to depressions of approximately 2°C. Nevertheless, there appeared to be a tendency thereafter for a progressive change with time irrespective of the predominating vegetation type. Thus, for example, stand 14, despite its predominant herb layer, had similar daily maximum air temperatures and radiation percentages to stands 11 and 12, of similar age but markedly different cover.

Reasons for these changes appear to be a tendency for all vegetation types in the area to form an increasingly complete foliage cover that made progressively more efficient use of incident radiation and in so doing created an increasingly efficient barrier to the passage

Table 15. Linear correlation coefficients of twenty micro-environmental variables with stand age and log stand age. Coefficients significant at the .05 level of probability are underlined.

<u>Micro-environmental variable</u>	<u>Correlation coefficient</u>	
	<u>Stand age</u>	<u>Log stand age</u>
% total radiation	-. <u>689</u>	-. <u>608</u>
% blue radiation	-.329	-.205
% green radiation	-. <u>503</u>	-. <u>508</u>
% red radiation	-. <u>708</u>	-. <u>614</u>
Daily max. temp. depressions ($^{\circ}\text{C}$)	+. <u>724</u>	+. <u>738</u>
Daily min. temp. differences ($^{\circ}\text{C}$)	-.408	-.174
Soil moist. spatial instability (cm tens.)	-.126	-.009
Soil moist. temporal instability (cm tens.)	-.189	-.134
Mean annual soil moist. condition (cm tens.)	+.056	-.022
Soil pH (H_2O)	-.146	+.094
Soil pH (KCl)	-.109	+.019
% carbon in surface soil	+.204	+.132
% nitrogen in surface soil	+.443	+.200
CEC of surface soil	+.400	+.126
P_2O_5 in surface soil (ppm)	-.144	+.102
Exch. Ca in surface soil (meq/100 gm)	+.026	+.254
Exch. Mg in surface soil (meq/100 gm)	+.273	+.388
Exch. K in surface soil (meq/100 gm)	-.066	+.040
Exch. Na in surface soil (meq/100 gm)	+.308	+.344
C/N ratio of surface soil	-.030	+.123

Table 16. Linear correlation coefficients of micro-environmental conditions with the mass of stand vegetation. Coefficients significant at the 0.05 probability level are underlined.

<u>Micro-environmental variable</u>	<u>Correlation coefficients with vegetation mass characteristics</u>				
	<u>Ground layer</u>	<u>Intermed. layer</u>	<u>Overst.</u>	<u>Intermed. + overst.</u>	<u>Total</u>
% total radiation	+ .629	+ .069	- .381	- .381	- .380
% blue radiation	+ .319	+ .025	- .212	- .212	- .212
% green radiation	+ .427	+ .283	- .152	- .160	- .150
% red radiation	+ <u>.709</u>	+ .031	- .392	- .396	- .395
Daily max. temp. depressions ($^{\circ}\text{C}$)	- <u>.566</u>	- .066	+ .426	+ .426	+ .425
Daily min. temp. differences ($^{\circ}\text{C}$)	+ .096	+ .159	- <u>.490</u>	- <u>.490</u>	- <u>.490</u>
Soil moist. spatial instability (cm tens.)	+ .242	+ .004	- .103	- .103	- .103
Soil moist. temporal instability (cm tens.)	+ .036	- .117	- .120	- .121	- .121
Mean annual soil moist. condition (cm tens.)	- .107	+ .356	+ .007	+ .005	+ .005
Soil pH (H_2O)	+ .011	+ .276	- .378	- .376	- .377
Soil pH (KCl)	+ .096	+ .239	- .153	- .152	- .152
% carbon in surface soil	- .146	- .349	+ .269	+ .268	+ .268
% nitrogen in surface soil	- .029	- .258	+ <u>.619</u>	+ <u>.618</u>	+ <u>.618</u>
CEC of surface soil (meq/100 gm)	+ .121	- .311	+ <u>.570</u>	+ <u>.569</u>	+ <u>.569</u>
$\text{P } \frac{0}{2} \frac{5}$ in surface soil (ppm)	+ .113	- .093	+ .074	+ .074	+ .074
Exch. Ca in surface soil (meq/100 gm)	- .116	+ .239	- .223	- .232	- .232
Exch. Mg in surface soil (meq/100 gm)	- .002	- .081	+ .126	+ .125	+ .125
Exch. K in surface soil (meq/100 gm)	+ .104	+ .132	- .080	- .079	- .079
Exch. Na in surface soil (meq/100 gm)	- .217	- .383	- .016	- .018	- .018
C/N ratio of surface soil	- .245	- .237	- .208	- .209	- .084

Table 17 Linear correlation coefficients of micro-environmental conditions with relative prominence of plant life-forms in sampled stands. Coefficients significant at the 0.05 probability level are underlined.

<u>Micro-environmental</u> <u>variable</u>	<u>Correlation coefficients with</u> <u>plant life-form types</u>					
	<u>Hardwood</u> <u>trees</u>	<u>Tree</u> <u>ferns</u>	<u>Softwood</u> <u>trees</u>	<u>Large</u> <u>zing.</u> <u>herbs</u>	<u>Large</u> <u>musac.</u> <u>herbs</u>	<u>Small</u> <u>herbs</u> <u>etc.</u>
% total radiation	-.358	+.223	-.115	+.381	+.163	+.067
% blue radiation	-.342	+.323	-.125	+.339	+.094	+.065
% green radiation	-.149	-.020	-.264	+.506	+.066	+.224
% red radiation	-.363	+.179	+.016	+.120	+.236	-.044
Daily max. temp. depressions ($^{\circ}\text{C}$)	+.319	+.276	+.050	-.444	-.217	-.303
Daily min. temp. differences ($^{\circ}\text{C}$)	-.621	+.338	+.199	+.127	+.206	+.180
Soil moist. spatial instability (cm tens.)	-.170	+.084	+.071	+.469	+.229	-.125
Soil moist. temporal instability (cm tens.)	-.311	-.070	+.070	-.110	+.153	+.279
Mean annual soil moist. condition (cm tens.)	+.075	-.076	+.043	-.301	+.329	-.131
Soil pH (H_2O)	-.670	.000	-.017	-.282	-.255	+.610
Soil pH(KCl)	-.557	-.158	+.126	+.334	-.202	+.670
% carbon in surface soil	+.410	+.002	+.359	-.395	-.072	-.593
% nitrogen in surface soil	+.718	-.183	-.052	-.336	-.134	-.455
CEC of surface soil (meq/100 gm)	+.795	-.152	-.098	-.315	-.104	-.591
P_2O_5 in surface soil (ppm)	+.184	-.224	+.159	+.114	-.138	-.092
Exch. Ca in surface soil (meq/100 gm)	-.097	-.119	+.352	+.254	-.263	+.315
Exch. Mg in surface soil (meq/100 gm)	+.107	-.114	+.312	+.080	-.306	-.078
Exch. K in surface soil (meq/100 gm)	-.189	-.379	+.233	+.259	-.154	+.227
Exch. Na in surface soil (meq/100 gm)	+.347	+.140	+.014	-.228	+.180	-.243
C/N ratio of surface soil	-.188	+.332	+.425	-.173	-.023	-.293

Table 18. Linear correlation coefficients of micro-environmental conditions with the relative prominence of individual species in sampled stands. Coefficients significant at the 0.05 probability level underlined.

Micro-environmental variable	Hardwood trees				Softwood trees		
	<u>Lithocarpus sp.</u> (1732)	<u>Ficus sp.</u> (1867)	<u>Indet. sp.</u> (1877)	<u>Lithocarpus sp.</u> (1886)	<u>Melastoma cf.</u> <u>polyanthum</u> (1520)	<u>Omalanthus cf.</u> <u>surigaense</u> (1535)	<u>Clerodendrum sp.</u> (1547)
% total radiation	-. <u>503</u>	+.100	-.259	-.357	-.057	+.068	-.015
% blue radiation	-.298	-.156	-.217	-.220	-.100	-.054	+.012
% green radiation	-.355	-.199	-. <u>520</u>	-.386	-.099	-.164	+.151
% red radiation	-. <u>502</u>	+.110	-.202	-.327	-.005	+.179	+.052
Daily max. temp. depressions (°C)	+. <u>492</u>	-.194	+.155	+.301	+.015	+.080	-.034
Daily min. temp. differences (°C)	-. <u>672</u>	-.013	+.323	-. <u>562</u>	+.105	+.231	+.252
Soil moist. spatial instability (cm tens.)	-.110	-.074	-.079	-.034	+.042	-.085	+.321
Soil moist temporal instability (cm tens.)	-.250	-.180	-.014	-.225	+.015	+.120	+. <u>498</u>
Mean annual soil moist. condition (cm tens.)	+.085	+.064	-.133	+.177	-.604	-.092	+.287
Soil pH (H ₂ O)	-.367	-. <u>531</u>	+.074	-.371	+.086	-.147	+.113
Soil pH (KCl)	-.395	-. <u>486</u>	+.235	-.439	+.044	-.061	+.086
% carbon in surface soil	+.282	+.262	+.082	+.179	+.151	+.366	-.204
% nitrogen in surface soil	+. <u>743</u>	+.090	+.138	+.402	-.207	+.104	-.174
CEC of surface soil (meq/100 gm)	+. <u>771</u>	+.156	+.002	+. <u>496</u>	-.114	+.005	-.116
P ₂ O ₅ in surface soil (ppm)	+.165	-.042	+.144	+.207	-.215	+.342	-.236
Exch. Ca in surface soil (meq/100 gm)	-. <u>339</u>	-.427	+.364	-.221	+.226	-.025	+.156
Exch. Mg in surface soil (meq/100 gm)	+.169	-. <u>500</u>	+. <u>490</u>	+.139	-.017	+.125	+.072
Exch. K in surface soil (meq/100 gm)	-.116	-.121	-.179	-.069	+. <u>693</u>	-.024	+.272
Exch. Na in surface soil (meq/100 gm)	+.348	+.053	+.086	+. <u>584</u>	+.153	-.165	+. <u>523</u>
C/N ratio of surface soil	-.316	+.161	-.087	-.143	+.419	-.207	-.098

Table 18.

Softwood trees (contd.)					Zingiberaceous herbs		Musaceous herbs	
<u>Trema orientalis</u> (1596)	<u>Ficus sp.</u> (1662)	<u>Onalanthus cf. populneus</u> (1734)	<u>Mallotus paniculatus</u> (1735)	<u>Laportea sp.</u> (1736)	<u>Costus speciosus</u> (1519)	<u>Hornstedtia sp.</u> (3440)	<u>Musa sp.</u> (3432)	<u>Musa textilis</u> (3442)
+ .119	-.050	+ .371	-.257	-.049	+ .218	+ .445	+ .052	+ .240
-.209	-.072	+ .514	-.136	+ .009	+ .193	+ .400	-.022	+ .243
-.109	-.071	-.081	-.223	-.346	+ .125	+ .508	-.120	+ .382
-.031	-.011	+ .381	-.245	+ .030	+ .212	+ .488	+ .100	+ .303
+ .193	-.008	-.455	+ .069	+ .090	-.494	-.282	-.179	-.124
+ .046	+ .067	-.207	+ .005	+ .330	-.049	+ .277	+ .001	+ .387
-.110	-.007	+ .074	+ .187	-.075	+ .028	+ .763	-.026	+ .556
-.067	-.035	-.081	-.150	+ .103	-.058	-.132	-.066	+ .490
-.262	-.253	+ .263	+ .229	-.052	-.246	-.286	+ .203	+ .292
-.225	-.117	-.114	+ .110	+ .033	+ .252	+ .250	-.377	+ .212
+ .532	+ .150	-.119	+ .172	+ .097	+ .344	+ .255	-.299	+ .170
+ .407	-.052	-.244	-.176	+ .195	-.397	-.309	+ .099	-.352
+ .424	-.156	-.203	+ .162	-.010	-.301	-.295	-.025	-.236
+ .191	-.071	-.107	-.166	-.041	-.327	-.237	-.015	-.192
+ .725	-.172	-.155	-.227	+ .073	+ .188	+ .024	-.075	-.142
+ .460	+ .334	-.334	+ .302	-.042	+ .221	-.230	-.330	+ .102
+ .647	+ .101	-.375	+ .156	+ .139	-.040	+ .140	-.385	+ .123
-.119	+ .773	-.069	+ .080	-.030	-.157	+ .262	-.119	-.089
+ .272	+ .159	-.223	-.038	-.200	-.339	-.100	+ .025	+ .332
-.019	+ .112	-.143	+ .422	+ .188	-.247	-.102	+ .088	-.226

Table 18.

Tree ferns	Grasses		Vines						
<u>Cyathea spp.</u> (3430, 3431)	<u>Paspalum</u> <u>conjugatum</u> (1742)	<u>Imperata</u> <u>cylindrica</u> (3436) var. <u>major</u>	<u>Daemonorops</u> spp. (1518)	? <u>Poikilogyne</u> sp. (1541)	<u>Stietocendra</u> <u>filifolia</u> (1721)	<u>Aristolochia</u> sp. (1764)	<u>Rubus</u> sp. (1769)	<u>Freycinetia</u> sp. (1786)	<u>Rubus moluccana</u> (1771)
+ .233	+ .220	+ .026	- .005	- .145	+ .172	- .218	+ .329	- .138	- .131
+ .323	- .060	+ .082	- .257	- .045	+ .348	- .245	+ .510	- .289	- .213
- .020	+ . <u>503</u>	+ .022	- .024	- .019	- .157	- .199	- .014	- .094	- .154
+ .179	+ .260	- .106	+ .0 <u>31</u>	- .090	+ .086	- .122	+ .252	- .112	- .014
+ .276	- . <u>678</u>	- .216	+ .082	+ .145	+ .293	- .040	- .307	- .014	.000
+ .338	- .008	+ .155	+ .005	+ .233	+ .344	+ .369	+ .022	- .166	+ .124
+ .084	- .120	- .109	- .091	- .138	+ .358	- .124	- .085	- .053	- .140
- .093	+ .145	+ .430	- .262	+ . <u>593</u>	- .302	+ . <u>570</u>	- .026	- .240	+ .276
- .076	- .159	+ .054	+ .003	+ .306	- .297	+ .232	+ .147	+ .222	+ .086
+ .193	+ .335	+ .466	- .399	- .113	+ .300	+ .192	- .030	- . <u>513</u>	- .099
- .158	+ . <u>532</u>	+ .463	- .444	- .098	+ .045	+ .267	- .153	- . <u>504</u>	- .047
+ .002	- .392	- .400	+ .228	+ .202	- .207	- .079	- .027	+ .262	+ .192
- .183	- .241	- .332	+ .031	+ .174	- .226	- .128	- .021	+ .081	- .075
- .152	- .250	- . <u>495</u>	+ .107	+ .004	- .277	- .127	- .013	+ .166	- .038
- .244	+ .139	+ .012	+ .081	+ .137	- .319	- .194	- .198	- .095	- .007
- .119	+ .255	+ .171	- .282	+ .075	+ .061	+ .243	- .344	- .401	+ .138
- .114	+ .041	- .047	- .248	+ .130	- .115	+ .167	- . <u>470</u>	- .410	+ .011
- .379	+ .365	+ .109	- .156	- .372	- .256	+ .260	- .112	- .110	+ . <u>489</u>
+ .140	- .399	- .309	+ .195	+ . <u>518</u>	- .248	+ .281	+ .053	+ .232	+ .290
+ .332	- .289	- .206	+ .316	- .032	- .016	- .024	+ .126	+ .250	+ .267

Table 18.

Ferns		Other herbs				Micro-environmental variable
<u>Nephrolepis</u> sp. (1759)	<u>Cyclosorus</u> sp. (1784)	<u>Elephantopus</u> <u>mollis</u> (1500)	<u>Scleria</u> cf. <u>scrobiculata</u> (1524)	<u>Spathoglottis</u> sp. (1659)	Araceae (1791)	
+ .002	-.094	+ .066	-.017	-.045	+ .151	% total radiation
-.070	-.127	+ .064	-.201	-.081	-.023	% blue radiation
+ .439	+ .219	+ .113	+ .031	-.091	+ .140	% green radiation
+ .009	+ .070	-.057	+ .044	-.037	+ .206	% red radiation
-.312	-.406	-.312	-.245	-.054	-.329	Daily max. temp. depressions (°C)
-.017	+ .164	+ .172	+ .045	+ .003	+ .032	Daily min. temp. differences (°C)
-.056	-.171	-.103	-.083	-.076	+ .035	Soil moist. spatial instability (cm tens.)
-.137	+ .359	+ .425	-.119	-.025	+ .053	Soil moist temporal instability (cm tens.)
-.443	-.159	-.025	-.001	-.266	-.166	Mean annual soil moist. condition (cm tens.)
+ .328	+ . <u>570</u>	+ . <u>549</u>	-.248	+ .193	-.233	Soil pH (H ₂ O)
+ .407	+ . <u>652</u>	+ . <u>567</u>	-.140	+ .184	+ .293	Soil pH (KCl)
-.340	+ .348	-. <u>484</u>	+ .080	-.037	-.188	% carbon in surface soil
-.292	-.391	-.394	-.135	-.163	-.174	% nitrogen in surface soil
-.375	-.414	-. <u>533</u>	-.129	-.102	-.022	CEC of surface soil (meq/100 gm)
+ .193	+ .041	-.028	-.023	-.112	-.189	P ₂ O ₅ in surface soil (ppm)
+ .421	+ .449	+ .252	-.159	+ .310	+ .267	Exch. Ca in surface soil (meq/100 gm)
+ .069	+ .134	-.042	-.351	+ .061	+ .067	Exch. Mg in surface soil (meq/100 gm)
+ .315	+ . <u>696</u>	+ .275	+ .119	+ . <u>826</u>	+ . <u>851</u>	Exch. K in surface soil (meq/100 gm)
-.308	-.335	-.378	-.092	+ .033	-.008	Exch. Na in surface soil (meq/100 gm)
-.135	-.053	-.252	+ .198	+ .129	-.067	C/N ratio of surface soil

of radiation to the ground. With a decline in total radiation reaching the stand floor, a concomitant depression of daily maximum temperatures was to be expected. It is surprising that a corresponding rise in daily minimum temperatures was not produced; this suggests that this type of foliage insulation may have been effective only on shortwave incoming radiation, and was incapable of restricting outgoing longwave nocturnal radiation. Ratios of the radiation receipts in separate wavebands to total receipts are given in Table 19 where the lack of a consistent change in the spectral composition of shade radiation in the stands is illustrated. Because of sampling difficulties only the ratios of red to total radiation can be regarded as reliable and these varied haphazardly about unity with a slight prevalence of higher values, indicating that stand floor radiation was slightly, but consistently, more "red" than external radiation. It must be concluded that the spectral quality of stand floor radiation varied less than could be accurately detected with the instruments used.

There appears, then, to have been a tendency for a gradual reduction in radiation and daily maximum air temperatures over a period of at least 30 years. If species occurred locally with differing tolerances of these phenomena, there would have been a tendency for gradual changes to take place in the stand floras with species more tolerant of low light intensities and less tolerant of high temperatures replacing those less well equipped to establish under these conditions.

The effects of vegetation mass

Linear correlation coefficients computed between the total plant mass of each stand, the mass of each layer (separately and in various combinations) and stand micro-environmental conditions are given in Table 16. Although included in the analysis speculatively, the ground layer mass yielded significant correlations with total and red radiation as well as with maximum daily air temperature depressions. As these coefficients were the converse of those produced by stand age, it is postulated that a cause and effect relationship existed, with ground layer mass tending to decline as stands aged, because of lower radiation receipts and air temperature.

Table 19. Ratios of blue, green and red radiation receipts to total radiation receipts at the stand floors

<u>Stand</u>	<u>Blue/total</u>	<u>Green/total</u>	<u>Red/total</u>
1	1.12	0.92	1.12
2	3.86	0.41	1.07
3	1.14	0.68	1.25
4	1.13	0.92	1.17
5	0.14	1.93	1.15
6	0.73	1.01	1.28
7	3.08	0.67	1.05
8	0.89	2.02	1.30
9	4.40	0.62	0.89
10	1.19	0.67	1.05
11	1.47	0.61	1.10
12	0.90	1.26	1.26
13	0.68	3.39	0.98
14	2.16	1.39	0.92
15	2.80	0.78	0.88
16	0.92	1.55	1.13
17	1.03	0.98	1.04
18	0.33	0.97	1.15

The importance of the intermediate layer as an influencer of micro-environmental conditions appears to have been small as no correlation coefficients significant even at the 0.1 probability level were recorded. Thus, despite the undoubted importance of this layer during the early period of rejuvenation when small herbs predominated, it was relatively insignificant over longer periods.

Overstorey mass in some way influenced daily minimum air temperatures and CEC and nitrogen content of stand surface soils. In no instance did the addition of the masses of the two subordinate layers, individually or in combination, produce an appreciable increase in the correlation coefficients. However, no structural feature of vegetation is fully independent of floristic composition and the higher coefficients recorded between these three environmental phenomena and hardwood trees, considered either as individual species or as a life form type (Tables 17, 18), suggest that these were the more probable "causers" and that weight per se was of secondary importance to the relationship. Plotting the results as a scatter diagram revealed that the forest site (13) played a disproportionately large part in the coefficient; this site had considerably more overstorey mass than any other stand and the regrowth stands themselves showed considerable variation in the supposedly dependent (micro-environmental) variables within a limited range of the supposedly independent (overstorey mass) variable. The tentative conclusion is drawn, therefore, that the overstorey mass of stands was, in itself, of secondary importance in altering the stand floor minimum air temperatures and surface soil CEC and nitrogen, these changes having been more closely related to detailed changes in the vegetation.

The effects of plant life form

The structural succession of distinct life forms that was taking place in the study area suggested that each life form may have been altering its micro-environment in some way to produce a staged succession of micro-environments that may have effectively induced a staged floristic succession. To examine whether these life forms possessed unique properties of micro-environmental alteration, their prominences, expressed as percentages of the intermediate and overstorey layer mass in each

stand, were correlated with the micro-environmental phenomena measured (Table 17). Almost all coefficients significant at the 0.05 level of probability were associated with the two "terminal" groups of hardwood trees and small herbs. It must therefore be concluded that the successional "intermediate" plant life form groups of softwood trees, tree ferns and large zingiberaceous herbs did not produce any unique micro-environmental conditions during their periods of predominance. They may, however, have played a more subtle role in combination with the "terminal" life form types.

The single significant correlation in the "intermediate" groups, that between large zingiberaceous herbs and soil moisture spatial instability, can be discounted for two reasons. Firstly, the inter-stand differences in this variable were not significant; secondly, excessive weight was contributed to the coefficient by a single high co-occurrence of the two variables in stand 7. The apparent high instability of the moisture régime in this stand is attributable to the high tension measurements recorded by a single cell embedded in soil impregnated with tree fern roots. Phenomena showing significant relationships with "terminal" life form groups included minimum air temperature differences, carbon content, CEC, percentage nitrogen and pH of the surface soil. Minimum air temperature differences showed a significant correlation only with the relative prominence of hardwood trees. This coefficient must be interpreted with caution, however, for, as discussed above, topographic position may have been an important determinant of this phenomenon. Stands 12 and 13, in which the greatest temperature depressions were measured, were also the highest stands sampled while stand 11, which had over 40% of its mass made up of hardwood trees, showed one of the highest minimum temperature elevations. It would therefore seem unwise to draw any firm conclusion about the reality of this relationship, particularly when temperature differences were in fractions of a degree C.

Changes in surface soil carbon content

The significant negative correlation between carbon content of the surface soil and the relative prominence of small herbs bespeaks the inability of this life form to induce appreciable soil carbon accretion

either through an inherent low productivity or rapid litter decomposition in the peculiar micro-environment beneath it. Whether the low carbon levels measured in these stands were inherited from prior periods of clearance or were induced by the stands themselves is not clear from the data. The rapid decline in soil organic matter following clearance of rain forest for shifting cultivation is well documented (Nye and Greenland 1960); litter additions cease and decomposition continues, possibly at an accelerated rate. However, different vegetation covers could equally well have the same effect if occupying a rain forest site for sufficient time. Whatever the initial origin of the low soil carbon levels, the herb stands in the study area were clearly incapable of producing appreciable quantities beneath them, even over extended periods, and levels stabilized at low values. In stand 14, for example, the soil carbon level after 23 years of regeneration remained at only 4%, only half the figure for forest soils. Of the two possible causes of this relationship, low productivity or a unique micro-environment, the first is thought to be the more probable. Temperature and moisture conditions beneath a grass cover were not appreciably different from those beneath other vegetation types (Table 14), and the data presented below suggests low litter production in grassland.

Annual litter fall/sq. m/year in each stand is listed in Table 20. For the younger regrowth stands, the figures given provide a fairly accurate measure of organic matter additions to the soil surface, but in older stands and forest some allowance for timber fall is necessary. Nye and Greenland (1960) point out that annual wood production may be used as a measure of this, and use Weck's (1956) figure of 10,000 lb/acre/year for lowland tropical rainforest to compute the nutrient cycle at Kade, Ghana, where this figure represented 106% of the measured annual litter fall in high forest. A similar percentage is used here to increase the litter production of the primary forest stand (13) from 527 to 1086 gm/sq. m/year. Stand 12, the floristic composition of which was closely similar to that of primary forest, is assumed to have had a similar total annual organic debris fall with a proportionately lower timber fall of 382 gm/sq. m/year.

Litter production in a stand of small herbs is not easily measured; the only result that was comparable with those from woody regrowth was

Table 20. Annual litter fall in sampled stands. a, estimated total debris fall with annual timber fall added; b, grassland stands, figures discarded as over-estimates.

<u>Stand</u>	<u>Measured annual litter fall (gm/m^2 per year)</u>	
1	203.6	
2	716.2	
3	697.2	
4	935.6	
5	1,252.6	
6	1,280.2	
7	947.8	
8	761.0	
9	1,111.0	
10	1,215.8	
11	997.2	
12	704.0	(1,086.0) ^a
13	527.4	(1,086.0) ^a
14	1,916.7 ^b	
15	1,926.4 ^b	
16	1,723.1 ^b	
17	752.0	
18	492.0	

obtained in stand 1, where an annual production of only 200 gm/sq. m/year was measured. The rise to prominence of woody vegetation brought with it an abrupt increase in litter production, and in stand 2 this had already exceeded 700 gm/sq. m/year at the time of measurement. In older stands, in which softwood trees or tree ferns predominated, it exceeded 1000 gm/sq. m/year, a figure that was maintained when high forest re-established itself. As would be expected, carbon content of the surface soil showed a similar increase, attaining levels similar to, or in excess of, those found under primary forest soon after the emergence of woody regrowth. In the younger stands, in which small herbs predominated, surface soil carbon content approximated 3%; this rose to exceed 9% under softwood trees. The fall to somewhat lower levels under tree ferns is difficult to explain; it may be that a less easily decomposed litter was produced by these pteridophytes leading to a temporary accumulation of surface litter and a consequent failure of the replenishment of the soil carbon.

In summary, low soil carbon contents were inherited or induced by stands of small herbs and thereafter maintained at a low level. The rise to prominence of woody plants of any life form resulted in a rapid increase in soil carbon which was thereafter maintained at a fluctuating level similar to that found under primary forest. Consequently, the occurrence of a change in soil carbon was dependent upon whether an initial decline had occurred at some time after forest clearance, either because of cultivation or a prolonged grassland stage. Where this had not occurred, as, for example, in stands 17 and 18, little change was taking place during re-vegetation and there was no potential for an autogenic floristic succession to take place with soil carbon as the determining factor.

Changes in surface soil CEC

Changes in CEC of the surface soil may be expected to show a fairly close correlation with changes in soil carbon. This relationship, plotted in Fig. 16, indicates that while some correlation did exist ($r=0.63$), this was not high. Stands of small herbs tended to have jointly low, and stands of hardwood trees jointly high, values; most chronologically intermediate stands possessed CEC values approximating 40 meq/100 gm

Figure 16. The relationship between the CEC and % carbon in the surface soil of sampled stands. ($r = 0.63$; $P < 0.01$.)

irrespective of soil carbon content. The initial rise in CEC with increasing soil carbon and its stability thereafter is expected; most surprising is the continued rise of CEC values after the establishment of hardwood trees, demonstrated both in Fig. 16 and by the high positive correlation between these two variables (Table 17). The sole postulate that can be advanced for this is the possibility that hardwood trees produce litter more amenable to transformation into organic colloids. As in the case of soil carbon, variation in CEC levels during revegetation would have depended upon their decline during prior disturbance. They appear to have been more susceptible to alteration than soil carbon levels for the soils of both stands 17 and 18 showed appreciable declines from primary forest levels despite only slight disturbance (Table 14).

Changes in surface soil pH

In a way analagous to soil carbon and CEC levels, soil pH showed significant correlations with the "terminal" life form groups of small herbs and hardwood trees (Table 17). High values (4.8/5.7) were recorded under stands of small herbs, falling to approximately 4.4/5.2 as the herbs were replaced by woody vegetation, and again to about 4.0/4.7 as hardwood trees finally rose to predominance (Table 14).

Two possible reasons can be advanced for these pH changes during the course of succession. They may have been related to an increasing soil CO_2 content as soil carbon and microbiological activity increased; this would not explain the continued fall under hardwood trees. Alternatively, the two-stages lowering of pH may have been related to a comparable change in base saturation produced by an enlarging exchange capacity with no comparable increase in exchangeable cations. As the correlation between these two variables is high ($r=0.78$ and 0.70 , for the KCl and H_2O methods of pH measurement respectively), the latter hypothesis seems the more likely.

The origins of the high pH values beneath small herb stands are obscure. They could have been induced by a burn after the site was cleared, a well documented phenomenon associated with shifting cultivation (Nye and Greenland 1960), or by the vegetation of the stands themselves.

Whatever the initial cause of these high values, small herbs clearly favoured their maintenance; soil in stand 15, for example, after 13 years of re-vegetation still recorded values of 4.8/6.0. However, in young stands that had not been burned and were not herb covered (stands 17 and 18), soil pH's were low and no significant changes would be expected there during the course of their re-vegetation.

Changes in surface soil nitrogen content

Percentage nitrogen in the surface soil was significantly positively correlated only with the prominence of hardwood trees (Table 17) and relatively low nitrogen levels occurred in all stands where other life forms predominated (Table 14). The decline in nitrogen contents from pre-clearance levels cannot be attributed to losses in eroded sediments and have tentatively been identified as the result of bacterial denitrification (Kellman 1969). This decline apparently took place with relative ease and no regrowth seemed capable of increasing nitrogen to its former levels. With the re-establishment of forest trees, however, a rise took place, albeit slowly; under primary forest contents of 1.09 - 1.30% were measured, while in stand 12, although at the time of sampling composed almost totally of hardwood trees, the nitrogen content was only 0.89%.

Reasons for this relationship are obscure. Jenny (1950) remarks upon the high nitrogen levels present in Colombian forest soils which he relates, on a world scale, to high nitrogen gains from rain water and to a high rate of symbiotic and non-symbiotic fixation, believing the latter to be the more important. As gains from rainfall must have been relatively constant throughout the study area, only the second sources could have been significant there. The possibility that the hardwood trees were fixing nitrogen symbiotically exists, although none of them were legumes. If so, transfer to the soil must have been taking place directly, either by excretion, the decay of old nodules, or by rainwash leaching, because the nitrogen content of the forest litter was no greater than that of the regrowth litter (Table 21). Nitrogen fixation by free-living organisms cannot be discounted in the unusual environmental conditions, such as lower temperatures and pH, on the forest floor.

There are no data on the availability to plants of nitrogen in the surface soils of the sampled sites.

Conclusions: the micro-environmental effects of different life forms

Only a limited number of micro-environmental phenomena were linearly correlated with the proportions of distinct life form types in the sampled stands. None of these life forms, save hardwood trees, definitely induced special micro-environmental conditions beneath them. Small herbs may have played a comparable role, but it is possible that they merely maintained certain soil conditions at levels inherited from prior periods of disturbance. Three aspects of these changes need emphasis.

a) Only soil conditions varied. It is conceivable that soils in the study area possessed a resistance to rapid change resulting from forest clearance. If this were the case, clearing per se may well have been of minor significance to soil changes during re-vegetation, whereas the nature of soil treatment during the period of disturbance would have assumed a much more important role. Stands 17 and 18 had undergone clearance but not burning and cropping and so serve as a useful check on this hypothesis. In both stands pH had remained at levels comparable to those of primary forest soils and carbon content had also been maintained at forest levels. CEC showed some change, however, particularly in stand 18, where a change in litter type may have been responsible. Nitrogen levels had dropped considerably in both stands indicating appreciable instability of this factor. Thus, while a change in nitrogen content, and possibly CEC, accompanied any re-vegetation, changes in carbon content and pH only took place where burning and cropping preceded abandonment of the site, or stabilized grasslands succeeded it. The possibility of at least two courses of succession thus existed.

b) None of the four phenomena which changed is likely to have had a direct effect upon any plant but the magnitude of the changes and the correlations strongly suggest that they were related, albeit indirectly.

c) It is important to distinguish between those phenomena that changed before the emergence of the "terminal" life form group of hardwood trees, and those that changed only when this group became predominant. The first type includes carbon content, CEC and pH of the surface soil and may possibly have been important in a floristic succession in that

some preliminary changes in them were necessary before species of the "terminal" life form could establish themselves. The second type of change, exhibited only by soil nitrogen, was apparently wrought by the terminal group itself, the species of which must therefore have been capable of establishing in low nitrogen conditions. The only role these phenomena could have played in a floristic succession would have been the exclusion of species of earlier structural stages from the terminal state.

The effects of individual species

The role of individual species in altering micro-environmental conditions is of interest in indicating the extent to which the direction of floristic succession may be determined by chance entry of particular taxa. The species here considered are those that occurred in the overstorey or intermediate layer of at least 5 stands to each of which they contributed not less than 0.01% of the total mass. Correlations were computed using data from all stands; the species' prominences were measured by their percentage contribution to the total mass of the two "influencing" layers of a stand and, where absent from the stand, a zero value was scored. The resultant coefficients are listed in Table 18. The limitations of these coefficients are similar to those mentioned earlier, namely the excessive weight that is contributed by a single high co-occurrence. In addition, the absolute masses of some species were small in all stands and effects apparently produced by these should be treated with caution; while some appreciable effects may, conceivably, have been produced by a small plant, the probability of a large plant being responsible is a priori far greater.

Significant relationships of two kinds may be distinguished: those in which the effects of an individual species paralleled that of the life form group to which it belonged, and those which were independent of the group. The effects that paralleled life form group effects are of interest in confirming the reality of the latter; where a number of separate species of the same life form exhibited similar effects, their joint significance can hardly be doubted.

The relative prominence of certain small herbs appears to have borne some relationship to high pH, and both of the hardwood trees

Lithocarpus sp. and Indet. (1877) appear to have been correlated with CEC of the surface soil (Table 18). All other parallel relationships appear to have been more restricted. Only Spathoglottis sp. of all the small herbs, had a negative correlation with soil pH, and only Lithocarpus sp. had a positive correlation with the nitrogen content of the surface soil. While the implication of this is that the effects of plant life forms recognized earlier may have been more apparent than real, the evidence is not conclusive. Moreover, most of the coefficients calculated for individual species effects are somewhat lower than those calculated for life form group effects, indicating a degree of group independence.

There was a wide range of species effects that seem to have been operating independently. A few possibly significant correlations were recorded between individual species prominences and insolation receipts. Those involving green and blue radiation cannot be regarded as important because of the low accuracy of measurement; where there were significant correlations between species and total or red radiation receipts, the coefficients were well below those recorded between time and these phenomena. It seems most probable, therefore, that the presence and relative prominence of these species was dependent upon stand age and that the measured correlations were spurious. The same generalization holds for species correlations with depressions of daily maximum air temperatures. Daily minimum air temperature differences, for reasons already outlined, were probably more closely related to topography and the correlations between this factor and the occurrence of the hardwood Lithocarpus spp. (1732, 1886) were probably spurious. Individual species effects upon soil moisture conditions of stands appear to have been small. Measured effects upon soil moisture spatial instability cannot be relied upon as this phenomenon was not significantly different between the stands (Table 14); the apparent high correlation between it and Hornstedtia sp. has already been explained by a single high, and unrelated, co-occurrence in stand 7. The same explanation dispenses with the apparent effect of Clerodendron sp. and Musa sp. on this phenomenon. The relationship that apparently existed between Dissochaeta sp. and Rubus sp. and soil moisture temporal instability are unrealistic as both species were of low total mass in all stands. No significant correlation was recorded between mean annual soil moisture condition and any species.

In contrast to the absence of any significant effects upon soil nutrient status by the groups of plants of similar life form, several individual species appear to have affected this condition. For these relationships to be meaningful, they had to fulfill two requirements. Firstly, they had to be positive correlations, as negatives would have suggested a restriction on the species by the nutrient; all save one of the relationships satisfied this requirement. Secondly, the species must have occurred in the vegetation with a sufficient absolute prominence; since nutrient increase in the surface soil by a plant normally involves nutrient cycling, it is unlikely that a plant of small stature and litter production would have been capable of achieving this. If a minimum figure of 1% of total plant mass in at least one stand is required, then three further species can be eliminated as insignificant, namely Indet. (1877), Rubus sp. and Rubus moluccana. All other correlation coefficients were weighted heavily by single high co-occurrences. The chemical analyses of the litter collections made in all stands may be used to check each apparent correlation by indicating whether an excessive nutrient return to the soil was taking place in the stands where the appropriate species occurred prominently. The correlation coefficient recorded between Lithocarpus sp. and exchangeable Na in the surface soil was heavily weighted by the high values of both variables in stand 12. Table 21 indicates, however, that Na returns to the soil in the litter of this stand were not exceptionally high, forcing one to conclude that the correlation was spurious. A scatter diagram of the relationship between the relative prominence of Melastoma cf. polyanthum and % K in litter (Fig. 17) indicated some positive correlation ($r=+0.39$) suggesting that the effect of this species on surface soil potassium was probably real. However, a similar comparison between Clerodendrum sp. and Na content of the litter ($r=+0.21$) indicates little correlation and a possible spurious relationship between this species and surface soil Na. The correlation of Trema orientalis with P and Mg in the surface soil is dependent upon the high co-occurrences of these variables in stand 6. Table 21 indicates a low Mg content in the litter of this stand but a more promising relationship with P (Fig. 18, $r=+0.52$) justifying Trema orientalis as a phosphorous-enriching species. The correlation between Ficus sp. and K content of litter is low ($r=+0.15$) and there seems little justification for regarding

Figure 17. The relationship between the prominence of Melastoma cf. polyanthum in a stand and the K content of the litter of that stand. ($r = 0.39$; $P > 0.05$.)

Figure 18. The relationship between the prominence of Trema orientalis in a stand and the P content of the litter of that stand. ($r = 0.52$; $P < 0.05$.)

Ficus sp. as a potassium-enriching species. A similar conclusion can be drawn about the apparent effects of Mallotus paniculatus, Spathoglottis sp. and Araceae sp. upon this element. Finally, it must be emphasized that although several apparent correlations have been dismissed as spurious on the basis of litter fall results, a remote possibility exists that nutrient cycling may have been effected by rainwash independently of the litter and so have gone undetected.

In summary, the identifiable effects of individual species on the stand micro-environment were few. While too few species were tested to enable firm conclusions to be drawn, it does appear that species of the same life form tended to have similar effects on a particular phenomenon, producing the "group effects" detected in a foregoing section. In instances where individual species seemed to be producing unique effects, closer scrutiny suggests that many of the high correlations were spurious. There is some evidence, however, to suggest that Trema orientalis acted as a phosphorous restorer and that Melastoma cf. polyanthum acted as a potassium restorer. The importance to floristic succession of changes induced by individual species depended, of course, upon the sensitivity to these elements of any other species in the area. Assuming this to have existed, the data give limited support to the idea that the direction of floristic succession was determined by the chance entry of a nutrient-enriching species at some early date.

Summary of micro-environmental changes

When micro-environmental conditions in the sampled stands were related to stand age and certain independent vegetation variables, a number of significant linear correlations appeared. Stand age seemed to affect radiation receipts and daily maximum air temperatures at the soil surface. Plant life form groups appeared to have no unique effects upon micro-environmental conditions except that high nitrogen levels were attained in the soil beneath stands of hardwood trees; stands of small herbs (grasslands) may possibly have induced low soil carbon levels, low CEC's and high pH's but these conditions could also have been inherited from prior periods of disturbance. Surface soil carbon content increased with the rise of woody vegetation and thereafter stabilized. The CEC and pH of surface

soils showed a two-stepped change; woody re-growth life forms induced a partial change and thereafter maintained an equilibrium for long periods between the extremes experienced under small herbs and hardwood trees. A number of species acted in parallel to produce these life form group effects but the degree to which an apparent group effect was produced by a single constituent species is unclear. There was limited evidence of a few individual species producing effects on soil nutrients that were unrelated to any effects of distinct life form types.

Micro-environmental changes and the factors promoting them were evidently complex. The existence of some "life form effects" indicated a potential for a staged floristic succession determined through carbon content, CEC and pH of the surface soil. The existence of other micro-environmental changes, induced independently by stand age or individual species, complicated the model of a distinct staged floristic succession. Finally, it must again be emphasized that the occurrence and severity of most changes depended upon the site conditions at the time of abandonment, and this upon the type of disturbance that the site had undergone. A gradual radiation- and temperature-induced succession was most likely to have occurred provided some clearance had taken place. Soil carbon content and CEC were more resistant to change and therefore less likely to have determined a floristic succession. Soil pH was apparently unaffected by disturbance that did not involve burning and therefore was insignificant in determining succession on all but burned sites.

Species' environmental tolerances

The micro-environmental changes that were taking place on abandoned sites in the study area during their re-vegetation indicated some potential for a self-induced floristic succession. Whether this potential was being realized in this way depended on how different were the tolerance ranges of the species composing the stands.

The investigation of tolerance ranges of species has been limited to their environmental requirements for establishment. The term "establishment" as used here refers to germination and maintenance of a plant beyond

Table 21. Percentage nutrient contents of litter samples (leaves and twigs only)

Stand	N	P	Ca	Mg	K	Na
1	1.39	0.117	0.94	0.306	0.19	0.068
2	1.24	0.088	1.11	0.216	0.52	0.052
3	2.00	0.144	1.38	0.331	0.41	0.056
4	1.46	0.116	2.26	0.272	0.51	0.051
5	1.38	0.072	1.10	0.187	0.25	0.043
6	1.78	0.158	1.31	0.168	0.26	0.073
7	1.76	0.114	0.99	0.209	0.32	0.061
8	1.60	0.090	1.27	0.221	0.21	0.040
9	1.25	0.047	0.76	0.173	0.29	0.029
10	1.29	0.058	0.73	0.207	0.29	0.029
11	1.71	0.108	1.28	0.325	0.33	0.053
12	1.30	0.059	0.70	0.207	0.27	0.046
13	1.68	0.091	1.15	0.173	0.31	0.021
14	0.42	0.071	0.74	0.166	0.16	0.020
15	0.36	0.034	0.26	0.085	0.26	0.011
16	0.67	0.055	0.40	0.135	0.47	0.019
17	1.45	0.073	0.99	0.227	0.19	0.020
18	2.40	0.150	1.83	0.421	0.64	0.033

the stage of dependence on seed food reserves. As the micro-environment measured represented conditions only at or below 70 cm above the soil surface, this height was used as the criterion of establishment of a plant. Such juvenile plants, having only recently established, almost certainly did so under conditions very like those actually measured. Thus, if a plant was sampled which was independent of seed food reserves but under 70 cm in height, it was assumed that it could establish under the conditions measured at the site; if absent, it was assumed that the plant had been excluded from the stand, possibly by one of the measured micro-environmental phenomena. While it can be argued that the exclusion of a species from a stand may take place at a later stage of plant development, my own observations in the study area led me to believe that it was an uncommon event there. The total absence of juvenile regrowth plants from the ground flora of primary forest stands was evidence of this as was the persistence of hardwood tree seedlings in logged-over forest. In the first instance, the inability to establish under forest conditions seemed to have excluded regrowth species whilst in the second case, hardwood tree seedlings, having established themselves, thereafter resisted elimination. Moreover, if a mechanism can be demonstrated whereby pre-establishment exclusions can account for autogenic floristic succession in the study area, this assumption will have been justified.

Data handling

Analysis of variance was used to determine the level of significance of differences in the environmental requirements for establishment of species. The recorded occurrences of species that were used in the analyses may not have represented the full range of their tolerances either because of the plant's inability to reach the site or because an insufficient range of environments could be sampled. The first difficulty can be ignored temporarily if the assumption of a constant propagule rain on all sites is maintained. The second was a more serious inadequacy the correction of which would have involved extensive sampling outside the selected stands. If, however, the error is recognized, it can be allowed for when interpreting the result of analyses. Thus, for example, if an "early" regrowth species appeared to have a tolerance to radiation extending to 25% of external conditions (the highest percentage recorded)

it would also be necessary to recognise that this range may have extended to 100%; that the plant might, in fact, have established on bare ground.

The species considered in the analyses were restricted to those which were sampled in the intermediate or overstorey layer of at least one stand, enabling these to be placed into life form types with some objectivity. Because of the small size of the environmental samples and the probable variation of values within each stand, only those species which had juvenile forms in at least three ground layer quadrats of at least two stands were considered. Results from stands 17 and 18 were omitted from the analyses because it was thought that many of the ground-layer plants occurring there had established prior to disturbance. Results from these stands are, however, of great interest when considered individually and they are used when the results of the analyses are interpreted. To summarize, therefore, only the species which occurred in the overstorey or intermediate layer of at least two stands other than 17 and 18 were used in the analyses. The 33 species that fulfilled these requirements are listed in Table 22 together with their stands of ground layer occurrence.

Analysis

The analysis was carried out in three parts to detect both significant differences in the environmental requirements for establishment of individual species and any significant groupings of species in this respect. The initial analysis dealt with individual species, each of which was treated as a statistical "group" and each stand-occurrence as an "item". Twenty identical analyses were carried out using data on each of the twenty environmental variables measured. The results of these analyses, when considered in isolation, are not very informative as they merely give an indication of the phenomena to which the species concerned tended to respond. However, they contribute very considerably when compared with the results of analyses in which the species were grouped into various classes.

The second series of analyses, using species grouped according to the life form to which they belonged, was designed to test whether

Table 22. Species included in the analyses of differences in environmental tolerances at establishment and their stands of ground-layer occurrence

<u>Species</u>	<u>Stands of ground-layer occurrence</u>
<u>Ardisia</u> sp. (1903)	5, 13.
cf. <u>Shorea almon</u> (3433)	5, 3.
<u>Melastoma</u> cf. <u>polyanthum</u> (1520)	1, 5, 9.
<u>Ficus</u> sp. (1662)	1, 3, 4, 5, 8, 9.
<u>Ficus</u> sp. (1698)	1, 2.
<u>Cyathea</u> spp. (3430), (3431)	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13.
<u>Hornstedtia</u> sp. (3440)	3, 4, 5, 6, 7, 8, 9, 10, 11.
<u>Elephantopus mollis</u> (1500)	1, 2, 4, 7, 9, 10, 14, 15, 16.
<u>Microglossa pyrifolia</u> (1516)	1, 2.
<u>Scleria</u> cf. <u>scrobiculata</u> (1524)	2, 3, 5.
<u>Cyrtococcum accrescens</u> (1533)	1, 4, 5, 7, 8, 9, 10.
<u>Setaria palmifolia</u> (1534)	7, 16.
<u>Lycopodium cernuum</u> (1542)	14, 15.
<u>Spathoglottis</u> sp. (1659)	1, 4, 15.
Marantaceae (1678)	3, 11.
<u>Paspalum conjugatum</u> (1742)	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 14, 16.
<u>Nephrolepis</u> sp. (1759)	1, 2, 4, 6, 7, 8, 9, 10, 11, 14, 15, 16.
? Gesneriaceae (1760)	1, 4, 5, 8, 9.
<u>Rubus moluccana</u> (1771)	2, 5, 9.
<u>Cyclosorus</u> sp. (1784)	1, 3, 4, 5, 6, 7, 10, 15, 16.
<u>Blumea riparia</u> (1525)	3, 5.
<u>Gleichenia truncata</u> (1808)	8, 9.
? <u>Cayratia</u> sp. (1811)	3, 9.
? <u>Cyclosorus</u> sp. (1830)	8, 11.
<u>Imperata cylindrica</u> var. <u>major</u> (3436)	1, 2, 7, 10, 14, 15, 16.
<u>Elatostema</u> sp. (1508)	8, 12, 13.
<u>Daemonorops</u> spp. (1518)	5, 8, 9, 10, 11.
<u>Leucostegia</u> sp. (1637)	12, 13.
Indet. (1780)	3, 5, 6, 12, 13.
<u>Freycinetia</u> sp. (1786)	3, 5, 12, 13.
<u>Athyrium</u> sp. (1947)	6, 12, 13.
<u>Aristolochia</u> sp. (1764)	1, 5, 9.
<u>Costus speciosus</u> (1519)	1, 5, 9.

all species of the same life form tended to have similar tolerances. If they did, and if the tolerances of these life forms corresponded to their order of appearance in the structural succession, then there would be an indication that the succession of life forms observed was the product of a "staged" floristic succession. The data used for this analysis were identical with those used for the analysis of individual species' tolerances with one exception; in the "small herb" group consideration was restricted to those species which occurred in the intermediate layer of stands where this layer was predominant, namely 1, 2, 14, 15, 16, 18. This served to separate the species of the group which were structurally prominent in some stands from those other species (such as small forest herbs and vines) which never made up more than a minute proportion of any stand mass. The small herbs which fulfilled this requirement are listed in Table 23. One item was scored in each life form group for each species occurrence in the ground layer of a stand. As a minimum of at least two attributes per sample was always ensured, the scores for those species that occurred with a three quadrat frequency in the ground layer of only one stand were added to the analysis. The extra species so included are listed in Table 24.

A final series of analyses used the same data re-grouped into only two classes, namely hardwood trees and all other species excluding tree ferns. This separation was based on the observation, made during the sampling of early regrowth vegetation, that most regrowth species were present, if only as seedlings, at, or soon after, site abandonment and that it was perhaps only hardwood trees which were delayed in establishment. Testing for significant differences between the two groups was designed to establish the reality of this observation and to investigate whether the grouping was statistically more significant than those of the two previous analyses. The exclusion of tree ferns from both groups was arbitrarily determined. Table 22 indicates the wide range of ground layer occurrence of this group in all stands from those of small herbs (and indeed the weed growth of cultivated fields) to high forest. It was thus clear that these species were of wide tolerance and their inclusion as members of either major group would only have served to obscure real differences in others.

Table 23. Small herbs present in the intermediate layer of stands 1, 2, 14, 15, 16 and 18.

<u>Elephantopus mollis</u> (1500)	<u>Paspalum conjugatum</u> (1742)
<u>Microglossia pyrifolia</u> (1516)	<u>Nephrolepis</u> sp. (1759)
<u>Impatiens</u> sp. (1517)	<u>Aristolochia</u> sp. (1764)
<u>Scleria</u> cf. <u>scrobiculata</u> (1524)	<u>Rubus</u> sp. (1769)
<u>Cyrtococcum accrescens</u> (1533)	<u>Pteridium aquilinum</u> (1672)
<u>Setaria palmifolia</u> (1534)	<u>Cyclosorus</u> sp. (1784)
<u>Lycopodium cernuum</u> (1542)	<u>Cissus</u> sp. (1819)
<u>Imperata cylindrica</u> var. <u>major</u> (3436)	

Table 24. Species sampled in the intermediate or overstorey layer of at least one stand and also occurring with a 3-quadrat frequency in the ground layer of at least one stand

<u>Saurauia</u> sp. (1731)
<u>Indet.</u> sp. (1922)
<u>Lithocarpus</u> sp. (1732)
? <u>Syzygium</u> sp. (1878)
<u>Cinnamomum</u> sp. (1888)
<u>Omalanthus</u> cf. <u>populneus</u> (1734)

Results

The results of the three groups of analyses of variance are summarized in Table 25, and the means used in the computations in Tables 26, 27 and 28. When treated individually, the species appear to have possessed distinctly different environmental requirements for establishment in a limited number of phenomena. If the 0.05 probability level is taken as the criterion of significance, species appeared to possess distinct tolerance ranges in terms of:

- total radiation,
- red radiation,
- daily maximum air temperature depressions,
- daily minimum air temperature differences, and
- surface soil carbon, CEC, nitrogen and pH.

Because of non-independent variation, differences in terms of daily minimum air temperatures were probably not real and will not be discussed further.

When the species were grouped into 5 life form classes, some increase in significance levels of establishment tolerance differences resulted (Table 25). These increases were restricted mainly to those phenomena for which the individual species showed significant differences in tolerance range. In addition, differences in terms of blue and green radiation showed an increase in significance level, although the importance of this was probably slight. Tolerance differences to exchangeable Ca also showed an increase in significance level with grouping, while a converse fall in terms of exchangeable Na occurred. Diagrammatically, therefore, species tolerance ranges may be pictured as clustering into groups with some intervening vacant spaces. This grouping would indicate a staged floristic succession only if the positions of the life form group tolerances along the environmental gradient correspond to their observed period of structural predominance in the vegetation. If the mean tolerance of each group is taken as indicating its position on these gradients, Table 27 indicates that, while hardwood trees were consistently at one extreme of the gradient, the regrowth groups were all closely similar and exchanged their relative positions from gradient to gradient. The mean tolerances for tree ferns tended to be intermediate, but Table 22

indicates that this was a product of wide tolerance rather than anything else. One must therefore conclude that the evidence does not strongly support the hypothesis of a multi-staged floristic succession.

Further grouping of the individual species into two classes revealed more significant differences (Table 25). In many instances the levels of significance produced by this grouping dropped well below the 0.001 probability which is the lowest for which tables exist; some indication of the increase in significant difference that did occur is given, however, by the increase in F values. Again these differences were restricted to those phenomena for which individual species' tolerances differed. Differences in terms of exchangeable Ca increased to the required 0.05 probability level; in some characteristics of soil moisture, differences increased, but not to the required level of significance. In terms of other phenomena, tolerance differences remained insignificant. Species tolerance ranges can therefore be taken to have been relatively distinct along certain environmental gradients clustering somewhat according to life form type, but with the greatest inter-group discontinuity between hardwood tree species and species of all other life forms.

One must therefore conclude that there was an overwhelming tendency for the species to operate ecologically as two distinct groups in terms of tolerance to radiation, air temperature, soil pH, carbon content, CEC, nitrogen content and exchangeable Ca. In Table 29 the tendency of one group toward "early" micro-environmental conditions and the other towards "late" conditions on each gradient can be seen. If it is assumed that the species tested represented an unbiased sample of all species encountered, then the same conclusions can be extended to this wider population. There was, therefore, an overwhelming tendency for any floristic succession to have been two-phased, provided that the necessary micro-environmental alterations took place during re-vegetation. To interpret the floristic succession that was occurring, therefore, it is necessary to consider these results in conjunction with those on micro-environmental changes arrived at in the preceding section.

Table 25. Results of analyses of variance on the establishment requirements of plants in the study area. F values and probability levels (P).

<u>Micro-environmental variable</u>	<u>33 Species</u>		<u>5 Life-form groups</u>		<u>2 Life-form groups</u>	
	F	P	F	P	F	P
% total radiation	1.50	<.05	7.15	<.001	28.10	<.001
% blue radiation	0.69	>.02	2.53	<.05	8.94	<.01
% green radiation	1.22	<.2	2.34	<.1	8.33	<.01
% red radiation	1.34	<.1	6.74	<.001	26.75	<.001
Daily max. temp. depressions ($^{\circ}\text{C}$)	1.51	<.05	4.88	<.01	16.21	<.001
Daily min. temp. differences ($^{\circ}\text{C}$)	2.04	<.001	12.43	<.001	54.29	<.001
Soil moist. spatial instability (cm tens.)	0.77	>.2	0.22	>.2	0.89	>.2
Soil moist. temporal instability (cm tens.)	0.43	>.2	0.65	>.2	2.15	>.2
Mean annual soil moist. condition (cm tens.)	0.77	>.2	1.36	>.2	3.47	>.1
Soil pH (H_2O)	3.59	<.001	12.42	<.001	46.71	<.001
Soil pH (KCl)	1.54	<.01	3.69	<.01	11.92	<.001
% carbon in surface soil	2.02	<.001	6.01	<.001	18.19	<.001
% nitrogen in surface soil	2.92	<.001	12.11	<.001	50.16	<.001
CEC of surface soil (meq/100 gm)	3.72	<.001	15.49	<.001	60.23	<.001
P_2O_5 in surface soil (ppm)	1.03	>.2	0.69	>.2	0.47	>.2
Exch. Ca in surface soil (meq/100 gm)	0.86	>.2	2.10	<.1	6.23	<.05
Exch. Mg in surface soil (meq/100 gm)	0.95	>.2	0.96	>.2	0.69	>.2
Exch. K in surface soil (meq/100 gm)	0.48	>.2	0.25	>.2	0.45	>.2
Exch. Na in surface soil (meq/100 gm)	1.44	<.1	1.55	<.2	2.03	<.2
C/N ratio of surface soil	0.93	>.2	0.67	>.2	0.30	>.2

Table 26. Mean micro-environmental conditions under which various species establish

Micro-environmental variable	Hardwood trees		Softwood trees			Tree ferns
	<u>Ardisia sp.</u> (1903)	<u>cf. Shorea almon</u> (3433)	<u>Melastoma cf. polyanthum</u> (1520)	<u>Ficus sp.</u> (1662)	<u>Ficus sp.</u> (1698)	<u>Cyathea spp.</u> (3430, 3431)
% total radiation	3.67	8.42	12.28	14.19	18.94	11.48
% blue radiation	1.19	7.15	27.08	31.52	47.64	25.48
% green radiation	8.89	8.78	11.46	11.87	12.12	10.21
% red radiation	3.99	10.27	12.71	15.74	20.72	13.40
Daily max. temp. depressions ($^{\circ}\text{C}$)	6.40	5.33	4.16	4.49	2.16	5.00
Daily min. temp. differences ($^{\circ}\text{C}$)	-1.00	-0.01	-0.14	+0.36	-0.31	+0.05
Soil moist. spatial instability (cm tens.)	49.21	55.66	53.57	99.88	48.75	73.05
Soil moist temporal instability (cm tens.)	45.95	64.45	61.73	75.80	72.85	60.93
Mean annual soil moist. condition (cm tens.)	166.75	162.70	157.60	130.03	154.20	127.79
Surface soil pH (H_2O)	4.95	5.20	5.40	5.43	5.50	5.35
Surface soil pH (KCl)	4.25	4.30	4.40	4.42	4.55	4.39
% carbon in surface soil	9.11	9.38	6.81	5.64	3.07	6.15
% nitrogen in surface soil	0.76	0.52	0.50	0.49	0.44	0.56
CEC of surface soil (meq/100 gm)	59.33	44.25	43.43	43.67	44.54	49.06
P_2O_5 in surface soil (ppm)	30	34	16	22	24	32
Exch. Ca in surface soil (meq/100 gm)	3.52	3.85	3.70	4.02	3.35	4.23
Exch. Mg in surface soil (meq/100 gm)	0.86	0.75	0.50	0.73	0.57	0.91
Exch. K in surface soil (meq/100 gm)	0.51	0.51	0.49	0.59	0.62	0.53
Exch. Na in surface soil (meq/100 gm)	0.10	0.07	0.08	0.12	0.04	0.12
C/N ratio of surface soil	14.45	18.50	13.63	11.18	7.00	11.70

Table 26 (contd.)

Zingiberaceous herbs		Small herbs etc.							
<u>Costus speciosus</u> (1519)	<u>Hornstedtia</u> sp. (3440)	<u>Elephantopus mollis</u> (1500)	<u>Microglossa pyrifolia</u> (1516)	<u>Scleria cf. scrobiculata</u> (1524)	<u>Cyrtococcum accrescens</u> (1533)	<u>Setaria palmifolia</u> (1534)	<u>Lycopodium cernuum</u> (1542)	<u>Spathoglottis</u> sp. (1659)	<u>Marantaceae</u> (1678)
12.28	11.62	14.96	18.94	12.52	13.31	18.06	10.06	13.13	8.81
27.08	23.19	36.50	47.64	31.41	27.75	43.41	25.58	22.07	10.95
11.46	9.96	12.05	12.12	8.65	11.83	17.03	10.38	11.56	5.83
12.71	12.99	15.50	20.72	14.34	14.42	19.83	8.37	13.57	10.60
4.16	5.36	4.32	2.16	4.48	4.76	3.61	5.43	3.62	5.40
-0.14	+0.28	-0.15	-0.31	-0.23	-0.19	+0.37	+0.33	+0.12	+0.69
53.57	82.60	80.25	48.75	53.89	98.39	194.85	48.35	44.99	51.25
61.73	60.52	54.09	72.85	62.13	64.57	37.05	79.35	85.53	63.75
157.60	122.26	105.57	154.20	164.90	136.43	73.15	113.10	116.87	110.60
5.40	5.39	5.61	5.50	5.23	5.49	5.60	5.85	5.73	5.45
4.40	4.38	4.50	4.55	4.30	4.40	4.60	4.65	4.70	4.55
6.81	6.57	4.26	3.07	7.22	5.56	3.73	3.35	4.01	6.61
0.50	0.52	0.41	0.44	0.48	0.44	0.40	0.36	0.41	0.56
43.43	43.66	37.72	44.54	43.55	42.13	36.13	27.12	37.79	43.02
16	33	26	24	31	19	42	25	26	36
3.70	4.61	4.35	3.35	3.33	4.16	5.12	4.99	5.03	5.05
0.50	0.97	0.71	0.57	0.60	0.73	0.98	0.71	0.82	1.21
0.49	0.50	0.60	0.62	0.49	0.59	0.61	0.50	0.89	0.43
0.08	0.13	0.07	0.04	0.06	0.12	0.07	0.04	0.07	0.09
13.63	13.14	10.67	7.00	14.70	12.99	9.45	9.10	9.63	11.75

Table 26 (contd.)

Small herbs etc. (Contd.)									
<u>Paspalum</u> <u>conjugatum</u> (1742)	<u>Nephrolepis</u> sp. (1759)	<u>Rubus</u> <u>moluccana</u> (1771)	<u>Cyclosorus</u> sp. (1784)	<u>Blumea</u> <u>riparia</u> (1804)	<u>Gleichenia</u> <u>truncata</u> (1808)	? <u>Cayratia</u> sp. (1811)	Dicot. (1830)	<u>Imperata</u> <u>cylindrica</u> var. <u>major</u> (3436)	<u>Elatostema</u> sp. (1508)
12.47	13.09	13.47	13.17	8.42	10.33	13.42	5.73	15.61	4.08
25.58	29.27	48.61	20.82	7.15	35.88	39.43	7.40	35.90	3.92
11.02	11.24	8.98	11.99	8.78	10.48	8.70	7.61	12.79	8.38
13.75	13.94	13.68	14.54	10.27	10.45	14.16	6.89	16.25	4.99
4.74	4.58	4.32	4.66	5.53	5.05	5.41	4.99	4.16	6.30
+0.14	+0.20	-0.39	+0.16	-0.01	+0.29	+0.45	+0.52	+0.18	-0.81
71.52	71.59	54.64	78.97	55.66	49.72	49.75	51.23	89.18	47.07
58.95	63.94	51.50	59.63	64.45	111.55	61.75	113.55	57.46	80.27
118.21	113.45	167.67	107.59	162.70	184.30	120.85	174.05	109.10	174.77
5.45	5.54	5.27	5.50	5.20	5.35	5.25	5.55	5.67	4.93
4.45	4.50	4.23	4.50	4.30	4.25	4.20	4.60	4.56	4.13
5.59	4.72	6.70	5.88	9.38	5.67	8.27	4.01	3.54	6.49
0.49	0.47	0.48	0.47	0.52	0.52	0.58	0.50	0.38	0.81
41.85	39.71	41.86	41.15	44.25	40.07	43.92	39.17	36.13	62.97
32	32	15	41	34	7	24	19	30	35
4.60	4.73	2.99	4.48	3.85	3.24	2.80	5.49	4.40	3.05
0.89	0.89	0.33	0.98	0.75	0.34	0.41	1.18	0.77	0.92
0.54	0.54	0.38	0.63	0.51	0.27	0.30	0.40	0.55	0.47
0.10	0.11	0.08	0.09	0.07	0.20	0.14	0.22	0.57	0.23
11.65	10.25	13.70	12.69	18.50	10.75	14.40	8.10	9.96	8.13

Table 26 (contd.)

Small herbs etc. (contd.)						Micro-environmental variable
<u>Daemonorops</u> spp. (1518)	<u>Leucostegia</u> sp. (1637)	<u>Indet. sp.</u> (1780)	<u>Freycinetia</u> sp. (1786)	<u>Athyrium</u> sp. (1947)	<u>Aristolochia</u> sp. (1764)	
9.26	3.22	6.84	5.82	5.79	12.28	% total radiation
19.75	2.63	5.50	4.90	4.40	27.08	% blue radiation
8.84	6.69	8.43	7.43	8.19	11.46	% green radiation
9.71	3.70	8.40	6.99	7.15	12.71	% red radiation
5.45	7.01	6.23	6.27	6.70	4.16	Daily max. temp. depressions ($^{\circ}\text{C}$)
+0.21	-1.39	-0.57	-0.70	-0.95	-0.14	Daily min. temp. differences ($^{\circ}\text{C}$)
51.82	46.32	47.66	50.99	42.33	53.57	Soil moist. spatial instability (cm tens.)
69.56	31.75	49.16	48.10	38.97	61.73	Soil moist. temporal instability (cm tens.)
152.92	140.35	133.86	151.53	114.63	157.60	Mean annual soil moist. condition (cm tens.)
5.48	4.70	4.94	4.95	4.77	5.40	Surface soil pH (H_2O)
4.38	4.00	4.18	4.15	4.10	4.40	Surface soil pH (KCl)
5.93	7.80	8.78	8.59	8.61	6.81	% carbon in surface soil
0.46	0.99	0.79	0.75	0.98	0.50	% nitrogen in surface soil
39.81	75.08	59.52	59.91	69.70	43.43	CEC of surface soil (meq/100 gm)
18	45	54	40	67	16	P_2O_5 in surface soil (ppm)
4.32	2.49	3.87	3.17	3.88	3.70	Exch. Ca in surface soil (meq/100 gm)
0.78	1.01	1.10	0.88	1.33	0.50	Exch. Mg in surface soil (meq/100 gm)
0.39	0.46	0.45	0.48	0.42	0.49	Exch. K in surface soil (meq/100 gm)
0.15	0.20	0.14	0.13	0.19	0.08	Exch. Na in surface soil (meq/100 gm)
13.76	7.90	12.72	13.20	8.87	13.63	C/N ratio of surface soil

Table 27. Mean micro-environmental conditions under which various life form types establish

<u>Micro-environmental variable</u>	<u>Hardwood trees</u>	<u>Tree ferns</u>	<u>Softwood trees</u>	<u>Large Zingiberaceous herbs</u>	<u>Small herbs</u>
% total radiation	3.43	11.48	14.53	11.79	13.69
% blue radiation	1.56	25.48	35.67	24.17	30.30
% green radiation	8.35	10.21	11.53	10.35	11.54
% red radiation	3.75	13.40	15.68	12.92	14.74
Daily max. temp. depressions ($^{\circ}\text{C}$)	6.65	5.00	4.05	5.06	4.46
Daily min. temp. differences ($^{\circ}\text{C}$)	-1.11	+0.05	+0.05	+0.17	+0.14
Soil moist. spatial instability (cm tens.)	47.07	73.05	74.14	75.34	99.02
Soil moist. temporal instability (cm tens.)	54.54	60.93	69.99	60.82	60.54
Mean annual soil moist. condition (cm tens.)	156.22	127.79	138.98	131.09	118.01
Surface soil pH (H_2O)	4.87	5.35	5.45	5.39	5.45
Surface soil pH (KCl)	4.19	4.39	4.43	4.38	4.48
% carbon in surface soil	8.75	6.15	5.18	6.63	4.96
% nitrogen in surface soil	0.86	0.56	0.48	0.52	0.45
CEC of surface soil (meq/100 gm)	64.75	49.06	42.81	43.61	39.96
P_2O_5 in surface soil (ppm)	34	32	21	28	31
Exch. Ca in surface soil (meq/100 gm)	3.19	4.23	3.81	4.38	4.43
Exch. Mg in surface soil (meq/100 gm)	0.91	0.91	0.62	0.85	0.68
Exch. K in surface soil (meq/100 gm)	0.49	0.53	0.55	0.50	0.54
Exch. Na in surface soil (meq/100 gm)	0.12	0.12	0.09	0.12	0.09
C/N ratio of surface soil	12.3	11.7	10.7	13.3	11.2

Table 28. Mean micro-environmental conditions under which two groups of species establish

<u>Micro-environmental variable</u>	<u>Hardwood tree species</u>	<u>Regrowth species</u>
% total radiation	3.43	13.57
% blue radiation	1.56	30.30
% green radiation	8.35	11.40
% red radiation	3.75	14.64
Daily max. temp. depressions ($^{\circ}\text{C}$)	6.64	4.47
Daily min. temp. differences ($^{\circ}\text{C}$)	-1.11	+0.13
Soil moist. spatial instability (cm tens.)	47.07	75.18
Soil moist. temporal instability (cm tens.)	54.54	61.53
Mean annual soil moist. condition (cm tens.)	156.22	122.26
Surface soil pH (H_2O)	4.87	5.45
Surface soil pH (KCl)	4.19	4.46
% carbon in surface soil	8.75	5.19
% nitrogen in surface soil	0.86	0.46
CEC of surface soil (meq/100 gm)	64.75	40.76
P_2O_5 in surface soil (ppm)	34	29
Exch. Ca in surface soil (meq/100 gm)	3.19	4.34
Exch. Mg in surface soil (meq/100 gm)	0.91	0.79
Exch. K in surface soil (meq/100 gm)	0.49	0.54
Exch. Na in surface soil (meq/100 gm)	0.12	0.09
C/N ratio of surface soil	12.3	11.4

Floristic succession; conclusions

The critical factors determining the occurrence and nature of a floristic succession (i.e. an elimination of established species and their replacement by other species) in the study area were those which prohibited either hardwood tree species or regrowth type species from establishing. The evidence available suggests that hardwood trees were prevented from establishing by the following factors:

- high radiation intensities,
- high air temperatures,
- high soil pH,
- low soil carbon levels, and
- low soil CEC.

Although hardwood trees tended to establish under conditions of soil nitrogen that were significantly higher than those under which regrowth species established, this factor is excluded from the list; it has been shown that high nitrogen levels were primarily a result of the predominance of hardwood trees which, to attain this predominance, must have been capable of establishing in conditions of relatively low nitrogen.

Conditions which appear to have prevented regrowth species establishing were:

- low radiation levels,
- low air temperatures,
- high soil nitrogen contents,
- low soil pH,
- high soil carbon contents, and
- high soil CEC.

This list can be refined using evidence from stand 17 where many regrowth species had established. There, soil pH had remained low and soil carbon content and CEC relatively high, indicating that these conditions were unimportant as regrowth species excluders.

The floristic succession that was taking place in the study area can be illustrated in two ways. Firstly, a table of all possible combinations of excluding factors can be prepared, the sites where these

Table 29. Possible combinations of high and low values of factors that prevented forest or regrowth type species establishing

Combinations of factors			Occurrence of combination	Establishing flora
1) High surface soil N	1) High max. air temps. 2) High rad. levels	1) Low surface soil C 2) Low surface soil CEC 3) High surface soil pH		
*	*	*	Nowhere	Neither
*	*		Nowhere	Neither
*			Forest	Forest spp.
	*	*	Abandoned fields	Regrowth spp.
	*		Logged-over forest	Regrowth spp.
*		*	Nowhere	Neither
		*	Established grassland	Neither
			Nowhere	Neither

combinations occurred noted, the flora likely to establish there predicted, and this compared with field data. Some of the apparent excluding factors can be eliminated from this table where measurement errors and non-independent variation made the measured stand means of doubtful accuracy; blue and green radiation and daily minimum air temperature differences can be excluded for these reasons. Several of the remaining factors tended to be co-linear and can be grouped as one factor. Red and total radiation receipts were closely correlated ($r = +0.96$), while a crude correlation existed between these variables and daily maximum air temperature depressions ($r = -0.55$). Similarly soil pH and CEC were correlated ($r = -0.84, -0.55$) and soil carbon was closely related to these (see above). Thus, the table can be reduced to a three-attribute configuration (Table 29).

Of the eight possible combinations of attributes, four were not found in the field; this apparently reflected the response of different attributes to the same influencing factor. Thus, for example, a combination of high soil nitrogen, high air temperatures and radiation, and low soil carbon, CEC and acidity was never found because high nitrogen levels required a hardwood tree cover which automatically lowered radiation and air temperature levels while raising soil carbon, CEC and acidity. Even if any of these four combinations had occurred, however, it seems that neither type of species would, in theory, have been capable of establishing in it, and it could only have supported an unique and alien flora. Of the four remaining combinations of attributes that did occur, one represents forest conditions where the combination excluded regrowth species but permitted hardwood trees to establish there (i.e. permitted the forest to regenerate in situ). Two other combinations represent conditions produced by forest clearance, with or without burning and cropping; in both instances regrowth species establishment was favoured. The final combination represents conditions found under long-established grasslands, such as stand 14, and is the most interesting. In such situations the insolation receipts at the ground surface and the temperatures experienced in the adjacent air layer were both low, excluding other regrowth species. Conversely, soil pH still remained high and carbon content and CEC low, discouraging the establishment of

hardwood trees. Thus, while the reasons for the initial establishment of these grasslands must have lain with other factors, the reason for their stability was the evolution of an unique micro-environment beneath them. Clearly, over a long period some establishment of woody species must have taken place as was happening in stand 16. This is to be expected as scattered chance breaks in the grass cover must have occurred and allowed the establishment of the woody plants (Plate 6). Woody growth initiation under such conditions is likely to be much more rare than it would be directly on to bare ground, however, and this perhaps accounted for the patchy distribution of softwood trees and tree ferns on site 7 which was probably covered by Imperata cylindrica var. major for some time after its abandonment. An anomalous feature was the poor establishment of young tree ferns in grasslands for, as a species of wide tolerance, it should, theoretically, have been an ideal colonist. It is possible that some form of compensation may have taken place between environmental variables affecting tree ferns, and that the appropriate combination did not occur in grassland.

Table 29 clearly represents an over-simplification of field conditions as all significant factors are treated at two distinct levels: high or low. Unfortunately, the analysis of variance results do not permit a more refined treatment, and insufficient data are available accurately to define the tolerance extremes of all species. A more realistic illustration of the floristic succession can be made, however, by showing changes in predominances and seedling numbers along each environmental gradient (Fig. 19). Points of the graphs are calculated as means for data falling within standard segments of the gradients. Shaded and un-shaded portions of each diagram represent percentage hardwood tree and percentage regrowth species predominance, respectively. Summed frequencies of hardwood tree seedlings, juvenile tree ferns and softwood tree seedlings (reduced to a standard 18-quadrat per stand sample) are superimposed on the diagram. For clarity, the seedling frequencies of small herbs and large zingiberaceous herbs have been omitted and the softwood curve taken as representative of the regrowth flora. The salient features of these diagrams are as follows.

Figure 19. Floristic succession: the changes in the prominence of hardwood trees and regrowth species and the changes in seedling frequencies along micro-environmental gradients.

a) Hardwood tree predominance and regrowth species predominance tend to occupy distinct portions of the environmental gradients. Only on the gradient of exchangeable Ca did this not hold, suggesting that this variable was unimportant in determining the general trend of the succession.

b) Hardwood tree seedlings tend to occur abundantly only at one end of all the gradients except that of exchangeable Ca.

c) Softwood tree seedlings tend to occur abundantly at the opposite end of gradients of radiation and daily maximum air temperature depressions. Their uniform occurrence along other gradients suggests that the variables represented were not effective in excluding them.

d) Despite this polarization there is considerable overlap, indicating that the distinctness of the two-phased floristic succession may have been considerably "blurred" by the tolerances of individual species going beyond those of the groups to which they were allocated.

e) Juvenile tree ferns tend to occur with uniform abundance along all gradients indicating a uniform establishment throughout the succession and within the forest.

These diagrams do not adequately define the environmental conditions under which hardwood trees established in abundance, as variations in seedling numbers along each gradient may not have been fully independent of other measured and un-measured environmental variables. On all gradients, however, a uniformly low abundance of hardwood tree seedlings was recorded at the extreme representing micro-environmental conditions at or soon after a site was abandoned. It is therefore safe to conclude that the establishment of hardwood tree seedlings was unlikely to have occurred immediately after abandonment. The time at which conditions did become suitable to hardwoods depended both on age and the type of secondary vegetation that came to predominate in the stand. Radiation and air temperature conditions gradually became more favourable irrespective of cover type while favourable soil conditions (carbon, CEC, pH) appeared only when woody regrowth began to predominate in the stand. However, unless abnormal circumstances intervened, woody species usually became prominent within a few years, or less, of abandonment, permitting at least some hardwood species to

establish in the stand from this early period. Woody regrowth species, therefore, although having similar environmental requirements for establishment to the small herbs predominant in young stands, played a distinct and vital role in the regeneration of forest. As they were capable of establishing under the same conditions as the "early" small herbs, one must conclude that this latter group of species was of minor importance in the process of forest re-establishment; in most cases they were field weeds that maintained themselves in the vegetation for some time by virtue of their rapid growth. Where few had in fact established, as in remote forest clearings, seedlings of softwood trees appeared exclusively and a stand similar to 18 was formed. However, a predominant herb stage could have been detrimental to the floristic succession (and hence, ultimately, to the structural succession) by prohibiting species of other life forms from establishing successfully beneath it.

The time at which regrowth species were prevented from establishing is also difficult to define. High radiation and air temperature appear to have been the main excluders of this flora and, while both underwent progressive alteration throughout the period measured, the most dramatic changes in these factors had already taken place in the stands before they were sampled. It is probable, therefore, that the seedling numbers recorded in the stands merely represented the terminal phase of scattered establishment and that, at the time of sampling, most were already effectively excluded from the vegetation.

STRUCTURAL SUCCESSION

The results presented above indicate that a successive change in flora cannot, by itself, have accounted for the successive changes of stand structures observed in the study area. The only aspect of the structural succession that is explainable as a necessary concomitant of the floristic succession was the replacement of regrowth life forms by hardwood trees. As it has been demonstrated that all of the predominating life forms of stages prior to the hardwood tree stage established at about the time of abandonment, the several distinct structural stages that did occur before the emergence of mature hardwood trees can only be attributed to differing growth rates among the secondary flora. The structural

succession may be termed self-induced or autogenic insofar as it was a reflection of the inherent properties of the species involved.

In what may be termed the "typical" succession in the study area, on land lightly cropped after clearance of forest, the following structural changes would have taken place.

a) During cropping of the site the weed flora would have included elements of all types of regrowth plant; small herbs, softwood tree seedlings, juvenile zingiberaceous herbs and juvenile tree ferns. (It is assumed that hardwood tree seedlings were completely killed by burning and cropping.)

b) During the cropping period, the rapid growth of the small herbs would have led to their predominating in the stand; this situation would have persisted for up to a year after abandonment. Many of these small herbs would have reproduced vegetatively and so maintained themselves on the site despite an altered micro-environment. Plant mass at this time would have approximated 3 kg/sq. m.

c) After a year, young softwood trees would have begun to overtop the herb layer, closing rapidly to form a complete cover that would soon have eliminated the small herbs. Beneath the softwood trees, tree ferns would have continued to grow slowly. When the stand age had reached 6-7 years, the plant mass would have approximated 12 kg/sq. m with tree density varying considerably from stand to stand. If the invaders had been small trees such as Omalanthus cf. surigaoense, a high density even-canopied stand would have resulted; as these are shorter-lived, death would have taken place at between 10 and 15 years of age and the stand would have passed directly to tree fern predominance. If the invaders had been large trees such as Trema orientalis or Mallotus paniculatus, tree density would have been lower and the canopy more uneven and broken. As these are relatively long-lived, tree ferns would have remained suppressed indefinitely beneath them and predominance would have passed directly to hardwood trees.

d) In stands where tree ferns had become predominant, plant mass would have changed little from that of the foregoing stage. These tree ferns, unlike the softwood trees, would have been able to reproduce in situ and so maintain the stand in a stable structural state until such

time as hardwood trees migrated to and established in the stand, matured, and eventually overtopped the tree ferns. Thereafter the tree ferns would have maintained themselves in a subordinate position in the forest. Tree ferns were thus the only species occurring locally to which Van Steenis' (1958) analogue with lymph is in any way applicable, the plants circulating within the "body" of the forest and forming a "scab" where necessary.

A structurally similar, but floristically distinct, succession took place where disturbance had been minimal, such as in logged-over forest. Here, already established hardwood seedlings maintained themselves and were thus present throughout the succession, although a similar staging of predominating life forms took place. The herb stage tended to be floristically distinct with few field weeds; sparser herbs, typified by Impatiens sp., temporarily predominated and occasional dense stands of juvenile Musa sp. occurred. Thereafter, the structural succession proceeded as described previously with the difference that the re-establishment of hardwood trees took place more rapidly.

In addition to these stages in the "typical" structural succession in the area a number of aberrant structural types occurred. Established stable stands of small herbs were the most common of these. While the reasons for their stability have been described, the causes of their initial establishment are less clear; fire is the most widely cited explanation and, in stand 15, may have been responsible for the death of young softwood tree seedlings. In stand 14, it seems likely that few woody species established at the time of abandonment as there was no record of fire there. As this was a former house-site and as it was the only stand in which Panicum maximum was found, it seems probable that this bunch-grass was the sole species capable of establishing successfully on the compacted soil there.

Stands of large zingiberaceous herbs are more difficult to explain. Both species were widespread and it is possible that, where abundant at the time of sampling, they had merely proliferated vegetatively filling a structural gap. Where softwoods were dying and no tree ferns or hardwood trees were replacing them, as in stand 4, colonies of Hornstedtia

sp. were appearing. In stand 7 this species had probably extended to fill all gaps between the scattered softwoods and tree ferns. As these stands did not possess conditions unfavourable to softwood or tree fern establishment, it is surprising that they were not replaced; it is possible that the exclusion mechanism was some un-measured environmental phenomenon. Exclusion of hardwood seedlings was expected because conditions were very different from those of forest. Thus, with all structurally higher life forms excluded and self-maintenance assured by vegetative propagation, these stands appear to have been destined for long periods of stability.

CONCLUSIONS

The secondary plant succession that took place during the re-vegetation of abandoned sites in the study area was, therefore, of far greater complexity than first appearances suggested. The apparent multi-staged succession of structures could be shown, by detailed sampling, to be a real phenomenon. Its explanation lay in two distinct processes:

a) differing growth rates of an established population of species most of which, except for tree ferns, could not reproduce themselves sexually in situ, and

b) a successive change of floras from one of regrowth species to one of forest species, the hardwood trees of the forest flora serving as the predominating life form of the terminal structural stage of succession.

The floristic succession in the area showed an overwhelming tendency to be two-phased. Because of this, the flora of any stand tended to be composed of two distinct elements:

a) those species which established before or shortly after site abandonment and which, through longevity or vegetative reproduction, had succeeded in maintaining themselves in the stand, and

b) those forest species which, subsequent to the start of re-vegetation, had succeeded in establishing in the altering micro-environment and maintaining themselves thereafter.

Despite the distinct two-phased nature of this floristic succession it cannot be satisfactorily described as two-staged. All

stands, save those at the extremes of the succession, showed an intermingling of the two floras in varying proportions. Even in so small an area, location of a stand and chance entrants produced distinct floristic differences between stands of similar ages and site treatments. Floristic succession in the study area can, in some degree, be likened to Whittaker's (1953) "change of populations with time", although polarization of the species into two ecologically distinct groups means that the combinations were not entirely random. A "typical" succession is described for convenience only; succession followed many courses even when the treatment of sites had been identical. The recognition of a "sere" or "unit succession" in the study area cannot be justified, however.

The insignificance of soil nutrients (at least as measured by the methods used) and soil moisture conditions in the general process of re-vegetation in the study area contradicts the often-repeated statement on the importance of these factors to the course of secondary rain forest succession. It is possible that changes of these phenomena may have taken place with re-vegetation on individual sites, although these were masked by greater site-to-site differences. If species sensitivity to these phenomena existed (although undetected in the analysis), there is the possibility that an "individualistic" succession was taking place on each site.

FACTORS COMPLICATING THE SUCCESSION

The successional processes demonstrated in the foregoing section were clearly only trends: a rigidly organized "sere" did not occur and stand characteristics could not be accurately predicted solely from their age. The importance of site locational and environmental differences, differing degrees of disturbance and chance floristic entrants in complicating the succession have already been mentioned. While the first three of these can be estimated, allowing some assessment of their effect on stand morphology, the last cannot be, and the amount of unexplained variation in stand characteristics that remains after the effects of these three have been allowed for gives some measure of the importance of this chance intrusion.

STAND FLORISTIC CHARACTERISTICS

It is clearly not possible accurately to predict the floristic composition of a stand given the flora of the region in which it is situated; too little is known of the individual properties of species and the factors affecting colonization. However, the floristic data collected suggests that the numbers of the species of the two ecological groups distinguished (regrowth and forest) were varying in an orderly manner. The total species population of the study area has been divided into these two groups, inevitably a somewhat subjective process. The separation was based on the tolerance differences among 30 widespread species detected previously and, whilst the extension of these conclusions to the whole species population is speculative, it nevertheless conforms to field observations. Widely occurring species of either forest or regrowth could be allotted to one group or the other with some objectivity, but for the sizeable number of infrequent minor species, the allocation was less certain. Field notes made at the time each plant specimen was collected have been used extensively; these were based on the author's observations and the recommendations of a local helper familiar with the flora. To avoid retrospective judgements, the separation was made prior to analysis and maintained without alteration thereafter (see Appendix). Of the total population of 346 species considered, 189 were designated as forest and 157 as regrowth. Although the size of these

two groups seems similar, because of more extensive sampling the number of regrowth species probably represented a high proportion of those actually occurring in the area whereas the number of forest species was certainly only a small proportion of the total. The size of the two groups in each stand is given in Table 30. In stands where a 21-quadrat sample was taken, the sizes of the groups were reduced proportionately, making them comparable, on a unit-area basis, with the remaining 18-quadrat samples.

Regrowth Species

Regrowth species may be thought of as a widely dispersed and highly mobile population. As most of the herbs of this group are common field weeds, this high mobility is a prerequisite for their survival. Many of them also possess seeds capable of prolonged dormancy in forest soil (cf. Symington, 1933) judging from their rapid appearance in considerable numbers in isolated openings in the forest. Conversely, subsoil exposures along logging trails, while re-vegetated more slowly than undisturbed soil, were usually well colonized within a year of exposure, suggesting moderately quick migration of propagules over the short distance to such sites. It is not surprising, therefore, that most young stands possessed a sizeable complement of species of this highly mobile group. What is notable, however, is the consistency of species numbers per unit area on similarly treated sites. Stands 1, 2, 17 and 18, all of comparable age and similarly light treatment, possessed closely similar numbers of regrowth species while on two other sites, one a corn field just abandoned and the other a one year old site formerly cleared twice without cropping, similar numbers were also recorded (39 and 32 respectively). This uniformity in species numbers may have reflected a random distribution of propagules throughout the area although data are insufficient to test this. On the other hand, it may have represented the maximum number of ecologically distinct units (species) that could be integrated on the given area of ground. As the regrowth group made up a major proportion of the total species in most stands, this uniformity in numbers per unit area was probably responsible for the constant sample size that was found necessary in order to sample stands with equal intensity.

Table 30. Numbers of forest and regrowth species in sampled stands.

Cyathea and Coffea spp. omitted; all samples reduced to 18 quadrats.

<u>Stand</u>	<u>Regrowth spp.</u>	<u>Forest spp.</u>	<u>% of forest spp. that were trees</u>
1	44	3	0
2	40	3	33
3	50	26	58
4	41	12	33
5	35	43	74
6	37	27	59
7	42	2	50
8	44	15	47
9	33	17	30
10	27	15	65
11	42	35	74
12	8	61	46
13	17	67	37
14	21	1	0
15	19	1	0
16	26	0	0
17	37	53	55
18	53	49	43
Abaca plantation	23	2	0
Corn field	39	0	0
Young woody regrowth	32	12	50

While the presence of so uniform a number of colonizing species is difficult to explain, it is possible to propose factors which could account for reductions in this number, provided the constituent species possessed differing tolerances of these factors. Differences in site environment at the time of abandonment may affect this but insolation and air temperatures at that time were similar at all sites and it has also been shown that regrowth species were insensitive to variation in most soil conditions. A second significant factor may have been a diminution in the store of viable propagules in the soil as a result of repeated cleanings (weedings) during cultivation. If a significant proportion of the regrowth species on each site arose from dormant propagules, it is conceivable that repeated cleanings removed seedlings from these and led to a progressive depauperization of the viable propagule store. The effects of such a process would be expected most severely to have influenced the longer maturing and more slowly migrating species, whilst having favoured the rapid maturing and freely migrating types. The approximate number of cleanings (including initial clearings and burnings) before abandonment of stands of comparable ages has been determined and plotted against the number of regrowth species in them (Fig. 20). While the relationship between the two variables is not clear, some joint variation does exist; linearity would not be expected as presumably a pool of resistant or ephemeral migratory species existed which were able to colonize sites irrespective of the number of times they had been cleaned. Annually burned grasslands, with their poor flora, probably come closest to stands entirely dependent upon such species. It is not possible, with the limited data available, to determine the exact nature of the relationship, however, and as only one of the sites (14) had undergone more intensive usage than those in Fig. 20, a linear relationship between cleanings and species numbers is assumed in the computations that follow.

The particular effects of the cleaning process on the trees of the group are demonstrated in Table 31. Because trees were the more slowly maturing members of the group and were likely to have migrated less freely than others, it is not surprising that a marked decline in numbers of tree species and particularly numbers of individuals, took

Figure 20. The relationship between the number of regrowth species in a stand and the number of times the site was cleaned, in sampled stands of comparable age.

Table 31. Prominence of softwood tree species in stands of similar ages, on sites that had undergone varied intensities of disturbance

<u>Stand</u>	<u>Cleanings</u>	<u>Species</u>	<u>Summed frequency</u>
18	1	9	59
17	1	7	29
2	2	16	69
Young woody regrowth	2	8	39
Corn field	2	8	38
1	6	6	17
15	18	4	5
Abaca plantation	25	4	6

place after repeated cleanings. Thus, while fire had been repeatedly cited as a determinant of the course of succession, it seems that the intensity of cleaning during prior disturbance may have a comparable effect.

Because few regrowth species established themselves in stands after the start of re-vegetation, stand age must also have affected the number present in any stand provided some gradation in species longevity existed. In Fig. 21 the numbers of regrowth species present in stands that had undergone similarly slight disturbances are plotted against the age of these stands. Whilst there is some hint of a decline in regrowth species numbers with age, the relationship is not close, and little can be said about its form. Species numbers were very low only in stand 12 and, were this stand omitted from the diagram, only a slow rate of species dropout from the stand would be indicated. The primary forest stand (13) contained 17 regrowth species, most of which were present in a tree fall site. This indicates that in primary forest considerable numbers of these species may have been kept in circulation, and that the low numbers in stand 12 may have been a temporary feature associated with the closure of the canopy. As the data do not permit the exact nature of the relationship to be determined, in the computations that follow a linear function is assumed to hold over the 27-year period of re-vegetation represented in the sampled stands.

Although it has been postulated that regrowth species were a highly mobile group, it is conceivable that forested areas were zones of low relative availability of these propagules while cultivated and regenerating areas represented a pool of readily available regrowth species. While it is desirable to test whether site location relative to the forest boundary affected the size of the regrowth species population in a stand, information of propagule dispersal is insufficient to permit any single measure of this to be postulated as most suitable. In lieu of any more specific hypotheses, mean site distance to the forest edge, whose measurement is described in the following section, has been used as a crude indication of the isolation of sites from the pool of regrowth species in cultivated and regenerating areas.

Figure 21. The relationship between the number of regrowth species in a stand and the age of the stand, in stands that underwent similarly light disturbances.

To assess the combined effects of these three factors on the numbers of regrowth species in the sampled stands, a multiple linear correlation was computed using regrowth species numbers as the dependent variable and stand age in years, number of cleanings prior to abandonment and mean site distance to the forest boundary in metres, as the independents. An arbitrary figure of 40 cleanings was assigned to stand 14, the former house site. A fourth independent variable, site altitude, was also added to assess whether the environmental gradients associated with altitude in the study area had any measurable effect upon regrowth species numbers. The four ingredients on combination gave a coefficient of $r = 0.591$; this accounts for only 35% of the variance in regrowth species numbers and indicates that other, un-measured, factors were having an appreciable influence on this variable.

An indication of the relative importance of these four factors is given by their partial correlation coefficients (Table 32). Of the four factors, number of cleanings was the single most important, and all other coefficients were well below the figure computed for it. The relatively low coefficient scored by the age variable may reflect a non-linear relationship, large numbers of regrowth species having been able to persist for an extended period during regrowth, then rapidly disappearing with forest tree canopy closure. Site altitude's low coefficient suggests that most regrowth species, despite many having probably recently migrated upslope from the lowlands, possessed sufficiently wide ecological amplitudes for environmental variation within the study area not to be an important factor in their occurrence. The location coefficient, besides being low, was negative, disproving the hypothesis as originally postulated; apparently there was a slight tendency for sites close to the forest boundary to have somewhat greater numbers of regrowth species than those far from it. However, the low coefficient does tend to support the concept of regrowth species as a highly mobile population. The regression equation for this relationship is:

$$X_1 = 92.070 - 0.33X_2 - 0.512X_3 - 0.001X_4 - 0.049X_5$$

Table 32. Relative importance of individual factors affecting regrowth species numbers

<u>Factor</u>	<u>Partial correlation coefficient</u>
Stand age	-0.306
Number of cleanings	-0.453
Distance to forest boundary	-0.241
Site altitude	-0.275

Table 33. Relative importance of individual factors affecting forest species numbers (a: one was scored if the site was burned and zero if not burned)

<u>Factor</u>	<u>Partial correlation coefficient</u>
Stand age	+0.567
If burned ^(a)	-0.634
Number of cleanings	-0.491
Distance to forest boundary	-0.198
Site altitude	+0.541

where

X_1 = number of regrowth species,

X_2 = stand age in years,

X_3 = number of cleanings,

X_4 = distance to forest boundary in metres, and

X_5 = site altitude in metres.

The adjusted standard error of the estimate for this equation is 11.65 species which, in view of the uniformity in regrowth species numbers in the sampled stands, makes this equation only a poor predicting device. There are several possible reasons for the low correlation: other unmeasured variables may have been affecting the numbers of regrowth species, the relationships may not have been truly linear and the original assumption that all species of this group established at or before abandonment may not have been true. Some new establishment may have taken place in the early stages of re-vegetation, maintaining species numbers at a higher level than that expected from the above method of estimation.

Forest species

In contrast with the generally uniform numbers of regrowth species in most stands, forest species numbers varied considerably from stand to stand. The size of the population immediately after abandonment appears to have depended upon whether the site was burned when cleared. Stands 17 and 18 were not burned but it is probable that all others were when originally cleared. While these two stands contained relatively large numbers of forest species (53 and 49 respectively), all other stands of similar age had almost none (Table 30). The subsequent size of the forest population in a secondary stand may depend upon two factors. It has been shown that environmental factors which prohibited the establishment of forest species changed favourably with the emergence of softwood tree predominance soon after abandonment. If the forest population had previously been exterminated by burning, the numbers establishing would have depended wholly upon the number of propagules reaching the site. This, in turn,

would have depended upon the age of the stand (if a spatially constant propagule rain was occurring throughout the area) and the distance from the forest (if such a constant propagule rain was not the rule).

A measure of site distance from forest has been arrived at by using a corrected planimetric map prepared from an aerial photograph (Fig. 2). A protractor was placed on the approximate centre of each stand with the cardinal point orientated northwards. Radiating lines were drawn every 30 degrees and extended to touch the nearest forest or logged-over forest boundary and along each of these twelve lines the distance from the edge of the stand to the forest boundary was measured in metres. Where stand edges abutted the forest a zero value for distance was scored. The mean of the twelve distances for each stand was then used as a crude measure of proximity to forest. There are several objections to this procedure. While the forest may have represented the seed source for forest tree species, more rapidly maturing and fruiting forest herbs in secondary stands may also have been seed sources. Moreover, direction itself may affect the facility with which propagules from forest reach a site, making the use of a mean figure, without weighting for direction, suspect.

To assess the importance of these three factors (burning, age and distance from forest) on the numbers of forest species in a stand, a second multiple linear correlation was computed. Because the softwood regrowth trees were responsible for creating a favourable micro-environment for forest plants and because the numbers of these were affected by the numbers of times the site was cleaned (Table 31), this variable was added to the analysis as a fourth independent. Site altitude was also added for reasons already described.

The five factors together gave a correlation coefficient of $r = 0.930$ which was far higher than that computed for numbers of regrowth species, 87% of the variance in forest species numbers being explained. Partial correlation coefficients are given in Table 33. Site burning appears to have been the single most important factor determining forest species numbers at a site. Coefficients for stand age, number of cleanings and site altitude are all somewhat less but of comparable magnitudes.

The relatively high coefficient scored by site altitude contrasts with its slight effect on regrowth species and suggests that the forest species population may have been of "mid-mountain" affinities, with sites at progressively lower altitudes falling beyond the tolerances of greater numbers of this population. The low coefficient scored by the location factor is of greatest interest. Apparently despite the obvious low seed mobility of certain forest species, such as Lithocarpus spp. and the large dipterocarps, a sufficiently large number of other forest species had adequate mobility over the distances involved to relegate this factor to a position of minor importance. This conclusion supports the basic assumption that propagule rain throughout the area was a relatively constant factor.

The regression equation for this relationship is:

$$X_1 = 0.69X_2 - 29.404X_3 - 0.445X_4 - 0.010X_5 + 0.088X_6 - 40.358$$

where

X_1 = number of forest species,

X_2 = stand age in years,

X_3 = if burned,

X_4 = number of cleanings,

X_5 = distance to forest boundary in metres, and

X_6 = site altitude in metres.

The adjusted standard error of the estimate for this equation is 10.69 species. Although very similar to the figure calculated for regrowth species numbers, the greater variation in forest species numbers means that the relative accuracy of prediction is greater.

The proportion of forest species that were trees is given in Table 30. Apart from the few stands with three or fewer forest species, the proportion of trees was consistently above 30% and in two stands 74% was recorded. This indicates that, even in young regrowth stands, the forest species population was not biased toward the smaller types but contained a high proportion of future trees.

The stand floras

The considerable variation in numbers of regrowth species on the one hand and forest species on the other which can be explained by combinations of habitat factors, adds weight to the earlier conclusion that the species of the study area were of two ecologically distinct types. The presence of these two groups, responding differently to habitat factors, explains, to a large degree, the differences in floristic richness of the sampled stands. The appropriate combination of conditions, as occurred in stands 17 and 18, resulted in a full complement of species from both groups, and produced an exceedingly rich stand. Thus, while the generalization that secondary vegetation is floristically poor in comparison with primary forest holds in many cases, the opposite relationship may occur.

All ecological evidence suggests that the successional change of these two species populations was reflected in a major floristic gradient in the secondary vegetation at any one time. While this cannot be tested in absolute terms (no sufficiently rapid computation method exists), the use of a gradient determined according to some standard mathematical model serves as a useful check on this assumption. Maximum gradients of floristic variation have been determined by two methods, both using species presence and absence data. In the first, the crude, but rapidly computed, ordination techniques developed by Bray and Curtis (1957) have been used, employing Sørensen's (1948) similarity coefficient and a geometric extraction of axes. A second, more complex and mathematically more correct, ordination, based on Gower's (1966) method and using a program developed by W.T. Williams was computed, using Pearson's ϕ (correlation) coefficient as a similarity value and extracting principal co-ordinates. The first five axes extracted are listed in Table 34.

In Fig. 22 the numbers of species of the two groups (forest and regrowth) in each stand are plotted against the first axis of floristic variation extracted by each method. In both, trends in the sizes of the two populations are opposed, particularly from low numbers of forest species to high numbers; this is particularly clear in the second, complex, ordination. It can thus be concluded that this successive change of species populations is reflected, to a large degree, in the major

Table 34. First five principal axes extracted from stand correlation matrix

<u>Stands</u>	<u>Axes</u>				
	I	II	III	IV	V
1	-0.405	-0.237	0.025	-0.080	-0.146
2	-0.353	0.032	0.114	-0.377	-0.003
3	0.034	0.254	-0.227	-0.108	0.126
4	-0.244	0.028	-0.198	-0.017	0.274
5	0.219	0.218	0.430	0.291	0.460
6	0.224	0.155	0.084	-0.327	0.382
7	-0.367	-0.012	0.011	-0.267	0.065
8	-0.128	0.007	-0.376	-0.042	0.116
9	-0.094	0.193	-0.063	-0.191	-0.355
10	-0.077	-0.020	-0.185	0.486	-0.131
11	0.131	0.307	-0.470	0.315	0.025
12	0.763	-0.517	-0.061	-0.090	0.046
13	0.710	-0.476	-0.126	-0.083	-0.131
14	0.355	-0.168	-0.108	-0.063	-0.048
15	-0.374	-0.243	0.101	0.273	0.108
16	-0.404	-0.308	0.312	0.136	-0.110
17	0.471	0.291	0.467	0.095	-0.192
18	0.249	0.495	0.052	-0.079	-0.396
Total variance extracted	2.429	1.332	1.057	0.925	0.859

Figure 22. Changes in the size of the two species populations distinguished along the principal axes of two ordinations.

Figure 23. The relationship between the distance of a stand from (18) and the position of the stand on the second axis of the complex ordination.

floristic gradient as illustrated in these two models. The results listed in Table 34 indicate, however, that this major axis does not extract a large proportion of the total variance from the matrix. This is evidence of the complexity of floristic variation in the sampled stands and further indicates the absence of a uni-directional floristic succession, or sere, in the study area. Variation represented by the second axis appears to have a crudely geographical centric tendency, dissimilar stands, such as forest and grassland, being placed close together. The distance from stand 18 (which is assigned the highest positive score on the axis) to all other stands has been measured and plotted against the axis values (Fig. 23). As stand 18 occurred near the geographic centre of the area, the suggestion is that the positions of stands on this axis correspond to their degree of removal from the common species pool. The remaining three axes of the second ordination represent variation which, with the data at hand, is incomprehensible. They apparently represent the variation caused by "chance floristic entrants" that cannot be accounted for.

CHANGES IN VEGETATION MASS

If a uni-directional succession existed in the study area, stand mass might be expected to have varied predictably with age even if in a complex and non-linear manner. Since this was not the case, the problem arises as to what other factors influenced this stand characteristic and with what accuracy it could be predicted. A first approach to the problem is the examination of growth characteristics of the main structural components of the vegetation, softwood trees, tree ferns, and hardwood trees, to determine whether each operated independently and, if so, the possibility of predicting total stand mass from the masses of its components. The growth curve of any life form group depends upon three factors:

- a) the degree of similarity in growth characteristics of the constituent species of the group which determines the uniformity of shape of the curve,
- b) the time at which the group establishes, determining the position of the curve on the time axis, and

c) the success with which the group establishes on a site, determining the absolute size reached by the growth curve.

The softwood tree and tree fern groups can be regarded as having established at the time of site abandonment, so eliminating the second factor from consideration. When the mass of the two groups was plotted against time it was evident that no clear growth curve existed, even among sites that had not undergone cropping and could be assumed to have been well colonized. However, there was some suggestion of two types of softwood growth curve and older stands (e.g. 5 and 11), which were composed of longer lived trees, exhibited the persistence of this element for a longer time. The complete absence of a softwood tree element in stand 12 suggested that this site was originally colonized by shorter lived species. There was no system in the arrangement of tree fern growth data; numerous apparent inconsistencies existed as, for example, between stands 3 and 6. It must therefore be concluded that neither of these two structural groups showed a sufficient consistency in growth to enable stand structural characteristics to be predicted from their sum. This variation may have resulted from differences in the factors listed above or from competition between, or even within, groups. A similarly negative conclusion must be drawn about the growth characteristics of the hardwood tree element. Only stands 11 and 12 possessed sufficient amounts of this element to permit comparison and the latter had more than twice the mass of the former. Presumably differing times and degrees of success of colonization account for most of the differences.

The apparent inter-dependence or haphazard variation of these structural elements suggests that total stand mass may be more accurately accounted for by relating it directly to habitat factors. In Fig. 24 total stand mass/sq. m is plotted against stand age. If only the slightly disturbed stands are considered, a bifurcation of the trend of structural change can be seen, which represents differences in type of colonizing tree that have already been mentioned. While mass continued to increase in stand 11, it had stabilized at approximately 12 kg/sq. m in the tree fern stands. This difference was apparently the result of

Figure 24. The relationship between stand mass and stand age. Stands on sites only slightly disturbed are plotted as dots, and those on sites more severely disturbed are plotted as triangles.

chance floristic differences and cannot be accounted for. However, it is possible that disturbance played a part in depressing the masses of the remaining stands by limiting the numbers of regrowth trees establishing while this, in turn, restricted the establishment of forest trees.

A multiple linear correlation of stand mass with age and number of cleanings prior to site abandonment yields a coefficient of $r = 0.802$; 64% of the variance in stand mass being accounted for. Data from stand 17 were omitted in this computation as the stand began regeneration with a large residual mass in the forest remnant. Partial correlation coefficients for the two independent variables are:

stand age	+0.781
number of cleanings	-0.472.

Thus, while stand age appears to be of greatest importance in determining stand mass, intensity of disturbance also has an appreciable effect. The regression equation for this relationship is:

$$100X_1 = 278.30 + 91.10X_2 - 31.14X_3$$

where

X_1 = stand mass in kg/sq. m

X_2 = stand age in years, and

X_3 = number of cleanings prior to site abandonment.

The adjusted standard error of the estimate for this equation is 4.43 kg, a moderately low figure in relation to the dependent variable.

CONCLUSIONS

In the study area, a variety of factors complicated the successional process leading to complex structural and floristic differences among the regrowth stands. Only some of these factors were measurable but their effects, when considered in combination, explained considerable proportions of the observed structural and floristic variation between stands. Evidence from two mathematical models suggests that a succession of two distinct species populations represented the main floristic change in the study area. There remained, however, considerable and unexplainable variation.

The floristic ingredients of the forest ecosystem in the study area could be present from an early stage of succession. If the site had not been burned, many forest species were present at the time of abandonment. If burned, the build-up of forest species numbers on a site depended upon site age, the number of cleanings and site altitude, but only slightly on distance from forest.

The development of a primary forest structure was, however, a lengthy process. Stand 12, after 27 years, appeared, superficially, to possess a typical forest structure but sampling revealed that it lacked the very large emergent trees that characterized primary forest. The time necessary for primary forest structure development depended, therefore, upon the growth rates of the large forest trees. Brown (1919) calculates that at 300 m elevation at the base of Mount Makiling in Luzon, the fast-growing dipterocarp Parashorea plicata, when open-grown, requires approximately 54 years to reach a diameter of 34 cm (907 sq. cm basal area). The two softwood trees Mallotus riccinoides and Macaranga sp. require only 17 and 15 years respectively to reach similar diameters. For Parashorea plicata to reach a diameter of 80 cm (5026 sq. cm basal area), 110 years is required. The same species when suppressed requires 107 and 142 years to reach diameters of 34 and 80 cm respectively. More rapid growth than this appeared to be taking place in the study area. In stand 12 (27 years old), one individual of Shorea cf. polysperma had a basal area of 1250 sq. cm, and other trees with up to 2300 sq. cm basal area were recorded. Even if this more rapid growth rate is allowed for, however, it seems likely that the two large emergents sampled in stand 13, each of 50,000 sq. cm basal area, were some centuries old. It must be concluded, therefore, that the re-establishment of a forest structurally similar to primary forest requires a time span of this order of magnitude.

DISCUSSION

The complexity of the functional relationships which existed in the secondary vegetation of an area so restricted as that of Gumate, amply justifies the intensive level at which the study was carried out. Indeed, these relationships were so complex, and the tendency toward individualistic stand characteristics so strong, that many more sites than the 18 actually sampled would have been desirable to ensure firm conclusions about general trends in the secondary vegetation of the area. The verbal reports on site histories which had to be used were not as full or as accurate as might have been hoped for. For example, the significance of burning in the extermination of the forest species population at a site could have been more accurately assessed if it were certain that all sites save 13, 17 and 18 had originally been burned. This difficulty in accurately dating stands of secondary tropical vegetation and determining the histories of disturbance of the sites on which they grow, where primitive shifting cultivators are responsible for the disturbance, suggests that more satisfactory results may be obtained if future research concentrates on abandoned plantations, written records of which should be available.

Despite the smallness of the area in which the study was carried out, environmental variation was sufficient to transgress the tolerance limits of some forest species, but few regrowth species. This subtle macro-environmental control emphasizes the need for great care to be exercised in selecting study areas that are uniform in this respect. However, most species were apparently of sufficient mobility to justify the basic methodological assumption that the accessibility factor did not vary greatly throughout the study area.

Although an attempt was made to reduce the explanation of vegetation characteristics to direct plant-environment interactions, this proved an impracticable task in the present state of knowledge. While it is reasonably certain that the significant relationships recorded between some plants and radiation or air temperatures involved direct cause and effect, none of the soil factors that were significantly correlated with vegetation characteristics were likely to have been

exercising a direct effect upon the plants involved. However, the high correlations recorded do suggest that rather positive indirect effects were involved and that the relationships were probably not spurious. In addition, because of the colinearity among several of the correlated environmental factors (e.g. radiation and air temperatures), it is possible that only some of these factors were having an ecological effect and that the effects of others were more apparent than real. It is, of course, impossible, with the data available, to separate the correlated factors into significant and insignificant.

As was to be expected, many of the environmental variables measured were not significantly correlated with any vegetation characteristic. The lack of significant effects of soil moisture can be attributed to the abundant and evenly-distributed rainfall which kept soil moisture tensions at low levels at all sites throughout the year. Had the rainfall régime been known before field work was started, its measurement could have been less detailed. As it happened, the area, when selected, was going through what, in retrospect, must be regarded as an exceptional dry spell, and although local informants at that time attested to the generally high rainfall of the area, it was thought that such a dry spell, even if occurring only once annually, may have been significant in eliminating less drought-resistant species from certain sites. However, in view of the annual variability of rainfall of the region it is possible that the unexplained features of some stands owed their origin to some unknown period of drought during their development (e.g. the absence of juvenile tree ferns from stabilized grasslands).

The lack of apparent differences in the spectral composition of shade radiation of different stands is probably more closely related to inadequate techniques of measurement than to a real absence of such differences. It does indicate that future attempts to measure this variable must make use of far more sophisticated techniques.

The apparent ineffectiveness of soil nutrient status upon the secondary vegetation can be attributed to one or more of three factors. Firstly, the soil parent material, a basic volcanic rock, probably

contained a relatively high proportion of nutrient elements, and the shallowness of the solum meant that the weathering zone was within reach of the roots of most plants. Many of the mature larger plants, therefore, were possibly drawing upon reserves from this zone and were insensitive to nutrient differences in the surface soil. Secondly, it is possible that most plants encountered in the study area were adapted to soils of low fertility and so were insensitive to variations in soil fertility encountered there, all of which were possibly above a limiting value. Thirdly, the inadequacy of the techniques of chemical analysis used doubtless also served to obscure the issue. This ineffectiveness of soil nutrient status implied a minimal effect, on re-vegetation, of soil erosion during prior periods of disturbance. Indeed, the single conceivably important effect that soil erosion may have had in the study area may have been the removal of viable seed. It is possible that some of the apparent reductions in numbers of regrowth species in a stand, seeming to result from repeated cleanings of the site, may be attributable to a removal of viable seed by surface wash-off. The role of erosion in reducing soil organic matter levels was also minor (Kellman, 1969).

The validity of having used spatial variation to elucidate a time sequence could only be determined by observations over an extended period. However, the importance of the vegetation changes that took place at about the time of site abandonment indicates that sequential observations over a period of several months at such sites may have provided valuable data confirming or confuting conclusions that had to be drawn from circumstantial evidence. Despite these methodological limitations, however, several conclusions can safely be drawn.

Most stands of secondary vegetation contained a single, distinct, life form which made up an overwhelming proportion of the plant mass; the life forms distinguished in this rôle included small herbs, large zingiberaceous herbs, large musaceous herbs, softwood trees, tree ferns and hardwood trees.

A comparison of the juvenile and mature plants present in each stand revealed that all stands, save those in which hardwood trees were predominant, were apparently unstable. In some stands, notably those

in which softwood trees predominated, little reproduction of the mature species was taking place. In other stands, in which the predominant plants were reproducing themselves, juvenile forms of other species which, when mature, would overtop the currently predominating life form, had established. It is concluded, therefore, that the secondary vegetation of the area was in a state of flux.

When the structures of these stands were compared with the time that had elapsed since their sites were abandoned, a general trend from small herb predominance in very young stands, to hardwood tree predominance in very old stands was evident. Stands of intermediate age had either softwood trees or tree ferns predominant. It is inferred, therefore, that a structural change will take place during re-vegetation of any abandoned site in the area from small herb predominance to hardwood tree predominance via softwood tree or tree fern predominance or both.

However, the multi-staged structural succession was not paralleled by a similarly multi-staged floristic succession. The floristic succession was two-phased as most species of the area appeared to belong to one of two distinct ecological groups. Those species in the regrowth group, including small and large herbs and softwood trees, established before or soon after the time of site abandonment but negligibly thereafter. Those species of the forest group established only at some time after site re-vegetation had begun. Tree ferns were a separate group of wide ecological amplitude, capable of establishing at any time during re-vegetation.

The environmental factors significant in this floristic succession included radiation intensity, air temperature, soil carbon, CEC, pH and nitrogen. As softwood trees were capable of inducing micro-environmental conditions favourable to hardwood tree establishment soon after site abandonment, most stands showed an inter-mingling of the two ecological groups in varying proportions.

The single structural change in the secondary vegetation that could be interpreted as a result of floristic change was the establishment,

and slow rise to predominance, of hardwood forest trees. Structural stages prior to this terminal state were interpreted as a reflection of the differing growth rates of the established population of regrowth species, all of which established at about the same time. Small herbs grew rapidly and so predominated in the stand at an early period, reproducing only vegetatively thereafter. Softwood trees grew more slowly, but, if well established, eventually rose to predominance and suppressed the herb layer. However, they were incapable of reproducing sexually in situ and were invariably there for one generation only. If short-lived, they died after 10-15 years and were replaced by slower-growing tree ferns already established beneath them. If longer-lived, they were usually replaced directly by hardwood forest trees, tree ferns remaining as a subordinate layer at all times. Tree ferns were capable of reproducing themselves in situ and maintaining a structurally stable stand until hardwood trees established beneath them, matured, and eventually overtopped them.

Although a general successional trend could be distinguished, several factors served to complicate this greatly. Whether or not a site was burned after clearance appeared to determine whether an established seedling population of forest species (and possibly any viable seed in the soil) was present from the start of succession. The number of times a site was cleaned during disturbance adversely affected the size of the regrowth population, and especially the number of softwood trees. An extended period of disturbance could lead to a depauperate stabilized herb stand the micro-environment of which did not favour the establishment of either woody regrowth species or forest species. The final, and possibly most important, complicating factor was chance presence or absence of particular species. Although this was strictly not a "chance" factor, no obvious reasons could be proposed to account, for example, for the fact that one species of softwood tree established in stand 3 and a different one in stand 6, or that tree ferns had not established in stand 4.

The floristic succession that was taking place at Gumate seems most closely to approximate Whittaker's (1953) concept of plant succession. However, there appeared to be less disorder in the change than he conceived

Table 35. Structural features of secondary stands in Malaya, Singapore, Nigeria and Trinidad, compared with those of similar age at Gumaté. Data from: a, Symington (1933); b, Burkill (1919); c, Ross (1954); d, Greig-Smith (1952); e, measurements made 1 ft. above the ground.

Area	Age (stand no.)	Canopy height in metres	Density of trees over 5 cm d.b.h. in metres ²	Density of trees over 9 in d.b.h. in metres ²
Malaya ^a	6 months	1.8		
	20 months	6.1		
	37 months	9.1		
Gumaté	12 months (18)	4.5		
	30 months (2)	5.5		
Singapore ^b	30 years	14-15		1/8.0
Gumaté	27 years (11)	20-25		1/4.1
	27 years (12)	20-25		1/5.8
Nigeria ^c	5 years	10	1/5.3	
	14 years	23	1/6.8	
	17 years	21-25	1/6.7	
Gumaté	7 years (3)	10-15	1/3.1	
	6-7 years (6)	15-20	1/7.6	
	21 years (21)	10-12	1/3.8	
Trinidad ^d	7 years	7.5	1/1.0 ^e	
	15-30 years	3-4.5	1/0.6 ^e	

of; the size of the two ecologically distinct species populations of the area did differ in an orderly manner in response to a limited number of factors, although the specific composition of the two populations was highly variable from site to site. The replacement of the regrowth species population by the forest species population was an orderly process, the latter group having required some "site preparation" by the former.

In contrast to the floristic succession, structural succession in the area did exhibit a series of distinct stages, although only the emergence of the hardwood tree stage was precipitated by a floristic change. The cause of structural succession on sites possessing an established population of regrowth species (of differing growth rates) was anticipated by Clements (1928), but this process has not received wide attention elsewhere. It is probable that this type of successional change is more common in secondary successions as the initial site condition is less drastically different from the "average" site condition of the area and there is, consequently, a greater number of species available, capable of establishing immediately. It is also more likely in the tropics, where a proportionately large flora is available in any given area. In both instances, the larger the population of species likely to colonize a site, the greater will be the variety of growth rates, and consequently, the greater the number of structural stages likely to appear sequentially.

The importance of viable seed stored in the soil in determining the population of regrowth species which would establish on a site in the area supports Egler's (1954) contention of the significance of this factor in secondary succession. Forest species, on the other hand, appeared either to lack the seed dormancy adaptation or, if possessing it, had seeds that were more easily exterminated by burning. The former possibility seems more likely for two reasons:

a) before the advent of man, neither group would have been subjected to fire, and it seems unlikely that the regrowth species' seed would have evolved a differential hardiness to fire in so brief a period, and

b) it seems likely that a seed dormancy adaptation was developed by regrowth species, but not forest species, before the advent of agriculture.

Before human disturbance of forest the regrowth species must have developed on scattered and only sporadically-available tree fall sites in the primary forest. By contrast, the seed of forest species would usually have been shed into a micro-environment favourable for its germination and would, therefore, have been less dependent for survival on seed capable of prolonged dormancy in the forest soil.

The results that have been achieved in this study support Decker's (1959) view that the critical first question to be answered when explaining a successional sequence is autecological. No amount of detailed phyto-sociological description of the secondary vegetation at Gumate would have revealed the factors determining the elimination of some species and their replacement by others.

APPENDIX: SUMMARY OF THE FLORA SAMPLED AT GUMATE. CLASSIFIED ECOLOGICALLY AND MORPHOLOGICALLY.

REGROWTH SPECIES

Softwooded trees

Caricaceae	<u>Carica</u>
Euphorbiaceae:	<u>Macaranga aleuritoides</u> F. Muell
	<u>Mallotus ricinoides</u> (Pers.) Muell. Arg.
	<u>Mallotus paniculatus</u> (Lamk) Muell. Arg.
	cf. <u>Mallotus</u>
	<u>Omalanthus</u> cf. <u>surigaoense</u> Elm.
	<u>Omalanthus</u> cf. <u>populneus</u> Merr.
Melastomataceae:	<u>Melastoma</u> cf. <u>polyanthum</u>
Moraceae:	<u>Ficus</u> (3 spp.)
	cf. <u>Ficus</u>
Papilionaceae:	<u>Erythrina</u>
Rhamnaceae:	<u>Alphitonia incana</u> (Roxb.) Kurz.
Ulmaceae:	<u>Trema orientalis</u> (L.) Bl.
Urticaceae:	<u>Acalypha</u>
	<u>Laportea</u> (2 spp.)
	<u>Pipturus</u> (2 spp.)
	Indeterminate Urticaceae (1 sp.)
Verbenaceae:	<u>Clerodendrum</u>
	Indeterminate Verbenaceae (1 sp.)
Indeterminate softwooded trees: (1 sp.)	

Large zingiberaceous herbs

Zingiberaceae:	<u>Costus speciosus</u> (Koen.) Sm.
	<u>Hornstedtia</u>

Large musaceous herbs

Musaceae:	<u>Musa textilis</u> Nee. (wild and cultivated varieties)
	<u>Musa</u>

Tree ferns

Cyatheaceae: Cyathea contaminans (Wall. et Hook.) Copel.
 Cyathea elmeri Copel.

Small herbs, vines and shrubs

Araceae: Indeterminate Araceae (3 spp.)

Aristolochiaceae: cf. Aristolochia (4 spp.)

Asclepiadaceae: Asclepias curassavica L.

Aspidiaceae: cf. Athyrium
Cyclosorus
cf. Cyclosorus

Balsaminaceae: Impatiens

Caryophyllaceae: Drymaria cordata (L.) Roem. et Schult

Compositae: Ageratum conyzoides L.
Bidens pilosa L.
Crassocephalum crepidioides (Benth.) S. Moore
Elephantopus mollis H.B.K.
Erethites valerianifolia (Wolf) DC. f. valerianifolia
Microglossa pyrifolia (Lamk.) Kuntze
cf. Oxalis
Syndrella nodiflora (L.) Gaertn.
Veronia
Indeterminate Compositae (2 spp.)

Convolvulaceae: Convolvulus
Steitocendra filiifolia (Desr.) Hallier f.

Cucurbitaceae: Indeterminate Cucurbitaceae (6 spp.)

Cyperaceae: Scleria cf. scrobiculata Nees

Davalliaceae: Nephrolepis
cf. Nephrolepis

Gesneriaceae: cf. Aeschynanthus
Cyrtandra
cf. Gesneriaceae (1 sp.)

Gleicheniaceae: Gleichenia truncata (Willd.) Spr. var. truncata
Gleichenia
cf. Hypolepis

- Gramineae: Cyrtococcum accrescens (Trin.) Stapf.
 cf. Cyrtococcum
Imperata cylindrica var. major Nees
Lopatherum gracile Brongn.
Miscanthus floridulus (Labill.) K. Sch. et Laut.
Panicum maximum Nees
Paspalum conjugatum (L.) Berg
Pennisetum macrostachyum (Brongn.) Trin.
Setaria palmifolia (Koen.) Stapf.
 Indeterminate Gramineae (1 sp.)
- Lycopodiaceae: Lycopodium
- Marantaceae: Indeterminate Marantaceae (1 sp.)
- Marattiaceae: Indeterminate Marattiaceae (1 sp.)
- Melastomataceae: Dissochaeta
 cf. Melastoma
- Orchidaceae: Spathoglottis
- Papilionaceae: Centrosema pubescens Benth.
- Piperaceae: cf. Piper
- Pteridaceae: Histiopteris incisa (Thunb.) J. Sm.
Pteridium aquilinum (L.) Kuhn
Pteris
 cf. Pteris
 cf. Pteridaceae (1 sp.)
- Rosaceae: Rubus moluccana L.
Rubus
 cf. Rubus
- Rubiaceae: Hedyotis
 cf. Hedyotis (2 spp.)
 cf. Psychotria
 cf. Uncaria
- Scrophulariaceae: cf. Lindenia
- Solanaceae: Physalis
Solanum nigrum L.
Solanum
- Urticaceae: cf. Boehmeria
 cf. Pilea
 Indeterminate Urticaceae (4 spp.)

- Violaceae: Indeterminate Violaceae (1 sp.)
- Vitaceae: cf. Cayratia
Cissus
 cf. Cissus
 Indeterminate Vitaceae (5 spp.)
 cf. Vitaceae (1 sp.)
- Zingiberaceae: cf. Alpinia
 Indeterminate Zingiberaceae (1 sp.)
 cf. Zingiberaceae (1 sp.)
- Indeterminate small herbs, vines and shrubs: (33 sp.)

FOREST SPECIES

Forest trees

- cf. Aquifoliaceae: cf. Ilex
- Buddleiaceae: Buddleia asiatica Lour.
- Burseraceae: cf. Canarium
- Clethraceae: Clethra cf. canescens F.-Vill.
- Compositae: Veronia arborea Ham.
- Daphniphyllaceae: cf. Daphniphyllum
- Dipterocarpaceae: Shorea cf. polysperma (Blco.) Merr.
 cf. Shorea almon Foxs.
 cf. Shorea
- Euphorbiaceae: cf. Glochidion
 cf. Macaranga (2 spp.)
 Indeterminate Euphorbiaceae (1 sp.)
 cf. Euphorbiaceae (1 sp.)
- Fagaceae: Lithocarpus (5 spp.)
- Gesneriaceae: cf. Cyrtandra
- Guttiferae: cf. Calophyllum
 cf. Garcinia
- Icacinaceae: Indeterminate Icacinaceae (1 sp.)
- Lauraceae: Actinodaphne
Cinnamomum
 cf. Cryptocarya (5 spp.)
 cf. Eniandra
Litsea

Lauraceae (contd.)	cf. <u>Litsea</u> Indeterminate Lauraceae (1 sp.) cf. Lauraceae (1 sp.)
Loganiaceae:	Indeterminate Loganiaceae (1 sp.)
Melastomataceae:	<u>Astryocalyx calycina</u> (Vid.) Merr. <u>Memecylon</u>
Meliaceae:	cf. <u>Aglaia</u> (2 spp.)
Monimiaceae:	cf. <u>Kibara</u> (2 spp.) cf. <u>Leviera</u>
Moraceae:	<u>Ficus</u> (2 spp.) cf. <u>Ficus</u> Indeterminate Moraceae (1 sp.)
Myrsinaceae:	<u>Ardisia</u> cf. <u>Rapanea</u> Indeterminate Myrsinaceae (2 spp.)
Myrtaceae:	<u>Syzygium</u> cf. <u>Syzygium</u> (2 spp.)
Palmae:	Indeterminate Palmae (2 spp.)
Pandanaceae:	<u>Pandanus</u>
Piperaceae:	cf. <u>Piper</u>
Proteaceae:	cf. <u>Helicia</u> Indeterminate Proteaceae (2 spp.)
Rubiaceae:	cf. <u>Hedyotis</u> <u>Lasianthus</u> Indeterminate Rubiaceae (1 sp.)
Sapindaceae:	Indeterminate Sapindaceae (2 spp.)
Saurauiaaceae:	<u>Saurauia</u>
Symplocaceae:	<u>Symplocos</u> (2 spp.)
Theaceae:	cf. <u>Eurya</u>
Urticaceae:	Indeterminate Urticaceae (1 sp.) cf. Urticaceae (1 sp.)
Verbenaceae:	cf. <u>Geunsia</u>
Vitaceae:	cf. <u>Vitex</u>
Indeterminate forest trees:	(34 spp.)

Other forest species

Acanthaceae:	<u>Staurogyne</u>
Aristolochiaceae:	cf. <u>Aristolochia</u>
Asclepiadaceae:	Indeterminate Asclepiadaceae (2 spp.) cf. Asclepiadaceae (1 sp.)
Aspidiaceae:	<u>Athyrium</u> cf. <u>Diplazium</u>
Aspleniaceae:	<u>Asplenium</u> cf. <u>cordatum</u> Forst. <u>Asplenium</u> cf. <u>decorum</u> Kunze cf. <u>Asplenium</u> (5 spp.) Indeterminate Aspleniaceae (1 sp.)
Chloranthaceae:	<u>Chloranthus</u>
Compositae:	<u>Blumea riparia</u> (Bl.) DC.
Davalliaceae:	cf. <u>Davallia</u> <u>Leucostegia</u>
Gesneriaceae:	cf. <u>Cyrtandra</u>
Hymenophyllaceae:	cf. <u>Hymenophyllum</u> Indeterminate Hymenophyllaceae (2 spp.)
Labiatae:	<u>Coleus</u>
Melastomataceae:	<u>Medinilla</u> cf. <u>Medinilla</u>
Moraceae:	Indeterminate Moraceae (1 sp.)
Orchidaceae:	<u>Bulbophyllum</u> Indeterminate Orchidaceae (1 sp.) cf. Orchidaceae (1 sp.)
Palmae:	<u>Daemonorops</u>
Pandanaceae:	<u>Freycinetia</u> (2 spp.)
Papilionaceae:	Indeterminate Papilionaceae (1 sp.)
Piperaceae:	cf. <u>Peperomia</u> cf. <u>Piper</u> (4 spp.)
Polypodiaceae:	cf. <u>Pyrrosia</u> Indeterminate Polypodiaceae (1 sp.)
Pteridaceae:	cf. <u>Lindsaya</u>
Rubiaceae:	cf. <u>Ophiorrhiza</u> cf. Rubiaceae (1 sp.)

Urticaceae:

Elatostemacf. Elatostema (2 spp.)cf. Pilea (2 spp.)Poikilospermum

Indeterminate Urticaceae (2 spp.)

Vitaceae:

cf. Cayratia

Indeterminate Vitaceae (1 sp.)

Indeterminate other forest species: (24 spp.)

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