THE MONTANE FORESTS AND SOILS OF JAMAICA: A REASSESSMENT

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WHEN FORREST SHREVE published his account of the forests of the Blue Mountains of Jamaica in 1914, it represented a landmark in the study of forests on tropical mountains. His detailed floristic and ecological account brought out the differences between ridges, slopes, and gullies and between windward and leeward sides of the range. He considered the forests particularly in relation to water supply, made comparative microclimatic records, and carried out simple experiments on certain species characteristic of ridge or gully sites. No detailed study of the forests has been made since his time, and nothing substantially new was added to his account of the Blue Mountain forests by Asprey and Robbins (1953) in their synopsis of the vegetation of the whole island.

Since Shreve's time, descriptions of the forests on many tropical mountains have been published, and it has been found possible to assign most of the forests to a small number of formation types on the basis of structure and physiognomy (cf. TABLE 1). The emphasis in interpretation of the factors limiting the distributions of forest types has moved away from almost exclusive reference to temperature and water relations, while the role played by differences in mineral supply has come to be appreciated more fully.

In the present paper we will show how the forests of the Blue Mountains and other major ranges in Jamaica fit into the world picture of formation types, and we will attempt to relate different forest types to different soil types. From the mountains of the Caribbean the formation of mor humus [1] will be described for the first time, as well as a distinct forest type that is associated with mor. Information from foliar analyses will also be used as a basis for discussion of the mineral factors limiting distributions.

This paper is based primarily on a reconnaissance made by both of us in December, 1973, in the Blue Mountains and Port Royal Mountains, but it incorporates some information gained by one of us (E. V. J. T.) during a year's detailed study of some of the sites visited then. It also includes the results of two reconnaissance trips by one of us (E. V. J. T.) to the John Crow Mountains in January and March of 1975.

[1] Mor humus is defined as humus which rests on the top of the mineral soil and is mixed with the mineral soil to a negligible degree; it is normally (perhaps always) very acid ($pH_{H_2O} < 4$, often ca. 3). Mull humus is defined as humus which is well mixed with the mineral material in the soil profile; the pH_{H_2O} varies from > 7 to < 4, but is usually > 4.

TABLE 1. Characters generally used in defining forest formation types on wet tropical mountains.*

FORMATION TYPE	LOWLAND RAIN FOREST	LOWER MONTANE RAIN FOREST	UPPER MONTANE RAIN FOREST	SUBALPINE RAIN FOREST
HEIGHT OF FOREST †	25–45(–67) m.	15–33(–45) m.	1.5–18(–26) m.	1.5–9(–15) m.
DOMINANT LEAF-SIZE CLASS ‡ OF TREES AND SHRUBS	*Mesophyll*	*Notophyll or Mesophyll*	*Microphyll*	*Nanophyll*
BUTTRESSES ON TREES	*Usually frequent and large*	*Infrequent or small or both*	Usually none	None
CAULIFLOROUS TREE SPECIES	Frequent	Rare	None	None
COMPOUND LEAVES ON TREES	*Abundant*	Occasional	Few	None
DRIP-TIPS ON LEAVES	*Abundant*	Frequent or occasional	Few or none	None
CLIMBERS	*Thick-stemmed woody species frequent*	*Thick-stemmed woody species usually none; other species often frequent*	Usually very few	Very few
VASCULAR EPIPHYTES	Frequent	*Abundant*	Frequent	Occasional

* Based on the system of Richards (1952), variously revised up to the time of Grubb and Stevens (in press); the most useful characters in italics.

† Emergents in parentheses.

‡ According to the systems of Raunkiaer (1934) and Webb (1959).

STUDY AREAS

THE BLUE MOUNTAINS. These run from east to west in the eastern part of Jamaica (FIGURE 1) and rise to 2265 meters. We studied two areas familiar to Shreve, that at about 1500 to 1600 meters west of Morce's Gap (northwest of Cinchona) and that above 1600 meters along the main route to the highest summit, Blue Mountain Peak, via Portland Gap (FIGURE 1). The geology of the range is complex, including granodiorite, "Blue Mountain Volcanics," "Blue Mountain Shales" (mudstones, sandstones, and conglomerates), and massive Eocene limestone in the first of the areas, and "Blue Mountain Volcanics" and "Shales" in the second (unpublished provisional map of Jamaican Geological Survey). According to Shreve, the annual rainfall is about 3300 mm. at sea level on the north side of the range, about 4270 mm. on Blue Mountain

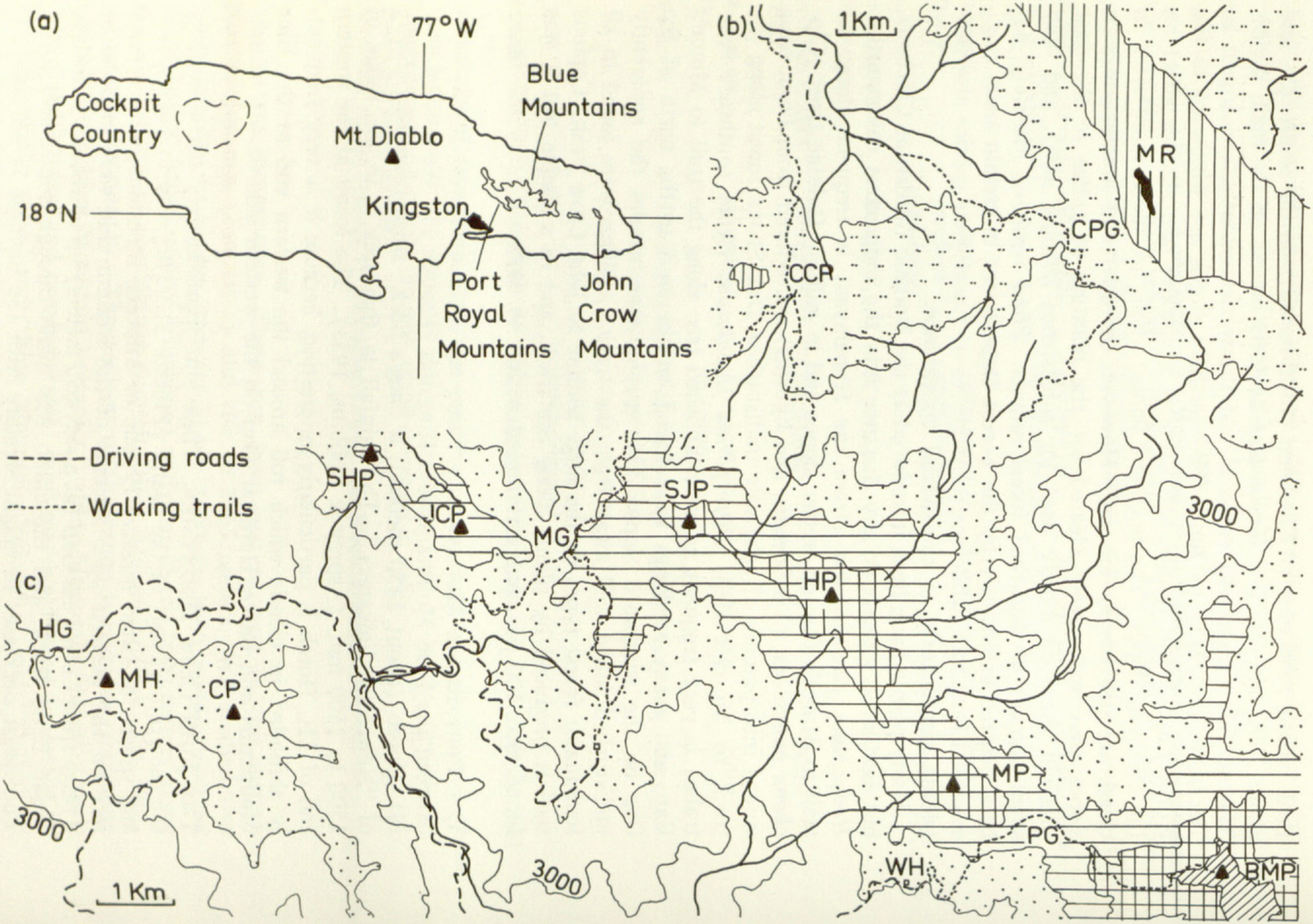
Peak, about 2690 mm. at Cinchona (1500 m. alt.) on the south side, and about 2890 mm. at New Haven Gap at 1705 meters on the main divide. The rainfall is markedly seasonal and the wettest months are August to December and May to June. The northern slopes are windward to the North East Trade Winds, and there is a marked rain shadow effect on the southern slopes. The northern slopes, which are much more often in cloud, are still largely forested. However, the drier and sunnier southern slopes were extensively cleared for the planting of coffee in the past (though they are mostly used for subsistence farming now), and only small patches of disturbed forest remain. *Pinus caribaea* Morelet [2] has been planted extensively by the Forest Department in certain areas (e.g., west of Cinchona), while scattered groves of *Eucalyptus* species also contribute significantly to the overall appearance.

Many plants have been introduced at the Botanic Garden at Cinchona, but few have spread for any distance into the indigenous communities. *Hedychium gardneranum* (from the Himalayas) is frequent along the trail to Morce's Gap on wetter slopes and in gullies. Quinine trees (*Cinchona pubescens*, *C. officinalis*, and hybrids), introduced from Peru, have spread into patches of relatively undisturbed DRY SLOPE forest along the track to Morce's Gap. *Pittosporum undulatum* (from southeast Australia) is very frequent as an established tree along the trail to Morce's Gap, and many seedlings were found on the trail to the north of the Gap on the windward slope. This species also invades the apparently undisturbed forest well away from the track; saplings were found in all four major forest types on the ridge leading to John Crow Peak. Copious seed is produced by plants along the track, and in a simple test it was found that 100 per cent germinated within 46 days.

THE PORT ROYAL MOUNTAINS. These run from northwest to southeast between the Blue Mountains and Kingston (FIGURE 1). We studied only Mt. Horeb (about 1450 meters), a "hog's back" ridge composed chiefly of "Newcastle Volcanics." The rainfall in this area is in the range of 1500 to 2500 mm. (Asprey & Robbins, 1953). The forest at the western end of Mt. Horeb is particularly interesting, because it is very frequently shrouded in clouds which roll around the western end of the Blue Mountains and on to Hardwar Gap on the western side of Mt. Horeb.

THE JOHN CROW MOUNTAINS. These run approximately north–south in the easternmost part of the island (FIGURE 1). They rise to 1100 meters and consist of tilted massive Eocene or Miocene limestone, with a scarp face on the western side. Ascents of the western side were made along a ridge from Corn Puss Gap (at about 650 meters) up to about 950 meters. There is no track, and the climb was made through continuous forest. The forest decreases in height steadily with the increase in altitude, but above about 950 meters a marked break was found, with the terrain becom-

[2] Unless otherwise indicated, nomenclature follows that of Adams (1972) and Proctor (1953).


(a)
77°W
18°N
Cockpit Country
Mt. Diablo
Blue Mountains
Kingston
Port Royal Mountains
John Crow Mountains
(b)
1Km
MR
CPG
CCR
SHP
ICP
MG
SJP
HP
3000
Driving roads
Walking trails
(c)
HG
MH
CP
C
MP
PG
WH
BMP
3000
3000
1 Km

ing distinctly steeper and more rugged. A closed canopy composed of trees rooted in the deep grykes [3] occurs between the huge outcropping rocks. The annual rainfall is said to be over 2500 mm. throughout the area, certainly over 5000 mm. at the northern end of the range and possibly over 7500 mm. (Asprey & Robbins, 1953). There are also said to be few rain-free days (C. D. Adams & G. R. Proctor, pers. comm.).

FOREST AND SOIL TYPES RECOGNIZED

Altogether ten forest types have been recognized (the names of which are also used here to designate soil types).

1. MOR RIDGE forest. Characteristic of knolls on ridges; known only between Morce's Gap and Silver Hill Peak.
2. MULL RIDGE forest. Widespread in the Blue Mountains up to about 1850 meters.
3. WET SLOPE forest. Very extensive on the northern slopes of the Blue Mountains; also found just over the divide on the southern side (clouds frequently roll just over the edge from the windward side and then disappear); also present on the northern slopes of the Port Royal Mountains.
4. GULLY forest. Widespread on northern and southern sides of the Blue Mountains up to about 1750 meters.
5. VERY WET RIDGE forest. Known only from the frequently fogged end of Mt. Horeb in the Port Royal Mountains.
6. HIGH ALTITUDE forest. Found on slopes and ridges above about 1850 meters on Blue Mountain Peak; probably also on the other highest peaks.
7. DRY SLOPE forest. Widespread on the southern slopes of the Blue Mountains.
8. DRY LIMESTONE scrub forest. Known only from the deeply dissected limestone outcrop at 1750 to 1800 meters on the southwest side of John Crow Peak in the Blue Mountains.

FIGURE 1. a, Outline map of Jamaica showing three main mountain ranges studied at the eastern end of the island; the contour is at 3000 ft. (915 m.). b, Details of the study area in the John Crow Mountains with areas above 2000 ft. (610 m.) and 3000 ft. (915 m.) shaded; CCP = Cuna Cuna Gap, CPG = Corn Puss Gap, MR = Main Ridge (> 3750 ft., 1143 m.). c, Details of Port Royal and Blue Mountain ranges with areas above 4000 ft. (1220 m.), 5000 ft. (1525 m.), 6000 ft. (1830 m.), and 7000 ft. (2135 m.) shaded. (BMP = Blue Mountain Peak; C = Cinchona; CP = Catharine's Peak; HG = Hardwar Gap; HP = High Peak; JCP = John Crow Peak; MG = Morce's Gap; MH = Mt. Horeb; MP = Mossman's Peak; PG = Portland Gap; SHP = Silver Hill Peak; SJP = Sir John Peak; WH = Whitfield Hall.) Based on the Ordnance Survey of Jamaica (1970).

[3] Grykes are cracklike hollows formed in hard limestone having karst-type topography; they are commonly 1–2 m. deep and 10–50 cm. wide.

9. WET LIMESTONE forest (lower) and (10) WET LIMESTONE forest (upper). Studied at 770 to 950 meters in the John Crow Mountains and probably widespread there.

The topographical distribution of types 1 to 4 and type 8 on the ridge from Morce's Gap to John Crow Peak is shown in FIGURE 2.

Shreve did not report on the Port Royal or John Crow Mountains. His account of the forests in the Blue Mountains is in close agreement with ours in respect to the WET SLOPE, DRY SLOPE, and GULLY forests, and it is in reasonable agreement with ours concerning the HIGH ALTITUDE forest and DRY LIMESTONE scrub forest. However, we present here a strongly revised assessment of the RIDGE forests; Shreve appears to have overlooked the development of mor humus on certain ridge sites.

During our study of the Blue Mountain forests, we found most of the tree, shrub, and climbing species mentioned by Shreve, although we missed a few recorded only at or near Blue Mountain Peak or only in windward ravines, a habitat which we did not have time to study. We saw only one specimen of *Citharexylum caudatum* (in MULL RIDGE forest next to the track at Morce's Gap), which Shreve noted to be a species of leeward (i.e. dry) slopes. We did not find *Eugenia harrisii* or *Myrcianthes* (*Eugenia*) *fragrans* (although we recorded *E. monticola* and *E. virgultosa*); nor did we find *Miconia rubens* or *Psychotria "brownei"* (although we did find *M. theaezans* and *P. sloanei*). In addition, we recorded a few more species missed by Shreve: *Calyptranthes rigida, Conostegia montana, Haenianthus incrassatus, Ilex harrisii* and *I. sideroxyloides* (both close to *I. macfadyenii* = *"I. montana"* of Shreve), and *Maytenus jamaicensis*.

DESCRIPTIONS OF THE SOIL TYPES

In the Blue Mountains the soils occupying the greatest area are those of the WET SLOPE and DRY SLOPE forests, and the next most widespread are those of the MULL RIDGE and GULLY forests. These all have a moderate organic matter content; on the slopes (but not on the ridges or in the gullies) there are frequent stones close to the surface and occasionally quite large rocks. All of these soils are freely drained. During a year's study no standing water was ever seen and no water table encountered. Streams are not seen much above an altitude of 1200 meters in the drier months in the Cinchona area, but they reach up to 1500 meters in wet spells. No marked differences were found between soils derived from "shale" and volcanic formations or granodiorite. Earthworms and ants appeared to be very rare — just one earthworm was seen (in a GULLY forest soil). Cockroaches are frequent and may be important in the breakdown of litter (cf. Murphy, 1973). Other mesofauna (centipedes, millipedes, termites, etc.) were not recorded. Burrowing mammals (mongooses and rats) are occasional.

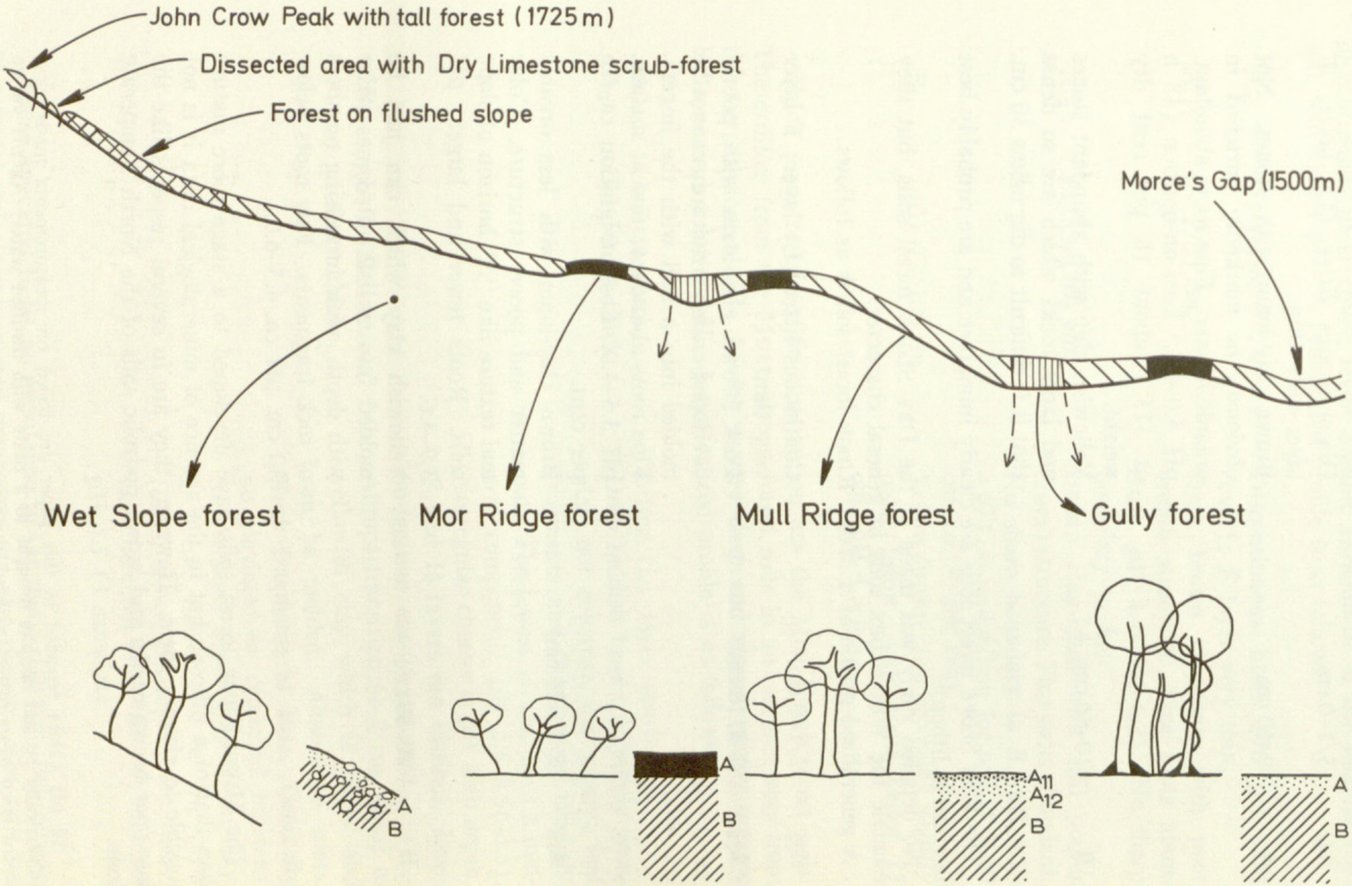


FIGURE 2. A transect of the ridge from Morce's Gap (east) to John Crow Peak (west) showing the main features of the four principal forest and soil types in the area.

The following is a generalized profile of a WET SLOPE forest soil.

A_{00}	5/1–0 cm.	Discontinuous litter (L) layer; F layer very thin.
A	0–10 cm.	Brown clay-loam with stones. Not obviously or markedly enriched in organic matter. Fine roots abundant. pH 4.0–4.5.[4] Loss-on-ignition (48 h at 375°) about 16 per cent dry weight.
B	10–30 cm. +	Yellowish clay with abundant stones and large rocks which are so dense that it is difficult to dig below 30 cm.

The WET SLOPE forest soils are clearly immature and are probably best classified as lithosols.

No detailed study was made of the DRY SLOPE forest soils, but they resemble the WET SLOPE soils in general character.

A generalized profile of a MULL RIDGE forest soil is as follows.

A_{00}	2/1–0 cm.	Continuous litter (L) layer; F layer very thin.
A_{11}	0–5/10 cm.	Dark brown clay-loam with poorly developed crumb structure; cannot be molded into a ball with the fingers. Fine roots abundant; few at surface. pH 3.5–4.0. Loss-on-ignition ca. 36 per cent.
A_{12}	5/10–20 cm.	Brown clay-loam with less organic matter and poorer structure. Color and texture like "A" horizon of slope soils. Roots fewer and larger. pH 3.9–4.6.
B	20–80 cm. +	Yellowish clay which can just be molded into a ball. Becomes paler with depth, with increasing numbers of rock fragments. Few roots below 30 cm. pH ca. 4.5–6.0.

The MULL RIDGE forest soils have developed to a stage more mature than that of a lithosol, but in the absence of mineralogical data it is not possible to classify them. However, they are in several respects like the base-poor brown earths and brown podzolic soils of the North Temperate Zone.

[4] All pH values reported in this paper are based on measurements made electrometrically on soil samples brought to a paste with distilled water. All pH values quoted from other papers without comment are based on some sort of measurement in distilled water.

The GULLY forest soils differ from the MULL RIDGE forest soils in their discontinuous litter cover, lesser organic enrichment of the mineral top-soil, and higher pH. A generalized profile is as follows.

A_{00}	2/1–0 cm.	Discontinuous litter (70 per cent cover); F layer very thin.
A_{11}	0–(1/3) cm.	Dark brown clay-loam with poor crumb structure. Fine roots abundant. pH 4.4–5.0(–6.2). No sharp boundary to A_{12}.
A_{12}	(1/3)–(10) cm.	Brown clay-loam with still poorer crumb structure. Fine roots abundant. No sharp boundary to B. pH 4.5–4.9. Loss-on-ignition for soil at 0–10 cm. ca. 36 per cent.
B	(10)–70/100 cm. +	Yellow brown clay becoming slightly paler below. Few roots below 25 cm. pH 4.5–6.0.

Much more restricted in distribution are the MOR RIDGE forest soils. These differ from the MULL RIDGE forest soils in an opposite way from the GULLY forest soils, having a very deep and almost wholly organic H layer and a lower pH. A generalized profile is as follows.

A_{00}	1–2 cm. thick.	Litter (L) layer continuous.
A_0	20–50 cm. thick.	Deep reddish brown, minutely granular, not coherent, not greasy; leaf fragments and living roots throughout. The lowest 10 cm. have a mineral component. pH 2.8–3.5(–3.8). No regular change in pH with depth. F and H layers not distinct. Loss-on-ignition ca. 96 per cent.
?B	Up to at least 100 cm. thick.	Abrupt transition (1–2 cm. deep) to yellowish clay which is sticky and can be molded. Almost no roots. Rock fragments at base. Generally no eluviated or cemented horizons. An A_e layer (pale gray-brown clay, 2–3 cm. thick) and a B_H layer (black-brown, cemented 1 cm. thick) were detected once but not refound. pH 4.5 (3 samples).

There appeared to be no mesofauna in the mor. However, the burrows of rats are quite common and mongooses are also present. The rats also nest in the trees.

The fully developed mor profile is easy to detect, because the soil is distinctly springy to walk on. However, many sites were found with early stages of mor development, indicating a continuum with the MULL RIDGE forest soils. Since there is no regular evidence of eluviated or very markedly illuviated horizons, the soils cannot be classified as podzols, and there is indeed no generally recognized world group of soils to which they can be assigned.

The mor humus might be termed peat by a casual observer. However, for a number of reasons presented in the discussion, we believe that this designation would be incorrect.

The VERY WET RIDGE forest soil on Mt. Horeb is quite unlike the MOR RIDGE forest soil and is indeed more like the GULLY soil type by virtue of its having only the top 1 to 2 cm. of the mineral soil markedly humus-enriched, dark brown, and with a strong crumb structure (pH 4.2). This soil differs from the GULLY forest soil in its 100 per cent litter cover. Below the humus-enriched layer the soil is first midbrown with much weaker crumb structure (pH 4.5), then paler and yellowish (pH 4.8).

The HIGH ALTITUDE forest soils studied were all on steep slopes or on the top of a knife-edge ridge. In general character they resemble the WET SLOPE forest soils. However, they vary a good deal in depth and in the apparent degree of enrichment with humus; above 2000 meters the soils derived from shales appeared to have a more marked crumb structure than those derived from tuffs. One earthworm was seen. The pH at 0 to 3 cm. and at 8 to 10 cm. is generally 4.1–5.9 (mean 4.8 at 0 to 3 cm., 5.0 at 8 to 10 cm., 14 sites recorded).

The WET LIMESTONE forest soils of the John Crown Mountains consist of sticky yellowish-brown clays 20 to 30 (to 50) cm. deep. There is a continuous litter cover, and the upper 10 cm. of the mineral soil are clearly enriched with humus (loss-on-ignition 17 to 37 per cent). The profile is heavily leached, since the pH throughout is 4.5–4.8, and it thus resembles that reported by Asprey and Robbins (1953, p. 387) from the bauxite areas developed over limestone farther west. Very surprisingly, in view of the present climate, the soil seems more similar to a Terra Fusca than to a Rendzina.

The soil of the DRY LIMESTONE scrub forest on the southeast slope of John Crow Peak, just below the summit, differs from that just described in its color (reddish-brown), in its lack of any obvious humus enrichment, in its being less leached (pH 6.4–6.8), and in its being generally shallower, most often 3 to 4 cm. deep (0 to 12 cm. in extremes). In addition, it has a marked clay-loam texture and a weak crumb structure. The litter layer is thin and discontinuous except under the denser stands of the bamboo *Chusquea abietifolia.* The obvious affinity of the soil is with the Terra Rossas.

We may summarize the salient points about the several soil types as follows. The SLOPE forest soils, whether wet or dry and whether at high altitudes or low, are lithosols moderately to strongly acid at the surface (pH mostly 4.0–5.5), while the more stable soils of the MULL RIDGE forest (at least in the Morce's Gap area) are deeper, less stony, and more mature, with a distinct accumulation of humus in the top 10 cm. and a surface pH of 3.5–4.0. The end point in this leaching series is found in the MOR RIDGE forest soils of knolls on the ridges where an H layer up to 50 cm. thick is found, and the pH throughout is 2.8–3.5(–3.8). The GULLY forest soils are also deeper and less stony than the SLOPE soils, but they have a discontinuous litter layer, and obvious humus enrichment extends to a depth of only 1 to 3 cm. (pH 4.4–5.0). The VERY WET RIDGE forest soil on Mt. Horeb is much more like the GULLY forest soil than the MOR RIDGE forest soil but is a little more acid (topsoil pH 4.2). The WET LIMESTONE forest soils are highly leached, moderately rich in organic matter, and in the same pH range as lithosols on nonlimestone rocks. The DRY LIMESTONE scrub forest soil is much shallower than that of the WET LIMESTONE forest, redder, and much less leached (pH 6.4–6.8); it also has a more loamy texture.

DESCRIPTIONS OF THE FOREST TYPES

The following account is of a preliminary nature and much further research needs to be done. A quantitative analysis of the composition and dynamics of the first four forest types listed in TABLE 2 will be given in a later publication.

It is convenient to deal with the forests in a somewhat different order from the soils, beginning with one of the types poorest in species.

MOR RIDGE forest. This has a rather open canopy (4 to)5 to 7 meters tall, made up of trees of small girth (mostly less than 30 cm. DBH). Almost all of the larger trees are leaning, apparently because of the poor support offered by the deep humus layer in which nearly all of the roots occur. The trees presumably develop their crowns a little unevenly and, when these become heavy, the roots fail to provide the resistance to displacement that is provided by roots in a firm, mineral soil. The trees in the MOR RIDGE forest lean in all directions, and windthrow does not seem to be involved. (It is significant that few of the trees in the MULL RIDGE forest lean over.) Sixteen dicotyledonous tree species were recorded (TABLE 2), three of them only once. Tree ferns are much less common and smaller than in the other forest types in the area — only two species are present (TABLE 3). The shrub layer is very poorly developed and contains only two species (both melastomes); *Blakea trinervia* is a scrambling species up to 4 meters tall, while *Miconia rigida* is upright and grows to about 2 meters.

The dicotyledonous tree species fall into two main groups, the "core" species found in gullies and on slopes, as well as on ridges, and a group confined to ridges and slopes (TABLE 2). None were found to be exclusive to MOR RIDGE forest in the Morce's Gap area. However, as shown in TABLE 3, the two tree ferns and the two shrubs are exclusive

FIGURE 3. **Mor Ridge forest.** Scale pole marked in feet. Sapling on left is *Lyonia* cf. *octandra.* Most bromeliads are *Tillandsia complanata* or *Vriesia sintenisii*; the one in flower is *Vriesia sintenisii.* February, 1975. Photo by E. V. J. Tanner.

to MOR RIDGE forest in this area; *Blakea trinervia* is often epiphytic elsewhere, and *Miconia rigida* is found elsewhere in VERY WET RIDGE forest and in HIGH ALTITUDE forest.

About half the "herb layer" (0 to 50 cm.), in terms of individuals, is made up of tree seedlings, and there are few herbaceous, regularly ground-dwelling species (TABLE 3). By far the most abundant are *Elaphoglossum latifolium* and *Peperomia* cf. *clusiifolia,* both somewhat succulent. In addition, it is characteristic of this forest type that several primarily epiphytic species are frequently found growing on the forest floor: the woody scrambler *Columnea hirsuta* (Gesneriaceae) and the orchids *Dichaea*

TABLE 2. **Trees (other than tree ferns) present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains.***

SPECIES	LEAF-SIZE CLASS †	MOR RIDGE FOREST	MULL RIDGE FOREST	WET SLOPE FOREST	GULLY FOREST	VERY WET RIDGE FOREST	HIGH ALTITUDE FOREST	DRY SLOPE FOREST	DRY LIMESTONE SCRUB FOREST	WET LIMESTONE FOREST (LOWER)	WET LIMESTONE FOREST (UPPER)
Core species											
Alchornea latifolia	No	+	+	+	+	+	−	+	−	−	+
Clethra occidentalis	No	+	+	+	+	+	−	+	(+)	−	+
Clusia havetioides	No	+	+	+	+	+	−	+	(+)	+	+
Cyrilla racemiflora	Mi	+	+	+	+	+	+	+	−	+	−
Ilex macfadyenii	Mi	+	+	+	+	+	+	+	−	−	−
Podocarpus urbanii	Na	+	+	+	+	+	+	(+)	(+)	−	−
Mor Ridge species (mostly also on Mull Ridges and some on Wet Slopes)											
Chaetocarpus globosus	Mi	+	+	(+)	−	+	−	−	−	−	−
Ilex obcordata	Na	+	(+)	(+)	−	+	+	+	−	−	−
Lyonia jamaicensis + *L. octandra*	Mi	+	+	+	−	(+)	(+)	+	−	−	−
Mecranium purpurascens	Mi	+	+	−	−	−	(+)	(+)	−	−	−
Persea alpigena	No	+	+	−	−	−	−	−	−	−	−
Schefflera sciadophyllum	Me	+	+	−	−	(+)	(+)	−	−	+	−
Vaccinium meridionale	Mi	+	+	+	−	+	+	+	−	−	−
Mull Ridge and Wet Slope Species (mostly extending to Gullies)											
Brunfelsia jamaicensis	Mi	−	+	+	+	−	−	(+)	+	−	−
Bumelia montana	Mi	−	+	+	+	−	−	−	−	−	−
Calyptranthes rigida	Mi	−	+	+	+	−	−	−	−	−	−

TABLE 2. Trees (other than tree ferns) present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains (*continued*).*

SPECIES	LEAF-SIZE CLASS †	MOR RIDGE FOREST	MULL RIDGE FOREST	WET SLOPE FOREST	GULLY FOREST	VERY WET RIDGE FOREST	HIGH ALTITUDE FOREST	DRY SLOPE FOREST	DRY LIMESTONE SCRUB FOREST	WET LIMESTONE FOREST (LOWER)	WET LIMESTONE FOREST (UPPER)
Cleyera theaeoides	Mi	−	+	+	+	−	−	−	−	−	+
Conostegia montana	No	−	+	+	+	−	−	−	−	+	+
Dendropanax arboreus	Me	−	−	(+)	−	−	−	−	−	−	−
D. pendulus + *D. nutans*	No	−	+	+	+	+	+	+	(+)	?	?
Eugenia marchiana	No	−	+	+	+	?	−	−	−	−	−
E. monticola	Mi	−	+	+	+	?	−	−	−	−	−
E. virgultosa	Mi	−	+	+	+	?	(+)	−	−	−	−
Eupatorium critoniforme	No	−	+	+	+	−	−	−	−	+	−
Gesneria alpina	Mi	−	−	(+)	−	−	−	−	−	−	−
Guarea swartzii	No	−	+	+	+	+	−	−	−	+	+
Haenianthus incrassatus	Mi	−	+	+	+	+	−	−	−	+	−
Hedyosmum arborescens	No	−	+	+	+	+	−	−	−	+	+
Ilex harrisii	Mi	−	+	+	−	−	−	−	−	−	−
I. sideroxyloides	Mi	−	+	+	−	−	−	−	−	−	−
Maytenus jamaicensis	Mi	−	+	+	−	−	−	−	−	−	−
Meriania leucantha	No	−	+	+	+	−	−	−	−	−	+
Miconia theaezans	No	−	+	+	−	+	−	+	−	−	−
Nectandra patens	No	−	−	(+)	−	−	−	−	−	−	−
Piper arboreum	Me	−	+	+	+	−	−	−	−	−	+
Xylosma nitida	No	−	−	(+)	−	−	−	(+)	−	−	−
Gully species (extending to Slopes; rarely Ridges)											
Laplacea haematoxylon	Mi	−	(+)	+	+	(+)	−	−	−	+	+
Meriania purpurea	Mi	−	(+)	(+)	+	−	(+)	−	−	−	−
Psychotria sloanei	Mi	−	−	+	+	−	−	−	−	−	−
Solanum punctulatum	No	−	+	+	+	−	−	−	−	−	−
Turpinia occidentalis	No	−	(+)	+	+	−	−	−	−	−	−
High Altitude species											
Clethra alexandri	Me	−	−	−	−	−	+	−	−	−	−
Eugenia alpina	Na	−	−	−	−	−	+	−	−	−	−
Senecio swartzianus	Ma	−	−	−	−	−	+	−	−	−	−
Dry Slope species											
Brunellia comocladiifolia	No	−	(+)	−	−	−	(+)	+	−	−	−
Cestrum diurnum var. *odontospermum*	No	−	−	−	−	−	−	(+)	−	−	−
Daphnopsis americana	No	−	−	−	−	−	−	+	−	−	−
Dodonaea viscosa	Mi	−	−	−	−	−	−	+	−	−	−
Garrya fadyenii	Mi	−	−	−	−	−	+	+	+	−	−
Juniperus barbadensis	Le	−	(+)	(+)	−	−	−	+	−	−	−
Miconia quadrangularis	No	−	−	−	−	−	(+)	+	+	−	−
Myrica cerifera	Mi	(+)	(+)	(+)	−	−	(+)	+	−	−	−
Myrsine coriacea	Mi	(+)	(+)	−	−	−	−	+	+	−	−
Oreopanax capitatus	Me	−	−	−	−	−	−	+	−	+	−
Rhamnus sphaerospermus	No	(+)	(+)	−	−	−	+	+	−	−	−
Viburnum alpinum	Mi	−	(+)	(+)	−	−	+	+	−	−	−
V. villosum	Mi	−			−	−		+	−	−	−
Species of scrub forest on Dissected Limestone											
Fagara hartii	Mi	−	−	−	−	−	−	−	+	−	−

TABLE 2. **Trees (other than tree ferns) present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains** (*continued*).*

SPECIES	LEAF-SIZE CLASS †	MOR RIDGE FOREST	MULL RIDGE FOREST	WET SLOPE FOREST	GULLY FOREST	VERY WET RIDGE FOREST	HIGH ALTITUDE FOREST	DRY SLOPE FOREST	DRY LIMESTONE SCRUB FOREST	WET LIMESTONE FOREST (LOWER)	WET LIMESTONE FOREST (UPPER)
Myrcia sp.	Na	–	–	–	–	–	–	–	+	–	–
Weinmannia pinnata	Na	–	–	–	–	(+)	(+)	–	+	–	–
Wet Limestone forest species											
cf. *Aegiphila trifida*	No	–	–	–	–	–	–	–	–	+	+
Ardisia brittonii	Me	–	–	–	–	–	–	–	–	+	+
Calophyllum calaba	Me	–	–	–	–	–	–	–	–	+	–
Calyptronoma occidentalis	Me	–	–	–	–	–	–	–	–	+	+
Clidemia plumosa	Me	–	–	–	–	–	–	–	–	+	–
Cordia elliptica	Me	–	–	–	–	–	–	–	–	+	+
Drypetes alba	Mi	–	–	–	–	–	–	–	–	+	–
Eugenia spp. (2)	Mi	–	–	–	–	–	–	–	–	+	+
Picramnia antidesma	No	–	–	–	–	–	–	–	–	+	+
Piper discolor	No	–	–	–	–	–	–	–	–	–	+
Psychotria dolphiniana	Mi	–	–	–	–	–	–	–	–	+	–
P. cf. *glabrata*	No	–	–	–	–	–	–	–	–	–	+
Solanum acropterum	No	–	–	–	–	–	–	–	–	–	+
Symphonia globulifera	Mi	–	–	–	–	–	–	–	–	+	–
Tabernaemontana rendlei	No	–	–	–	–	–	–	–	–	+	–
Tetrorchidium rubrinervium	Me	–	–	–	–	–	–	–	–	+	–

* + = present; (+) = present but rare and not included in the determination of leaf-size spectrum; – = absent.

† According to the systems of Raunkiaer (1934) and Webb (1959). Le = leptophyll; Na = nanophyll; Mi = microphyll; No = notophyll; Me = mesophyll *sensu stricto*; Ma = macrophyll.

TABLE 3. **Tree ferns, shrubs, herbs, and climbers present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains.***

Species	Leaf-size class †	Mor ridge forest	Mull ridge forest	Wet slope forest	Gully forest	Very wet ridge forest	High altitude forest	Dry slope forest	Dry limestone scrub forest	Wet limestone forest (lower)	Wet limestone forest (upper)
Tree ferns											
Blechnum underwoodianum		+	−	−	−	−	−	−	−	−	−
Cyathea fragilis		+	−	−	−	−	−	−	−	−	−
C. furfuracea		−	+	+	+	?	−	−	−	−	−
C. hystricosa		−	+	+	+	?	−	−	−	−	−
C. pubescens		−	+	+	+	?	−	−	−	−	−
C. dissoluta		−	−	−	−	?	−	−	−	+	−
C. grevilleana		−	−	−	−	?	−	−	−	−	+
Cyathea sp.		−	−	−	−	−	+	−	−	−	−
Lophosoria quadripinnata		−	(+)	+	+	−	+	+	−	−	−
Shrubs and tall woody herbs											
Blakea trinervia	No	+	−	−	−	−	−	(−)	−	(−)	−
Miconia rigida	No	+	−	−	−	+	+	−	−	−	−
Lisianthius latifolius	No	−	+	+	+	−	−	−	−	−	−
Palicourea alpina	No	−	+	+	+	+	+	(+)	−	−	−
Psychotria corymbosa	Mi	−	+	+	+	+	+	(+)	−	−	−
Senecio cf. *fadyenii*	No	−	+	+	+	−	−	−	−	+	+
Wallenia laurifolia	No	−	+	+	+	+	+	(+)	−	−	−
Besleria lutea	Me	−	−	+	+	−	−	−	−	(+)	−
Cestrum hirtum	No	−	−	(+)	(+)	−	−	−	−	−	−
Boehmeria caudata	Me	−	−	−	+	−	−	−	−	−	−
Callicarpa ferruginea	Mi	−	−	−	+	−	−	−	−	+	−
Datura suaveolens	Me	−	−	−	(+)	−	−	−	−	−	−

TABLE 3. Tree ferns, shrubs, herbs, and climbers present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains (*continued*).*

SPECIES	LEAF-SIZE CLASS †	MOR RIDGE FOREST	MULL RIDGE FOREST	WET SLOPE FOREST	GULLY FOREST	VERY WET RIDGE FOREST	HIGH ALTITUDE FOREST	DRY SLOPE FOREST	DRY LIMESTONE SCRUB FOREST	WET LIMESTONE FOREST (LOWER)	WET LIMESTONE FOREST (UPPER)
Piper fadyenii or *P. hispidum*	No	–	–	–	(+)	–	–	–	–	–	–
Tournefortia glabra	Me	–	–	–	(+)	–	–	–	–	–	–
Cephaelis elata	Me	–	–	–	–	+	–	–	–	+	+
Lobelia martagon (WH‡)	No	–	–	–	–	–	+	–	–	–	–
Vernonia pluvialis	Mi	–	–	–	–	–	+	–	+	–	–
Baccharis scoparia	Le	–	–	–	–	–	(+)	+	–	–	–
Bidens shrevei	No	–	–	–	–	–	+	+	+	–	–
Bocconia frutescens (WH‡)	Ma	–	–	–	–	–	+	+	–	–	–
Eupatorium parviflorum	No	–	–	–	–	–	+	+	–	–	–
E. triste	Mi	–	–	–	–	–	–	+	+	–	–
Satureja viminea	Le	–	–	–	–	–	–	+	+	–	–
Vernonia divaricata	Mi	–	–	–	–	–	–	+	–	–	–
Salvia jamaicensis	Mi	–	–	–	–	–	–	–	+	–	–
Verbesina nervosa	No	–	–	–	–	–	–	–	+	–	–
Mecranium virgatum	No	–	–	–	–	–	–	–	–	+	–
Neea nigricans	No	–	–	–	–	–	–	–	–	+	–
Psychotria foetida	Me	–	–	–	–	–	–	–	–	+	–
P. uliginosa	Me	–	–	–	–	–	–	–	–	+	–
Wallenia subverticillata	No	–	–	–	–	–	–	–	–	+	–
Conostegia pyxidata	Mi	–	–	–	–	–	–	–	–	–	+
Gesneria calycina	No	–	–	–	–	–	–	–	–	–	+
Herbs											
Elaphoglossum latifolium		+	+	+	–	(–)	–	–	–	–	–

Gleichenia bancroftii	+	+	+	–	(+)	–	–	–	–	–
Liparis neuroglossa	(+)	(+)	(+)?	–	–	–	–	–	–	–
Peperomia cf. *clusiifolia*	+	(–)	–	–	–	–	–	–	–	–
Polystichopsis denticulata	+	–	–	–	–	–	–	–	–	–
Polypodium loreum	+	+	+	+	+	–	–	–	–	–
Trichomanes robustum	+	+	+	–	+	–	–	–	–	–
Blechnum striatum	–	+	+	–	+	–	–	–	–	–
Calanthe mexicana	–	(+)	(+)	–	–	–	–	–	–	–
Erythrodes plantaginea	–	+	(+)	+	?	–	–	–	+	–
Gesneria mimuloides	–	–	(+)	–	–	–	–	–	–	–
Liabum umbellatum	–	+	+	–	–	–	–	–	–	–
Liparis harrisii	–	(+)	(+)	–	–	–	–	–	–	–
Lycopodium taxifolium	–	(+)	–	–	–	–	–	–	–	–
Pilea weddellii	–	(+)	(+)	(+)	(+)	–	–	–	–	–
Peperomia alpina	–	+	+	+	–	(+)	–	–	–	–
Prescottia stachyodes	–	+	+	+	?	–	–	–	+	–
Rhynchospora polyphylla	–	+	+	+	–	–	–	–	–	–
Zeugites americana	–	+	+	+	(+)	+	–	–	–	–
Diplazium brunneo-viride	–	–	–	+	–	–	–	–	–	–
D. centripetale	–	–	–	+	–	–	–	–	–	–
Marattia alata	–	–	–	(+)	–	–	–	–	–	–
Pilea cf. *grandiflora*	–	–	–	+	–	–	–	–	–	–
Polypodium lanceolatum	–	–	–	(+)	–	–	–	–	–	–
Ponthieva harrisii	–	–	–	+	–	–	–	–	–	–
Selaginella denudata	–	–	–	–	+	–	–	–	+	+
Pteridium aquilinum	–	–	–	–	–	+	+	–	–	–
Rhynchospora eggersiana	–	–	–	–	–	+	–	–	–	–
Psychotria discolor	–	–	–	–	–	–	–	–	+	+
Thelypteris deltoidea	–	–	–	–	–	–	–	–	+	–

TABLE 3. **Tree ferns, shrubs, herbs, and climbers present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains** (*continued*).*

Species	Leaf-size class †	Mor Ridge forest	Mull Ridge forest	Wet Slope forest	Gully forest	Very Wet Ridge forest	High Altitude forest	Dry Slope forest	Dry Limestone scrub forest	Wet Limestone forest (lower)	Wet Limestone forest (upper)
Diplazium costale		–	–	–	–	–	–	–	–	–	+
Pilea sp.		–	–	–	–	–	–	–	–	–	+
Climbers and scramblers											
Anthurium scandens		+	+	+	+	+	–	–	–	–	–
Odontosoria jenmanii		(+)	+	+	+	+	–	–	–	–	–
Schradera involucrata		(+)	+	+	+	+	–	–	–	+	–
Smilax balbisiana		+	+	+	+	+	–	–	–	–	–
Cassia viminea		–	+	+	+	–	–	+	–	–	–
Chusquea abietifolia		–	+	+	+	+	+	+	+	–	–
Manettia lygistum		–	(+)	–	–	–	+	+	–	–	–
Marcgravia brownei		–	–	–	+	–	–	–	–	+	+
Cionosicys pomiformis		–	–	–	–	–	–	+	–	–	–
Cynanchum harrisii		–	–	–	–	–	–	+	–	–	–
Anthurium cordifolium		–	–	–	–	–	–	–	–	+	–
Lomariopsis underwoodii		–	–	–	–	–	–	–	–	+	–
Solandra sp.		–	–	–	–	–	–	–	–	+	–
Syngonium auritum		–	–	–	–	–	–	–	–	+	+

* + = present; (+) = present but rare; – = absent; (–) = present only as an epiphyte.

† Listed for the shrubs; according to the systems of Raunkiaer (1934) and Webb (1959). Le = leptophyll; Na = nanophyll; Mi = microphyll; No = notophyll; Me = mesophyll *sensu stricto*; Ma = macrophyll.

‡ WH = woody herb.

glauca, *Dilomilis montana* (Sw.) Summerh. (= *Octadesmia montana* (Sw.) Bentham), *Pleurothallis oblongifolia*, *Stelis micrantha*, and *S. trigoniflora* (Sw.) Garay & Sweet (= *S. ophioglossoides* (Jacq.) Sw.). Hummocks of the moss *Leucobryum giganteum* C.M. 5 to 20 cm. across are frequent. However, *Sphagnum* is absent from Mor Ridge forest in the Morce's Gap area. In the Blue Mountains and Port Royal Mountains *Sphagnum* is generally a weed of paths, but it was seen once in apparently undisturbed Mor Ridge forest — on Silver Hill Peak about 1 km. west of John Crow Peak (obs. E. V. J. T.).

Climbers and scramblers are uncommon and all thin-stemmed. Only four species are found (Table 3), and of these *Anthurium scandens* is by far the commonest, creeping on the forest floor as often as up the trunks. The bamboo *Chusquea abietifolia* is absent.

Vascular epiphytes are very frequent. Bromeliads are particularly prominent (mostly *Tillandsia complanata* and *Vriesia sintenisii*, with some *Vriesia incurva* and a single plant of *Guzmania fawcettii*). Orchids are also very common (the five species listed above plus *Epidendrum ramosum*, *E. repens*, *Jacquiniella teretifolia*, and *Lepanthes ovalis*). So are the ferns, the most abundant (*Hymenophyllum polyanthos* and *H. sericeum*) being filmy and the others (*Grammitis curvata* (Sw.) Ching, *G. graminea*, and *G. trichomanoides*) mostly small-fronded. *Polypodium loreum* is occasionally epiphytic, *Lycopodium taxifolium* is rare, and *Columnea hirsuta* is occasional. Epiphytic bryophytes are common, but the degree of "mossing" is not very marked; the bryophyte cover on the trunks is never more than 50 per cent and usually less than 20 per cent. Epiphylls are rare. The lichen *Usnea* is common in the crowns.

Hemiparasites were not obvious from the ground, but when trees were felled for biomass estimation, they were found to be frequent, apparently especially on *Lyonia*. The species involved were *Dendropemon parvifolius*, *Dendrophthora opuntioides* (by far the commonest), and *Eubrachion ambiguum*. No parasitic or saprophytic vascular plants were seen in the herb layer.

There are no buttresses on the trees, no cauliflorous species, and no leaves with drip-tips. Compound leaves are seen only on *Schefflera* and the tree ferns. The leaf-size spectrum of the trees and shrubs (excluding the tree ferns and the three species represented by only one mature individual each) is shown in Table 4; microphylls and notophylls are most abundant. As in many other low-stature forests on tropical mountains, the leaves of the trees and shrubs are mostly thick and more or less coriaceous (cf. Howard, 1968; Grubb, 1974).

Fully developed Mor Ridge forest has been found by one of us (E. V. J. T.) on several knolls along the ridge from Morce's Gap over John Crow Peak to Silver Hill Peak. In addition, many sites along this ridge show stages in the development of mor.

Mull Ridge and Wet Slope forests. These two forest types are very similar and are treated together here. They differ from the Mor Ridge

TABLE 4. **Percentages of tree and shrub species in the various forest types in the leaf-size classes of Raunkiaer (1934) modified by Webb (1959).**

	Mor Ridge forest	Mull Ridge and Wet Slope forests	Gully forest	Very Wet Ridge forest	High Altitude forest	Dry Slope forest	Dry Limestone scrub forest	Wet Limestone forest (lower)	Wet Limestone forest (upper)
Leptophyll	—	—	—	—	—	11	8	—	—
Nanophyll	13	2	3	11	14	—	15	—	—
Microphyll	40	46	41	32	33	43	54	25	16
Notophyll	40	44	47	53	38	39	23	40	60
Mesophyll *sensu stricto*	7	7	9	5	5	4	—	35	24
Macrophyll	—	—	—	—	10	4	—	—	—
Megaphyll	—	—	—	—	—	—	—	—	—

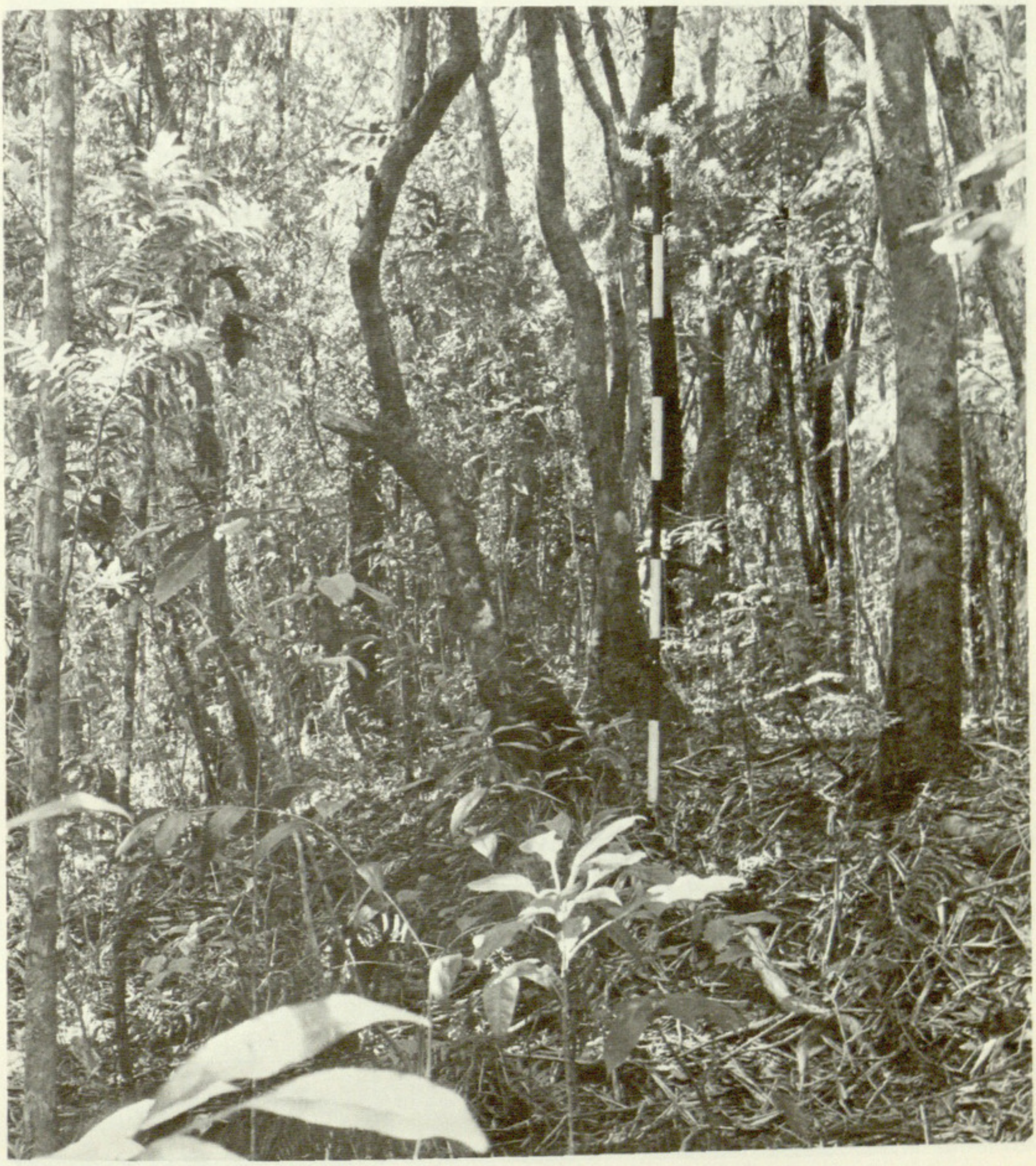


FIGURE 4. **Mull Ridge forest.** Scale pole marked in feet. Saplings of *Dendropanax pendulus* in center foreground; *Podocarpus urbanii* on left; *Cyathea furfuracea* in right background. February, 1975. Photo by E. V. J. Tanner.

forest type in being taller (8 to 13 meters), in having a closed canopy, and in having many fewer epiphytes, both vascular and nonvascular. The trees in the SLOPE forest are generally taller and frequently lean downhill. On the ridge tops there are occasional trees of larger girth (*Cyrilla racemiflora* to more than 70 cm. DBH, *Lyonia* cf. *jamaicensis* to more than 45 cm. DBH, and *Podocarpus urbanii* Pilger to more than 50 cm. DBH); such trees also occur less frequently on the slopes. The MULL RIDGE forest is notably easier to walk through than the MOR RIDGE forest because of the general lack of leaning trees and the greater height to the first branch on most trees. There are a much larger number of dicotyledonous tree species present — 47 were recorded, although of

FIGURE 5. **Wet Slope forest.** Scale pole marked in feet. Trunk arching over pole is of *Cyrilla racemiflora*. Upright trunk on left is of *Clethra occidentalis*; trunk with protuberances at top right is of *Hedyosmum arborescens*. Tree fern in foreground is *Cyathea pubescens* (always short-stemmed on slope). February, 1975. Photo by E. V. J. Tanner.

these 12 were represented by only very few individuals (TABLE 2). Several of the trees absent from the MOR RIDGE forest (TABLE 2) are frequent in the MULL RIDGE and WET SLOPE forests, e.g. *Calyptranthes rigida, Dendropanax "pendulus,"*[5] *Eugenia* spp., and *Hedyosmum arborescens*. Tree ferns are much more numerous, taller, and attain greater girths; the species are quite different (TABLE 3).

There is a well-developed though discontinuous shrub layer about 2 to 3 meters tall, containing seven species (TABLE 3) but composed chiefly

[5] Possibly including some *D. nutans*.

of *Palicourea alpina* and *Psychotria corymbosa* (both Rubiaceae). Herbs are present in greater variety than in the MOR RIDGE forest; most of the species present in the latter forest occur, in addition to quite a number of others (TABLE 3). The most frequent are the terrestrial orchids (*Erythrodes plantaginea* and *Prescottia stachyodes*). The hummock moss *Leucobryum* is decidedly less common than in the MOR RIDGE forest.

The climbers and scramblers are few in number (TABLE 3), and all are thin-stemmed. The bamboo *Chusquea abietifolia* is only occasional, but it forms localized, impenetrable thickets. The vascular epiphytic species are much as in the MOR RIDGE forest, although *Columnea hirsuta* is generally absent, while the bromeliad *Hohenbergia fawcettii* is present but rare. In addition, *Peperomia* cf. *clusiifolia* occurs here occasionally as an epiphyte. No critical observations were made on the hemiparasites; *Phoradendron flavens* was seen in the MULL RIDGE forest on the ascent of Blue Mountain Peak but not in the Morce's Gap area.

As in the MOR RIDGE forest, the trees have no buttresses and there are no cauliflorous species. Only two species represented by more than a very few individuals have drip-tips (*Dendropanax "pendulus"* and *Eugenia virgultosa*), and only two have compound leaves (*Guarea swartzii* and *Schefflera sciadophyllum*). The leaf-size spectrum of the trees and shrubs (excluding the tree ferns and the species represented by very few individuals) is similar to that in the MOR RIDGE forest (TABLE 4). However, the average leaf texture is decidedly less coriaceous.

The MULL RIDGE — WET SLOPE forest is certainly worthy of recognition as a separate association from the MOR RIDGE forest, since it contains many more species, including trees, shrubs, and herbs. We agree with Asprey and Robbins (1953) that this forest type (their "MONTANE MIST" forest) appears to be rather uniform floristically over wide areas, but we cannot agree with their statement (1953, p. 400) that "the dominants are *Podocarpus urbanii* and *Cyrilla racemiflora*." Dominance, in fact, seems to be shared by three, four, or five species at any one site, and it is perhaps unfortunate that Asprey and Robbins called this forest type the "*Podocarpus-Cyrilla* association."

GULLY forest. Our impression of this forest type in the Cinchona-Morce's Gap–John Crow Peak area and the Portland Gap–Blue Mountain Peak area agrees closely with the description given by Shreve. The GULLY forest differs from those so far considered in its greater height (12 to 18 meters), much taller boles, and fairly frequent buttresses (0.8 meters high), as well as in the presence of the woody liana *Marcgravia brownei*, which develops stems 3 cm. thick and climbs high into the canopy. The mean girth of the trees is certainly greater than on the slopes and ridges, but it seems that few trees (mostly *Solanum punctulatum*) exceed 40 cm. DBH. Twenty-six dicotyledonous tree species and four species of tree fern were recorded, all of them represented by many individuals. Floristically the forest is quite distinct from that on slopes and ridges, despite the occurrence of the six "core" species and many

FIGURE 6. **Gap forest (uppermost end of Gully forest).** Scale pole marked in feet. Tree on right with buttresses is *Clethra occidentalis*; seedling in front of it is *Eugenia virgultosa.* All tree ferns are *Cyathea pubescens.* February, 1975. Photo by E. V. J. Tanner.

of the species of MULL RIDGE — WET SLOPE forest (cf. TABLES 2 and 3). All of the MOR RIDGE species of trees (TABLE 2) are absent, while there are five species decidedly more common in gullies than on slopes and ridges and quite absent from mor sites. Of these latter species, three (*Laplacea haematoxylon, Solanum punctulatum,* and *Turpinia occidentalis*) are able to grow 15 to 18 meters tall, and these contribute significantly to the structure of the forest, especially the *Solanum.*

The shrub layer is similar to that in the MULL RIDGE — WET SLOPE forest but includes much more *Besleria lutea* and one additional frequent species, *Boehmeria caudata.* Isolated individuals of four more species were seen (cf. TABLE 3); two of them, *Datura suaveolens* and *Tournefortia glabra*, are more often seen in the mountains as weeds (C. D. Adams, pers. comm.). Compared with the shrub layer, the herb layer contains relatively more species absent from the MULL RIDGE — WET SLOPE forest and lacks more species widespread in the latter forest type (cf. TABLE 3).

The climbers are much as in the MULL RIDGE — WET SLOPE forest (with the addition of *Marcgravia brownei*). The same appeared to be true of the vascular epiphytes in the sites which we studied, although it appears from Shreve's account (pp. 38–41) that there are several additional species on the lower parts of the boles in many windward ravines. Certainly the growth of epiphytic bryophytes is appreciably greater in the more sheltered gullies.

The forest resembles the forests on slopes and ridges in its lack of cauliflory and paucity of species with compound leaves or drip-tips. The leaf-size spectrum shows a somewhat greater development of notophylls relative to microphylls (TABLE 4).

VERY WET RIDGE forest. Structurally and floristically this forest on Mt. Horeb is very like the MULL RIDGE — WET SLOPE forest of the Blue Mountains. The floristic resemblance is shown for the trees in TABLE 2 and for the shrubs, herbs, and climbers in TABLE 3. The forest differs in the greater abundance of epiphytic bryophytes (the cover on trunks is generally 50 per cent and may add 20 per cent to the apparent DBH) and in the abundance of the small-fronded *Selaginella denudata* on the forest floor. It also differs in the abundance of large bromeliads on the bigger, older trees. The commoner species of the Morce's Gap area (*Tillandsia complanata* and *Vriesia sintenisii*) are present, but the species less common there (*Hohenbergia fawcettii* and *Vriesia incurva*) were not seen on Mt. Horeb. The most abundant (and also the largest) species on Mt. Horeb (*Guzmania fawcettii*) was found only once near Morce's Gap. A further indicator of wetness is the presence of the shrub *Cephaelis elata*, common in the WET LIMESTONE forest and typical of "sheltered *facies* of montane woodland" according to Adams (1972).

This forest would perhaps best be classified as a distinct *facies* of the MULL RIDGE — WET SLOPE association.

HIGH ALTITUDE forest. This was visited only once, and our account is therefore less reliable than that for the other forest types. It is generally 3 to 6 meters tall, but reduced to 1.5 to 2.0 meters toward the summit of Blue Mountain (over 2000 meters). The trees are generally upright. On a few north-facing cliffs and on certain ridges we noticed severe wind-pruning of trees and shrubs, at least some of which had smaller and thicker leaves than usual.[6] However, most of the dwarfed forest, including that near the summit, shows no sign of wind-pruning. Twenty-

[6] The same was seen at a lower altitude (1670 meters) in Portland Gap.

three species of trees were recorded, including two tree ferns; nine were recorded as very rare, mostly found near the lower limit of the forest type. The species present are an interesting mixture (TABLE 2). Of the six "core" species of lower altitudes only three are present; of the ten ridge and slope species of lower altitudes only two are present other than as rare isolated individuals; and of the 23 ridge, slope, and gully species only one occurs. Of the five gully species only one is present. The three tree species confined to the HIGH ALTITUDE forest all have leaves which represent types characteristic of SUBALPINE forest on the high equatorial mountains: close-packed glabrous nanophylls in *Eugenia alpina*, densely hairy mesophylls in *Clethra alexandri*, and densely hairy macrophylls in *Senecio swartzianus*.

It is interesting that several DRY SLOPE forest species are found in the HIGH ALTITUDE forest, some of them (*Garrya fadyenii*, *Viburnum alpinum*, and *V. villosum*) repeatedly and others (*Brunellia comocladiifolia*, *Miconia quadrangularis*, *Myrica cerifera*, *Rhamnus sphaerospermus*, and *Weinmannia pinnata*) only as isolated individuals. Adams (1972) also records that *Myrsine coriacea* ascends as far as the top of Blue Mountain. All of these species occur in spite of the undoubted fact that the HIGH ALTITUDE forest is fogged for much longer periods than the MULL RIDGE forest of lower altitudes, where they do not normally occur. The high altitude slopes concerned have undoubtedly been disturbed to some extent as a result of their proximity to the long-used track to Blue Mountain Peak, but it seems most unlikely that the DRY SLOPE forest species have gained entrance to the community purely as a result of disturbance.

The shrubs show a similar pattern of development, with few of the species of moist forests at lower altitudes present (TABLE 3) and at least four of the species which are found in DRY SLOPE forest or DRY LIMESTONE scrub forest at lower altitudes. The one apparently obligate HIGH ALTITUDE "shrub" (really a woody herb), *Lobelia martagon*, again represents a life form characteristic of the Subalpine Zone on equatorial mountains. However, it should be noted that it is sometimes found below 1850 meters, even as low as 750 meters on occasion (Adams, 1972). *Lobelia alticaulis*, similarly woody but virtually unbranched, is found in the John Crow Mountains at 600 to 750 meters (Adams, 1972).

The HIGH ALTITUDE forest is deficient in tree ferns (no material of those present was collected), herbs, and climbers (TABLE 3). *Chusquea* and bracken (*Pteridium aquilinum*) are occasional, and a large-fronded species of *Gleichenia* (not collected) is locally abundant. Vascular epiphytes and hemiparasites are very few. "Mossing" is about the same as in the MULL RIDGE forest or less marked, except on certain north-facing slopes, where it is very obvious.

The leaf-size spectrum of the trees and shrubs (other than tree ferns and very rare species) shows a very wide spread (TABLE 4). Only two species, *Schefflera sciadophyllum* and *Weinmannia pinnata* (both very rare), have compound leaves, although two others, *Bocconia frutescens* and *Senecio swartzianus*, have deeply dissected leaves. Only one species, *Dendropanax* "*nutans*",[7] has drip-tips. There are no buttressed or cauliflorous species. The HIGH ALTITUDE forest clearly represents a distinct association.

The vegetation around the summit of Blue Mountain has been very severely disturbed. However, about 100 meters to the east, on a flat area of 1 to 2 hectares, there is a distinct *facies* of the HIGH ALTITUDE forest which does not appear to have suffered much human interference, unless it was by fire at some time in the distant past. *Clethra alexandri* (2(to 2.5) meters tall) is the most abundant tree, followed by *Eugenia alpina*, then *Dendropanax "nutans"*, *Ilex macfadyenii*, *Vaccinium meridionale*, and *Viburnum alpinum* or *villosum* (all of which are occasional), and finally *Podocarpus urbanii* and *Cyathea* sp. (both rare). There are two occasional shrubs, *Eupatorium parviflorum* and *Wallenia* sp. The tall woody herb *Lobelia martagon* is frequent and contributes significantly to the physiognomy of the community. In the herb layer *Rhynchospora eggersiana* is frequent, *Blechnum* sp. and *Lophosoria quadripinnata* are occasional (the latter with fronds dwarfed to less than 1 meter in length instead of the usual 1.5 to 2.0 meters), and *Lycopodium clavatum* is locally abundant. The soil appears to be more or less evenly and markedly enriched with organic matter (though not "peaty") to a depth of 30 cm., where stones are encountered. The surface pH is 4.3–4.5 and that at a depth of 30 cm. is 4.3 (two samples).

DRY SLOPE forest. This community, as mentioned earlier, has been almost totally destroyed by man. Its lower limit is now quite obscure, but the community seems to have stretched down to about 1000 to 1100 meters at least; the upper limit is about 1500 meters. The least disturbed remnants are 6 to 11 meters tall; most of the trees are upright and few attain a DBH of 40 cm.

Many of the most disturbed areas are now dominated by shrubs and low trees, some of which are markedly xeromorphic, in particular the switch plant *Baccharis scoparia*, the tiny-leaved *Satureja viminea*, and the sticky-leaved *Dodonaea viscosa*. Soft-leaved Compositae (*Bidens*, *Eupatorium*, and *Vernonia*) are locally prominent.

The forest and associated scrub contain 26 species of dicotyledonous trees, one tree fern, and ten shrubs. Of these, 13 trees and seven shrubs constitute a distinct suite, more common here than in any other forest type studied (TABLES 2 and 3). It is notable that fewer than half of the hard-leaved tree species of the ridges and wet slopes are present on the dry slopes. Of the species that are present (e.g., *Ilex obcordata*, *Podocarpus urbanii*, and *Vaccinium meridionale*), none are particularly common. It is, therefore, unfortunate that Asprey and Robbins called the community "Montane Sclerophyll." It is markedly less "sclerophyllous" than the MOR RIDGE forest and somewhat less "sclerophyllous" than the MULL RIDGE forest.

Tree ferns, apart from *Lophosoria quadripinnata* (which has only a

[7] Possibly including some *D. pendulus*.

short trunk), appear to be quite absent from the DRY SLOPE forest at the present time. We were told, however, that tall tree ferns with copious development of adventitious roots on the trunks had been cut out from the wettest parts of the DRY SLOPE forest along the path from Cinchona to Morce's Gap for sale to orchid-growers.

The herb layer was not studied in detail. It is extremely difficult now to determine what the original herbaceous species were because of the great influx of weeds. There are few climbers (TABLE 3) and relatively few epiphytes.

There are no cauliflorous or buttressed species; only one species (*Brunellia comocladiifolia*) has compound leaves and none have drip-tips. The leaf-size spectrum of the trees and shrubs (excluding the tree fern and very rare species) shows the widest spread of all the forest types studied by us, but the two most abundant leaf-size classes are as in the MULL RIDGE — WET SLOPE forest, i.e., microphylls and notophylls (TABLE 4). The forest clearly represents a further distinct association.

DRY LIMESTONE scrub forest. On the southeast side of John Crow Peak at 1750 to 1800 meters, growing amongst the deeply dissected limestone, is a distinctive scrub forest 2 to 4 meters tall, with most stems only 2 to 3 cm. thick at 1 meter in height (a few are 6 cm. thick). This community is remarkable for the almost complete absence of the more or less hard-leaved tree species of the RIDGE and SLOPE forests (TABLE 2). Apart from abundant *Chusquea abietifolia* (which covers about 75 per cent), the dominant shrub species are the soft-leaved *Eupatorium triste* and *Vernonia pluvialis*, the leptophyllous *Satureja viminea*, and the more or less succulent-leaved *Verbesina nervosa*. The soft-leaved *Salvia jamaicensis* is also characteristic, and the scrambling shrub *Bidens shrevei* (also soft-leaved) is present. The leaf-size spectrum shows a predominance of microphylls (TABLE 4), and in this sense the community is relatively xeromorphic. However, the leaf texture is mesomorphic (as is indeed the leaf texture of the dominant species on limestone in the lowlands in the dry southwestern part of Jamaica). The change from the hard-textured leaves of the MOR RIDGE forest to the soft-textured leaves of the LIMESTONE scrub forest in many ways parallels the change from bog to fen vegetation in northern Europe. One might expect the soft-leaved species of the LIMESTONE scrub forest to be at least facultatively deciduous. However, they were found not to have lost their leaves toward the end of the main dry season (in March) in 1974 (obs. E. V. J. T.). Of the few harder-leaved species present, the most interesting perhaps is *Weinmannia pinnata*, otherwise seen by us only in HIGH ALTITUDE forest, on Mt. Horeb, and in the John Crow Mountains, but described by Adams (1972) as "locally frequent in montane thickets and open woodlands, 3600–6500 ft."

Down in the grykes between the rugged blocks of limestone there is virtually no herb layer, although in solution hollows on the tops of the rocks a few herbaceous species are found (*Peperomia quadrifolia*, *Pilea microphylla*, *Relbunium hypocarpium*, and a few orchids and bromeliads).

Bryophytes are absent from the trunks of most of the shrubs, but the lichen *Usnea* is very frequent on emergent crowns. The hemiparasite *Eubrachion ambiguum* was noted.

WET LIMESTONE forest. On the summit of John Crow Peak in the Blue Mountains, the vegetation is quite different from that just described. The ground is not deeply dissected, although there are outcropping rocks of limestone. The vegetation is, in general appearance, like that of the MULL RIDGE forest, but we did not have an opportunity to study it critically.

The WET LIMESTONE forest was studied in some detail on the western slopes of the John Crow Mountains. Here there appeared to be a continuum, at the lower end of which the forest was 15 to 18 meters tall, with frequent buttresses more than 1 meter high and occasional prop roots, and at the upper end of which the forest was 8 to 11 meters tall without buttresses or prop roots. Two sites were chosen for detailed study (at 770 meters and 950 meters) to represent the extremes. Throughout the continuum the canopy is closed, the trees are upright, and there is no evidence of wind-clipping. At the lower end many trees with a DBH greater than 40 cm. are present, but at the upper end the forest is denser and there are few individuals with a DBH greater than 15 cm. The forest differs from all of those described so far in the presence of a species of palm, *Calyptronoma occidentalis*, which is generally frequent at the lower end of the continuum but more or less confined to gullies at the upper end.

Twenty-three species of angiospermous trees, one tree fern, and 11 species of shrubs were recorded at the lower site, of which only 12 angiospermous trees and one shrub were present at the upper site. Ten angiospermous trees, one tree fern, and two shrubs were recorded at the upper site and not at the lower. Although the list of herbs in TABLE 3 is certainly less complete than that for the other forest types, the herb layer is undoubtedly poor in species. This is especially true at the upper end of the continuum, where the herb layer is occupied almost exclusively (apart from tree seedlings) by the fern *Diplazium costale*, with upright stems 10 to 15 cm. tall.

Climbers are abundant at the lower end of the continuum and, though fewer species are present, they are still frequent at the upper end. *Syngonium auritum* (Araceae), which climbs to the lower part of the canopy, is particularly prominent throughout.

Vascular and nonvascular epiphytes throughout are approximately as abundant as in the MULL RIDGE forest of the Blue Mountains. The following vascular epiphytes were collected: *Catopsis nitida, Guzmania fawcettii,* and *Hohenbergia eriostachya* (all bromeliads); *Arpophyllum jamaicense, Epidendrum polybolbon, Maxillaria purpurea, Neourbania adendrobium,* and *Pleurothallis uncinata* (all orchids); *Polytaenium feei* (fern); *Blakea trinervia* (melastome); and *Columnea fawcettii* (gesneriad). Although our collections are again bound to be incomplete, it is notable that the bromeliad and orchid species involved are all different from those recorded in the Blue Mountains *sensu stricto* except the *Guzmania*, which is very rare in the latter range. The *Pleurothallis*, like the *Guzmania*, is found on Mt. Horeb, and the *Arpophyllum* occurs at Newcastle nearby (C. D. Adams, pers. comm.).

No cauliflorous species were found, only two species with compound leaves (*Calyptronoma occidentalis* and *Guarea swartzii*), and only one with drip-tips (*Psychotria dolphiniana*). The leaf-size spectrum of the trees and shrubs (other than tree ferns and very rare species) shows a clear preponderance of notophylls and mesophylls *sensu stricto*.

No detailed study was made of the community above 950 meters, where there was a steep, dissected slope with grykes 0.5–2.5 meters across and large blocks of limestone completely devoid of soil. The whole slope was covered by a low forest with a closed canopy, the very tortuous trunks and roots running over the rocks. Bryophytes are very abundant through the canopy and over the trunks, roots, and rocks. The trees present in the lowermost part of this community include *Guarea swartzii* and *Piper discolor* (also found in the continuous forest below) and *Conostegia icosandra*, *Viburnum alpinum*, and *Wallenia venosa*. Also found were the shrub *Gyrotaenia microcarpa*, the herbs *Lobelia grandiflora*, *Pilea grandiflora*, and *Psychotria discolor*, and the epiphyte *Elaphoglossum crinitum*. This community above 950 meters is termed "Elfin Woodland" by Asprey and Robbins (1953), who recorded *Clusia havetioides* (as *C. clarendonensis*) as the most abundant species. C. D. Adams and G. R. Proctor (pers. comm.) agree that this species is abundant over wide areas on the eastern (dip) slope of the mountains. *Clusia portlandiana* is also present, indeed confined to the John Crow Mountains, but it is not known whether it is a widespread and abundant species (C. D. Adams, pers. comm.).

It is notable that 15 of the tree species and two of the shrub species present in the WET LIMESTONE forest are also found in the MULL RIDGE — WET SLOPE forest of the Blue Mountains and/or the VERY WET RIDGE forest of Mt. Horeb; one more is known in the DRY SLOPE forest of the Blue Mountains (TABLES 2 and 3). Of the remaining 13 trees and seven shrubs in the WET LIMESTONE forest identified with certainty to species level, only nine trees and four shrubs are recorded by Adams (1972) as generally occurring on limestone. Most of these 13 apparently calcicolous species are rare or absent above 900 meters. Whether they are strictly calcicolous is doubtful, because relatively little rain forest remains in the appropriate altitudinal range on soils derived from rocks other than limestone, and such sites have not been studied critically. A high proportion of the species in the community above 950 meters are certainly found elsewhere off limestone, i.e. all of the 12 recorded by Asprey and Robbins (1953, p. 402) except *Conostegia balbisiana* and *Garcinia humilis* ("*Rheedia sessiliflora*") [8] and all of the ten recorded by us other

[8] *Clusia 'clarendonensis'* is excepted, since this was a misidentification of *C. havetioides*.

than *Conostegia icosandra, Lobelia grandiflora, Psychotria discolor,* and *Wallenia venosa.*

RESULTS OF FOLIAR ANALYSES

In December, 1973, mature, well-lit leaves were collected from the crowns of two individuals of almost all the major tree species in a stretch of MOR RIDGE forest on one of the knolls west of Morce's Gap. The leaves were oven-dried within two days of collection. In late July to early August, 1974, mature, well-lit leaves were collected from the crowns of three individuals of each of two "core" species (*Alchornea latifolia* and *Clethra occidentalis*) in the MOR RIDGE, MULL RIDGE, WET SLOPE, and GULLY forests in the same area west of Morce's Gap. The gully forest in which we collected grew in a slight dip in the ridge and represents the uppermost limit of what we have described as GULLY forest. The leaves were oven-dried within one day of collection. Leaves from both collections were analyzed by standard methods (cf. Tanner, in press).

The results are set out in TABLES 5 and 6. The interpretation of foliar analyses always presents problems, and these are discussed elsewhere (Grubb, in prep.). The level of N, on a dry-weight basis, is largely a measure of leaf structure, since it is lower in leaves with a coriaceous texture, which reflects the development of thick cell walls, especially in the epidermides and bundle sheaths. This is less completely true of P or K, and leaf cell-wall thickness is not generally the major determinant of the levels of other mineral elements. These generalizations seem to hold for the present results. Thus, on the whole, the lowest N levels are found in the species with the most coriaceous leaves and, almost certainly, the thickest walls, i.e. *Ilex obcordata,** *Clusia havetioides,** *Podocarpus urbanii, Ilex macfadyenii, Chaetocarpus globosus,** and *Lyonia* cf. *octandra.** Of these species, the four marked with asterisks all attain their greatest abundance in the MOR RIDGE forest and contribute very largely to the impression of a particularly coriaceous leafy canopy in this forest type. The six species with the lowest P levels include five of the six species named above (all except the *Lyonia*), and the six species with lowest K levels include four of the six named above (not the *Chaetocarpus* or the *Clusia*).

If we consider, by way of contrast, the five species that not only grow in the MOR RIDGE forest but also appear to be about equally frequent in the GULLY forest (*Alchornea latifolia, Clethra occidentalis, Cyrilla racemiflora, Mecranium purpurascens,* and *Podocarpus urbanii*), we find that three of these (the *Alchornea, Clethra,* and *Mecranium* species) show the highest levels of N and P and two of the highest levels of K.[9] These results suggest that the coriaceous-leaved species of the MOR RIDGE for-

[9] *Blakea trinervia,* which is commonly an epiphyte and only found as a ground-dwelling species in the Morce's Gap area in the MOR RIDGE forest, has notably high levels of N, P, and K; these are consistent with the somewhat succulent nature of the leaves and, therefore, the ratio of protoplast to wall material.

TABLE 5. The average foliar concentrations of various mineral elements in mature leaves collected in December, 1973, from Mor Ridge forest west of Morce's Gap.*

	N	P	K	Na	Mg	Ca	Mn	Fe	Zn	Cu
Aquifoliaceae										
Ilex macfadyenii	0.97	0.038	0.27	0.13	0.21	0.58	0.015	74	33	3.2
I. obcordata	0.72	0.028	0.22	0.31	0.18	0.44	0.011	96	22	4.2
Clethraceae										
Clethra occidentalis	1.27	0.051	0.42	0.08	0.71	1.47	0.047	93	41	4.1
Cyrillaceae										
Cyrilla racemiflora	1.14	0.045	0.37	0.25	0.15	0.20	0.005	74	19	2.0
Ericaceae										
Lyonia cf. *octandra*	1.06	0.047	0.32	0.05	0.15	1.05	0.024	93	61	7.7
Vaccinium meridionale	1.19	0.040	0.34	0.07	0.15	0.31	0.011	56	12	3.2
Euphorbiaceae										
Alchornea latifolia	1.57	0.100	0.46	0.03	0.21	0.94	0.017	107	24	5.7
Chaetocarpus globosus	1.00	0.041	0.38	0.04	0.16	0.22	0.009	89	25	3.5
Guttiferae										
Clusia havetioides	0.76	0.040	0.41	0.21	0.29	0.92	0.023	78	22	3.5
Melastomataceae										
Blakea trinervia	1.51	0.067	0.64	0.04	1.04	1.81	0.002	99	33	7.2
Mecranium purpurascens	1.49	0.053	0.33	0.18	0.55	0.34	0.003	78	14	3.5
Podocarpaceae										
Podocarpus urbanii	0.79	0.039	0.24	0.20	0.06	0.98	0.021	93	14	3.0

* Each value is the mean of two collections. Results are expressed as percentage dry weight for most elements, but as p.p.m. dry weight for Fe, Zn, and Cu.

est might be enabled to flourish there by an ability to withstand particularly low levels of N, P, and K supply, such as are commonly found in highly acid, highly organic soils in the temperate zones. The species concerned also tend to have the lowest foliar levels of Ca, Mg, and Mn, but the levels of these elements are not so consistently or markedly low.

The results in TABLE 6 for *Alchornea* and *Clethra* do not altogether confirm the above expectations. Certainly there is evidence from both species that the K supply is markedly worse in the MOR RIDGE forest soil than in the MULL RIDGE soil and notably better in the GULLY soil. However, only the results for *Alchornea* suggest any significant differences for N, and neither species yields any evidence of significant differences in P supply. The results for Ca and Mg are rather surprising, with the highest levels in both species being found at the MOR RIDGE and WET SLOPE sites. There are no consistent intersite differences in Mn, Fe, Cu, Zn, or Na. These results are considered later in relation to probable limiting factors.

DISCUSSION

THE FOREST FORMATIONS

We will now consider the classification of the Jamaican mountain forests in the scheme of formation types found useful in other parts of the wet tropics (summarized in TABLE 1) and tentatively relate the forests of the wetter parts of the lowlands to the same scheme.

The MOR RIDGE forest meets every criterion of the UPPER MONTANE rain forest in TABLE 1 except the predominance of microphylls (cf. TABLE 4). The same is true of the MULL RIDGE — WET SLOPE forest type, despite its greater stature and softer-textured leaves. The VERY WET RIDGE forest on Mt. Horeb is closely related to the latter type, separable merely as a *facies* in floristic terms, yet it shows a marked tendency toward a larger mean leaf size (TABLE 4). The HIGH ALTITUDE forest and DRY SLOPE forest are also clearly referable to the UPPER MONTANE rain forest formation type on all criteria except the leaf-size spectrum. All of these forests are notable for their lack of buttresses and thick-stemmed lianas. In contrast, the GULLY forest characteristically has these features, as well as significantly greater stature and a fairly clear preponderance of notophylls and mesophylls *sensu stricto*. Clearly, in the Jamaican situation, the leaf-size spectrum alone is not useful for the classification of MONTANE rain forests, but we consider that, taking all the positive features of the GULLY forest together, this association is best classified as an impoverished form of LOWER MONTANE rain forest. It is impoverished in the sense that it is of lower stature and contains fewer species (especially of woody climbers) than the LOWER MONTANE rain forests on most equatorial mountains (cf. Grubb *et al.*, 1963; Grubb & Stevens (in press); Whitmore, 1975). The fact that there is an appreciable overlap of tree species between the LOWER MONTANE and UPPER MONTANE forests in Jamaica emphasizes the importance of variations in plant per-

TABLE 6. The average foliar concentrations of various mineral elements in mature leaves collected in July and August, 1974, from four forest types west of Morce's Gap.

	N	P	K	Na	Mg	Ca	Mn	Fe	Zn	Cu
Alchornea latifolia										
MOR RIDGE	1.46	0.10	0.32	0.046	0.28	0.88	0.037	0.011	19	5.0
MULL RIDGE	1.59	0.09	0.59	0.034	0.16	0.64	0.039	0.010	19	4.1
WET SLOPE	1.64	0.11	0.68	0.036	0.24	0.75	0.012	0.011	6	1.4
GULLY	1.67	0.12	0.82	0.036	0.16	0.67	0.033	0.010	24	8.1
Clethra occidentalis										
MOR RIDGE	1.04	0.06	0.93	0.049	0.51	0.69	0.050	0.012	24	5.1
MULL RIDGE	1.07	0.06	1.25	0.033	0.26	0.47	0.031	0.010	22	4.3
WET SLOPE	1.27	0.08	1.38	0.054	0.49	0.73	0.033	0.012	22	5.8
GULLY	1.09	0.07	1.73	0.052	0.28	0.39	0.031	0.010	42	4.4

* Each value is the mean of three collections. Results are expressed as percentage dry weight for most elements, but as p.p.m. dry weight for Zn and Cu.

formance in the development of distinct forest formations. The same point is made by Grubb and Stevens (in press) for forest types in New Guinea.

The forest at the lower end of the continuum found on limestone in the John Crow Mountains is also clearly referable to LOWER MONTANE rain forest by every criterion in TABLE 1. The forest at the upper end of the continuum, however, is intermediate between LOWER MONTANE and UPPER MONTANE, having prominent climbers and a clear dominance of notophylls — mesophylls (typical of LOWER MONTANE forest), but low stature and an absence of buttresses (typical of UPPER MONTANE forest). We could not study the Limestone Pavement forest above 950 meters in any detail, but it is probably best assigned to the UPPER MONTANE rain forest formation. Asprey and Robbins included this forest type with our HIGH ALTITUDE forest in "Elfin Woodland," but since the communities are quite distinct in structure, physiognomy, and floristics, we do not find this treatment useful. As for our DRY LIMESTONE scrub forest, there is no widespread world vegetation type corresponding to it. It could possibly be regarded as an edaphically determined variant within the UPPER MONTANE rain forest formation.

It is interesting that the families of trees and shrubs involved in the different forest types show considerable parallels with those in other parts of the world. For example, those present in the MOR RIDGE forest are much the same as those in the UPPER MONTANE rain forest on peat in Malesia (Aquifoliaceae, Araliaceae, Clethraceae, Ericaceae, Guttiferae, Lauraceae, Melastomataceae, Myrsinaceae, and Podocarpaceae). The most notable absentees in the Jamaican MOR RIDGE forest are the Myrtaceae and Theaceae (both frequent in the MULL RIDGE forest) and the Symplocaceae (generally rare in Jamaica, cf. Adams, 1972). The most surprising family found to be represented is the Euphorbiaceae, with two abundant species, *Alchornea latifolia* and *Chaetocarpus globosus.* Of the three other families of trees present in the MOR RIDGE forest, the Cyrillaceae are found only in the New World, while the Myricaceae and Rhamnaceae were represented at our sites by only one individual each.

The 15 families represented by trees and shrubs, absent from the MOR RIDGE forest but present in MULL RIDGE — WET SLOPE forest, are also widespread in montane forests of the tropics. Those marked by asterisks in the following list are found in the UPPER MONTANE rain forest, with mull humus at relatively high altitudes, in the Andes [10] and/or New Guinea (cf. Cuatrecasas, 1958; Grubb & Stevens (in press)): Celastraceae,* Chloranthaceae,* Compositae,* Flacourtiaceae,* Gentianaceae,* Gesneriaceae,* Meliaceae, Myrtaceae,* Oleaceae,* Piperaceae,* Rubiaceae,* Sapotaceae, Solanaceae,* Staphyleaceae, and Theaceae.* The three families not marked by asterisks are typical of LOWER MONTANE as opposed to UPPER MONTANE rain forest on the higher equatorial mountains. All of the families mentioned in the previous paragraph (apart from the

[10] The *selva andina* of Cuatrecasas is almost certainly equivalent to our UPPER MONTANE rain forest and his *selva subandina* equivalent to our LOWER MONTANE rain forest.

Cyrillaceae) are also found in the higher-altitude UPPER MONTANE forests of the equatorial mountains.

The DRY SLOPE forest is particularly interesting because of the dominance of genera with marked dry-climate connotations. The following seven species belong to genera notable for their success in the Mediterranean-climate regions of Europe or California or in the neighboring mountains: *Garrya fadyenii*, *Juniperus barbadensis*, *Myrica cerifera*, *Rhamnus sphaerospermus*, *Satureja viminea*, *Viburnum alpinum*, and *V. villosum*. *Daphnopsis* is closely related to *Daphne*, which is also, in part, a Mediterranean-Montane genus. *Baccharis scoparia*, the switch plant, has many relatives in the dry inner valleys of the high Andes. In the case of *Dodonaea viscosa*, the same species is found on some of the drier slopes of the high mountains of equatorial South America and Africa.[11] Of the remaining species, *Bidens shrevei*, *Eupatorium parviflorum*, *E. triste*, and *Vernonia divaricata* are soft-leaved shrubs representative of a family (the Compositae) which is widespread on the limestone at lower altitudes in the dry southwestern part of Jamaica.

At present the mean annual rainfall in the DRY SLOPE forest is quite high (up to 2700 mm.), well over the 1400 mm. needed to sustain rain forest ("MOIST MONTANE" forest) in the Lower Montane Zone in Africa (Zamierowski, 1975) and even well above the 1800 mm. generally needed to sustain rain forest in the tropical lowlands (Richards, 1952). Before man opened up the community, there was probably a continuous forest made up of characteristic DRY SLOPE trees (*Brunellia*, *Daphnopsis*, *Myrica*, *Myrsine*, *Oreopanax*, *Rhamnus*, and *Viburnum*) and some of the MULL RIDGE and WET SLOPE trees (mainly *Alchornea*, *Clethra*, *Cyrilla*, *Ilex*, and *Vaccinium*). At that time the *Dodonaea viscosa*, the *Juniperus barbadensis* Thunb., and the various shrubs now so prominent (species of *Baccharis*, *Bidens*, *Bocconia*, *Eupatorium*, *Satureja*, and *Vernonia*) may have been more or less confined to rock outcrops or to land slips. The DRY LIMESTONE scrub forest on the southeast slope of John Crow Peak at the present time illustrates one natural habitat for several of the species. If the climate during the last Ice Age was much drier than it is at present in Jamaica, as seems to have been the case in South America (Vuilleumier, 1971), Africa (Van Zinderen Bakker & Coetzee, 1972; Hamilton, 1974), and northeastern Australia (Kershaw, 1970; 1974), the DRY SLOPE forest is likely to have been more widespread and the light-demanding shrubs may have grown widely on ordinary slopes as well as on rock outcrops.

It is also important to consider past climates in interpreting the distinctly subalpine features of leaf form and life form found in the HIGH ALTITUDE forest (cf. p. 340). If the forest limits were lowered by 1000 meters in the last Ice Age (cf. Walker, 1970; Vuilleumier, 1971; Flenley, 1972; Van Zinderen Bakker & Coetzee, 1972), the top of Blue Mountain Peak (now 2265 meters) would have reached a level at which SUBALPINE forest is found today in parts of the Andes (Vareschi, 1955). The colony

[11] In New Guinea it is found on river gravels, on natural forest margins, and in secondary forest (Grubb & Stevens, in press).

of the tussock grass *Danthonia domingensis* (*"D. shrevei"*) at about 1850 meters on the north side of High Peak (named Sir John Peak in Shreve's account) could be a relict of this period, but the factors controlling its persistence at the present time (and its absence from the appreciably higher Blue Mountain Peak) are obscure. Shreve (1914) reported that there is nothing obviously peculiar about the soil where the plant grows, but he noted the low growth of the trees and shrubs mixed with it.

Unfortunately we have made no new observations on the downward continuation of the MONTANE rain forests in Jamaica, and we can relate the lower-altitude types to the schema in TABLE 1 only on the basis of Asprey and Robbins's (1953) account and certain new facts provided by C. D. Adams (pers. comm.).

The major component of the "MONTANE MIST" forest of Asprey and Robbins is our MULL RIDGE — WET SLOPE forest, but it also includes our MOR RIDGE forest and GULLY forest. The lower limit of the "MONTANE MIST" forest on the northern slopes of the Blue Mountains is said to be at about 3500 feet (1050 meters), and this is presumably the lower limit of our UPPER MONTANE rain forest in that area. In the John Crow Mountains, which are wetter, there is a gradual transition from LOWER MONTANE rain forest at 700 meters to LOWER MONTANE — UPPER MONTANE transitional forest at 900 meters and possible UPPER MONTANE (Limestone Pavement) forest above 950 meters.

There seems to be a continuum in structure, physiognomy, and floristics between our GULLY forest at about 1500 meters on nonlimestone rocks in the Blue Mountains, our WET LIMESTONE forest at 700 to 800 meters in the John Crow Mountains, and the "LOWER MONTANE" rain forest described by Asprey and Robbins from sites at 550 to 750 meters on the slopes of the Rio Grande Valley between the Blue Mountains and the John Crow Mountains. It would appear that the forest is commonly 24 to 30 meters in height at an altitude of 550 to 750 meters. Asprey and Robbins report three species (*Ficus maxima* (*'suffocans'*), *Psidium montanum*, and *Symphonia globulifera*) as emergents to 36 meters near the lower limit, but according to Adams none of these species can be considered characteristic of this forest type and none grow commonly to more than 30 meters tall.

There is a further continuum in structure, physiognomy, and floristics from the "LOWER MONTANE" rain forest of Asprey and Robbins at 550 to 750 meters in the Rio Grande area to their "WET LIMESTONE" forest at 300 to 750 meters in the Cockpit Country, an area of karst limestone in the western part of the island, and in a similar area near the center of the island rising to 838 meters in Mt. Diablo (see FIGURE 1). Their "WET LIMESTONE" forest is described as about 18 meters tall with relatively few emergents to 30 meters; the trees do not have large buttresses. Asprey and Robbins's account suggests that thick-stemmed lianas are absent, but *Rourea glabra* (*R. "paucifoliolata"*), reported by them, can grow to a height of 30 meters and develop quite thick stems (Adams, 1972). Moreover, according to Adams (pers. comm.), there are other species present with substantial stems, e.g., *Chamissoa altissima, Clematis dioica, Ipomoea ternata,* and *Schlegelia parasitica.* Usually these species attain a DBH of no more than about 5(–10) cm. Taking the criteria of TABLE 1 as a whole, this forest must be assigned to the LOWER MONTANE rain forest formation.

It is notable that the forest contains a number of woody families usually more or less confined to lowland forests in other parts of the tropics: Anacardiaceae (*Comocladia* and *Mosquitoxylum*), Annonaceae (*Annona, Oxandra,* and *Xylopia*), Burseraceae (*Bursera,* rare in wet areas), Canellaceae (*Cinnamodendron*), Combretaceae (*Buchenavia, Bucida,* and *Terminalia*), Nyctaginaceae (*Neea* and *Pisonia*), Quiinaceae (*Quiina*), and Simaroubaceae (*Picrasma* and *Simarouba*). Of the genera listed here only one (*Oxandra*) was recorded by Asprey and Robbins from their "LOWER MONTANE" rain forest and only two (*Neea* and *Picrasma*) were recorded by us. However, all of the others except *Mosquitoxylum, Bucida,* and *Simarouba* are noted by Adams (1972) as being found, at least occasionally, above 2000 feet (about 600 meters). It thus appears that the lower part of the LOWER MONTANE rain forest in Jamaica shows the *mélange* effect of Grubb (1974) and Grubb and Stevens (in press) to a marked degree, i.e., the particular forest type, defined on structure and physiognomy and found at a lower altitude than it would be on a high mountain in the equatorial belt, contains floristic elements that are confined to lower-altitude forests in the high equatorial mountain situation. The same effect is seen in the LOWER MONTANE rain forest at 150 to 600 meters in Puerto Rico discussed in the work edited by Odum and Pigeon (1970) and in the LOWER MONTANE rain forests at 260 to 800 meters on various Caribbean Islands discussed by Beard (1944, 1955).

There is no typical LOWLAND rain forest, as defined by TABLE 1, in Jamaica at the present time. Possibly it existed at or near sea level before the coming of man in the areas with an annual rainfall of more than 1800 mm., e.g., where sugarcane is now grown. However, Adams believes that it would probably have been a marsh forest variant of LOWLAND rain forest. He says that the last remnants of high forest of this type at and near sea level are being destroyed at present in parts of the parishes of Westmoreland and Hanover in western Jamaica. Components include *Bucida buceras, Crudia spicata, Symphonia globulifera, Tabebuia angustata,* and *Terminalia latifolia,* with the massive liana *Dalbergia brownei.* A similar forest in the Black River plain in the parish of St. Elizabeth has, in addition, *Grias* (cauliflorous) and large bignoniaceous vines. These forests are the nearest in Jamaica to the LOWLAND rain forest associated with the great rivers of South America (cf. Adams, 1971, p. 56), but they are subject to distinct seasonal and edaphic constraints.

In summary, LOWLAND rain forest in the sense of TABLE 1 may have existed in the past in a few areas at an altitude below 300 meters, but it is now virtually impossible to be sure. The few remnants of high forest at or near sea level are of a distinctly marshy type. Relict areas of LOWER MONTANE rain forest are still found from 300 meters to 1750 meters. In the lower part of its range this forest type occurs on ridges and slopes, as well as in gullies, and it contains a wide range of species. Many of the woody families present have strong lowland affinities. At the upper end of its range this forest type is confined to gullies and is much poorer in species. On the slopes of the John Crow Mountains there is a continuum from LOWER MONTANE rain forest at 700 to 800 meters to what must probably be classified as UPPER MONTANE rain forest above 950 meters. The transition from LOWER MONTANE to UPPER MONTANE rain forest on the slopes of the Blue Mountains has not been studied in detail but apparently occurs at about 1050 meters. The UPPER MONTANE formation contains at least four different associations: MOR RIDGE forest (local in occurrence), MULL RIDGE — WET SLOPE forest (very widespread with a local VERY WET RIDGE forest *facies*), DRY SLOPE forest (formerly widespread, now mostly destroyed), and HIGH ALTITUDE forest (found only above 1850 meters and confined to a few peaks). These four forests are closely similar in structure and physiognomy to UPPER MONTANE rain forests elsewhere except for their possession of approximately equal numbers of tree and shrub species with microphylls and notophylls. They are also similar in their content of woody families, but they do contain a few families more characteristic of LOWER MONTANE forests in equatorial regions.

DEVELOPMENT OF THE MOR RIDGE FOREST

It is necessary to justify the term "mor," because many observers would describe the relevant soils in the Blue Mountains as "peat." In that part of Europe neither strongly oceanic nor strongly continental, e.g. southeastern England, mor and peat are quite distinct. Peat is formed under topographically determined waterlogged conditions; the drainage waters may be base-rich and the pH of the peat high or the waters may be base-poor and the pH of the peat low. In either case microbial breakdown is primarily inhibited by the waterlogged conditions. In contrast, mor is formed on strongly leached upland sites, nearly always on base-poor parent materials; the pH of the uppermost mineral soil where mor begins to form is always strongly acidic (pH less than 4.5, usually less than 4.0). The soil is more or less freely drained, and microbial breakdown is primarily inhibited, either by factors related to the low pH as such or by various phenolic compounds present in large quantity. Accumulations of mor humus seen in southern and central England at the present time are usually only 5 to 10 cm. thick (Watt, 1934; Ovington, 1954; Dimbleby & Gill, 1955; Mackney, 1961; Gimingham, 1972). However, accumulations 20 to 30 cm. thick under *Quercus* species and *Castanea sativa* Mill. have been found by O. Rackham (unpublished data) and similar accumulations (some more than 70 cm. thick) are known in Germany, Denmark, and Norway (Iversen, 1964). It appears that most sites at which such accumulations developed have been destroyed by human activity.

In the strongly oceanic parts of Europe, especially in the mountains (e.g., in western Ireland, Wales, and Scotland), the distinction between mor and peat becomes less clear. Acidic "blanket peat" develops over most surfaces where precipitation normally exceeds evaporation. Even in such areas normal podzols with mor humus are commonly found on the upper parts of steep slopes grading into thin iron-pan soils covered by peat on the ridges and deep peat-gley soils on the plateaux and dip slopes (Crompton, 1952; Crampton, 1963; Holding, Franklin, & Watling, 1965).

Even where forest mor and forest peat are quite distinct topographically, they are often similar in micromorphology. Both materials commonly contain substantial quantities of undecomposed plant fragments (parts of leaves, twigs, fruits, and pollen) and fungal hyphae. However, mor typically contains an appreciable fraction made up of the fecal pellets of mites (Kubiena, 1953; Kendrick & Burges, 1962), the actual proportion being higher in some kinds of mor than in others (Iversen, 1964). Peat frequently contains obvious remains of mosses, but only in certain bog-peats is the bulk of the material derived from them. Both mor and peat may become matted and both often blacken with age.

On well-drained soils in the lowland tropics there are many known occurrences of deep mor humus accumulations quite distinct from peats, e.g., in Borneo (Hardon, 1937; Richards, 1962, 1965; Brunig, 1969), in Guyana (Richards, 1952), and in Brazil (Klinge, 1965). There are also obviously waterlogged acid peat deposits, e.g., in Borneo and Sumatra (Polak, 1933; Coulter, 1950, 1957; Richards, 1952; Anderson, 1963, 1964). Intergrades between mor and peat do not seem to have been recorded explicitly but very probably occur in Borneo (cf. Brunig, 1969).

Despite the existence of topographic intergrades and resemblances between mor and peat in micromorphology, most organic accumlations can be ascribed to one or the other type on the basis of the genesis of the material, whether it is controlled primarily by waterlogging (peat) or by extreme acidity without waterlogging (mor).

In the UPPER MONTANE forest in Jamaica, surface accumulations of organic matter are not found in any of the manifestly very wet sites — on limestone in the John Crow Mountains, in GULLY forest or the HIGH ALTITUDE forest of the Blue Mountains, or in the VERY WET RIDGE forest of Mt. Horeb. This suggests that the accumulations that are found are not determined primarily by waterlogging.

However, the possibility of waterlogging in the upper layers of the soils on the knolls bearing MOR RIDGE forest has been considered carefully. During a year's observations it was found that the knolls certainly were not regularly in fog when the other parts of the ridge were free of low cloud (obs. E. V. J. T.). Indeed there is indirect evidence that the atmosphere within the forest on knolls was actually drier, largely as a result of the more open canopy — the minimum temperatures were lower and the maximum higher (obs. E. V. J. T.). Shreve's (1914) records emphasized the frequent occurrence of low relative humidities on the ridge forests, and this has been specifically confirmed by one of us (E. V. J. T.)

for a MULL RIDGE site. The accumulated organic matter was, of course, saturated after rain had fallen, but it was frequently less than saturated during sunny spells. There is no sign of gleying in the mineral soil beneath it. The only possible indicator of wetter conditions in the MOR RIDGE forest is the greater development of epiphytes, but we attribute this to the sloping trunks offering more suitable sites for establishment, the open canopy providing a more favorable light-climate at the level of the trunks, and, possibly, a greater average age for the trees affording a longer time for colonization.

While the evidence is against the involvement of waterlogging, there is a strong correlation between the degree of accumulation of organic matter and the pH in ridge soils — only 1 to 2 cm. in depth in the top of the "mineral" soil on Mt. Horeb (pH 4.2), through the top 5 to 10 cm. of the "mineral" soil in the MULL RIDGE forest of the Morce's Gap area (pH 3.5–4.0), and up to 50 cm. above the "mineral" soil in the MOR RIDGE forest of the same area (pH 2.8–3.5).

There is a basic difficulty in interpreting this correlation as evidence that humus accumulation is dependent on low pH, since the pH is unquestionably dependent on the accumulation of humus — the more humic acid carboxyl groups present and not occupied by bases, the lower the pH. This precise situation is met in the North Temperate Zone (see, for example, Gorham, 1953, for the Lake District in N. W. England). The usual analysis of the situation is based on the idea of a self-generating or autocatalytic system. It is generally supposed that once leaching of the topsoil has reached a certain critical level, there are important changes in the availability of major mineral nutrients (N, P) and that shortage of these induces the formation of mor-forming litter. The mor-forming litter (or even the living canopy) is then supposed to release substances which inhibit the microbial release of mineral nutrients still further, and so a stagnated system develops (cf. Handley, 1954; Coulson *et al.*, 1960; Davies *et al.*, 1964). An alternative explanation involves the mycorrhizal fungi of the dominant trees in the inhibition of the mineral-releasing and litter-decomposing microbes (Gadgil & Gadgil, 1971). Both hypotheses are useful in providing models of a self-generating system, and either could be applied to the Blue Mountain system. Many early stages in the development of mor were found, and there can be little doubt that there is an inevitable trend from mull to mor on the ridge near Morce's Gap at the present time.

One particularly interesting feature of the situation in the Blue Mountain forests is the considerable number of tree species which can produce mull or mor humus, depending on the soil conditions. This is reminiscent of the position in certain species-rich temperate deciduous forests of eastern North America (cf. Chandler, 1941).

In the North and South Temperate Zones certain trees and shrubs have the ability to acidify soils particularly rapidly and so precipitate the onset of mor formation (Watt, 1934; Scott, Thomson, & Simpson, 1936; Ovington, 1953; Burges & Drover, 1953; Grubb & Suter, 1971). There is no evidence that any of the species in the Jamaican montane forest have this ability; the processes of mor formation appear to be set in motion simply as a result of generalized leaching of the type, which occurs inevitably under any plant canopy where precipitation exceeds evaporation.

The only other case recorded from a tropical mountain in which mor is formed without any intergrading to peat is that reported by Pitt-Schenkel for LOWER MONTANE rain forest (*sensu* our TABLE 1) at about 1650–2280 meters in the western Usambara Mountains in Tanzania, where the annual rainfall is about 1250 to 1600 mm. (i.e. distinctly less than in the Blue Mountains) and rather markedly seasonal. The bedrock is gneiss. The mor humus (A_1 horizon of Pitt-Schenkel, 1938, p. 76) is about 10 to 12 cm. thick and has a pH of 3.0–3.2. The A_e horizon below it (A_1/A_2 of Pitt-Schenkel) is a friable loam with bleached quartz grains (pH 3.2–3.4). This African soil type is in need of more comprehensive investigation, but it appears to differ from that in Jamaica by the thinness of the mor layer and the presence of a clearly leached mineral layer. It is notable that although the forest trees do not grow as tall as those on mull sites elsewhere, most of the tallest individuals are still 23 to 24 meters tall.

The mor of the Usambara Mountains in Tanzania and the Blue Mountains in Jamaica may be contrasted with the peat found on mountains in Borneo, the Solomon Islands, Malaya, and New Guinea.

Askew (1964) described the development of peat on ridge crests of a shale/sandstone formation under heavily mossed forest (almost certainly UPPER MONTANE rain forest *sensu* TABLE 1) at about 1800 to 2700 meters on Mt. Kinabalu in North Borneo. The soil surface and tree branches were said to be "completely mantled in a thick layer of moss." The peat is very dark reddish brown, about 40 cm. thick, and has a fine-sized granular structure. The "pH" is recorded as 2.3; this is a pH measurement made in KCl solution (G. P. Askew, pers. comm.). A pH_{H_2O} value of 3.4 is given by Burnham (1974). Beneath the peat is a markedly gleyed, eluviated horizon, but only at certain sites are iron pans present.

Of particular interest in the present context is the transition from peat and gleying at 1800 meters to fibrous mor and nongleyed podzols under much less mossy forests at 1500 meters. Askew (1964, p. 69) describes the transition as gradual — it corresponds with the transition from UPPER MONTANE rain forest to LOWER MONTANE rain forest ("SCLEROPHYLLOUS MOUNTAIN" forest). Askew also records a fascinating series of stages of increasing mor development with the increase in altitude. At about 1250 meters thin mor and micropodzols are found only on the gentler sloping sites of ridge crests, but with the increase in altitude the mor layers and eluviated horizons thicken and spread to steeper sites. The pH_{KCl} of the mor is 2.0 and that of the eluviated mineral horizon 2.8; the organic carbon content of the mor is 40 per cent, about the same as in the peat. Askew, following Mohr and Van Baren, attributes the greater development of mor to a direct effect of temperature on litter decomposition. We would challenge this view. Mor formation can occur without doubt at sea level (cf. Hardon, 1937; Klinge, 1965; and others), and it seems more likely to us that the effect of temperature is mediated through the plants; under the increasingly less favorable growing conditions (lower temperatures and more cloud), either they produce litter more and more completely determined as potential mor (e.g., through a higher content of polyphenols), or their mycorrhizas are increasingly strong competitors with the micro-organisms which might otherwise decompose the litter.

One curious feature of the zone of peat-forming forest is the occurrence of mull soils rather than mor soils on the slopes. The situation is markedly different in this respect from that described for parts of oceanic Britain (Crompton, 1952) and from that in the Solomon Islands.

Lee (1969) has described in some detail the soils of Kolombangara in the western Solomon Islands. On the summit slopes of Kolombangara (1550 meters) there occurs what is probably one of the most continuously fogged UPPER MONTANE rain forests in the world. The rainfall is estimated at about 3000 mm. and is rather evenly distributed through the year, but the consistent fog is probably of more importance in pedogenesis. The bryophytes completely cover the trunks and major branches to a height of at least 3 meters and exaggerate the apparent DBH by more than 20 per cent (P. J. G. & T. C. Whitmore, unpubl. obs., 1963; see also Whitmore, 1969). The bedrock is andesite. On the ridges above 1000 meters a very dusky red, very greasy, and very wet moss peat is found; the pH is 3.0–3.3 and the thickness generally 10 to 20 cm., reaching 40 cm. at the summit. At most sites there is under this peat an eluviated and gleyed horizon; near the summit a very thin iron pan is found beneath the eluviated layer. It is particularly interesting in the present context that the uppermost slope sites beneath the UPPER MONTANE rain forest on the ridges were described by Lee as having accumulations of mor rather than peat (5 to 9 cm. thick). The pH of the mor is given for one site as 3.25 and the loss-on-ignition is 82 to 95 per cent. The texture varies considerably, as one might expect of a mor/peat intergrade, at one site "fibrous," at another "greasy," and at a third "peaty." There does not appear to be any obvious eluviated layer below it, where the mineral soil has a pH of 3.5–5.0. Apart from this lack of obvious podzolization under the mor, the situation is clearly very much like that described from oceanic parts of Britain by Crompton (1952).

In Malaya most UPPER MONTANE rain forest is found growing on peat, although there are some sites where it is not found (Holttum, 1924; Whitmore, 1975). Whitmore and Burnham (1969) have given an elegant account of the transition on granite from yellow latosol supporting LOWLAND rain forest at 300 meters to a peat soil supporting UPPER MONTANE rain forest at 1500 to 1600 meters. The annual rainfall in the area which they describe is about 2500 mm. Although this is distinctly seasonal, it is believed that frequent fogging in the season with less rainfall ensures that the soil very rarely dries out. Bryophytes are frequent on the forest floor in the better lit sites, but they extend up the trunks generally only to about 1 meter and do not form as thick a cover as on Kolombangara. The peat covers all the ridge and plateau sites, often 20 to 50 cm. thick and sometimes 1 meter thick. It is black, massive, spongy, greasy, and lacking in pores. Beneath it there is a very wet eluviated layer (A_e) and beneath that an iron pan; very often the A_e layer is distinctly gleyed. The peaty podzol soils are thus very much like those described from Mt. Kinabalu and Kolombangara.

In the upper part of the Malayan LOWER MONTANE rain forest (above about 1200 meters), there is frequently a rather thinner surface accumulation of organic matter, termed "peaty" by Whitmore and Burnham but distinguished by them as dusky red rather than black, as friable and not greasy, and as having a considerable inorganic component. During a visit with Dr. T. C. Whitmore in 1970, one of us (P. J. G.) suggested that the deposit might better be described as a hydromor. We found at several sites in the Cameron Highlands a marked eluviated layer beneath but no obvious illuviated layer or gleying, much as in some of the iron podzols described by Kubiena (1953). The pH of the putative mor was found to be 3.6 by Whitmore and Burnham and that of the mineral soil below it 4.6. The putative mor is found on the slope soils at the same altitude as the peat on the ridges, so the position in this respect is more like that on Kolombangara than on Mt. Kinabalu. However, there is apparently a tendency toward deeper mor formation with increasing altitude on the ridges below the zone of peat-formation, much as on Mt. Kinabalu.

The first report of typical podzol-profiles in the mountains of Southeast Asia was that of Hardon (1936) from the Vogelkop Peninsula of northwestern New Guinea. At an altitude of 2000 to 2400 meters in the Mt. Koebré area at the south end of the Arfak mountains, under what we would call UPPER MONTANE rain forest (cf. Grubb & Stevens, in press), typical podzols develop over shales and sandstone. The annual rainfall is believed to be between 1500 and 2500 mm., and persistent fog is very frequent. On the summit the "raw humus" cover consists of 40 cm. of gray-brown spongy fibrous peat over 30 cm. of brown compacted peat. On the lower slopes, which have been much affected by man, the "raw humus" cover is only 20 to 25 cm. thick. It is not clear whether any areas carry well-defined mor as opposed to peat. Further east, in the main ranges of West Irian where the climate is similar, most "podsols" are said to have "moder" humus, while peat develops only in topographically suitable sites (Haantjens, Reynders, Mouthaan & Van Baren, 1967, pp. 36, 37). Even further east, in Papua-New Guinea, true peats appear to be rare in the Montane Zone (cf. Grubb, 1974).

The gradation between peat and mor is thus poorly documented for New Guinea, but a spectrum of humus types has been shown clearly to exist in the other three areas of Southeast Asia considered. The existence of this spectrum of types of humus accumulation must be taken into account when schemes are put forward to explain the mechanisms of accumulation.

SPECIES GROUPS AND LIMITING FACTORS

As a result of our floristic account, summarized in TABLES 2 and 3, we can isolate various groups of species and consider the factors most likely to be limiting their distribution.

First we have the species recorded only from low altitude LOWER MONTANE rain forest. The information available is least complete for these species, but since there appears to be a continuum of change in floristic composition with altitude in a single kind of topographic site (e.g., gullies in the Blue Mountains), it is suggested that some function of temperature is the effective factor limiting the upward spread of these species.

It is convenient to consider next three groups of species: (a) those exclusive to LOWER MONTANE (GULLY) forest at higher altitudes (e.g., *Boehmeria caudata*), (b) those much more frequent and much taller in such forest (*Solanum punctulatum* and other GULLY species in TABLE 2), and (c) those about as frequent in LOWER MONTANE (GULLY) forest at 1500 meters as on slopes and ridges but less tall in the latter situations and most markedly reduced in performance in MOR RIDGE forest (the "core" species of TABLE 2). For these three groups, presence and performance at their upper limit are strongly related to topography, and it seems most unlikely that temperature determines the upper limit. Neither air temperature nor leaf temperature seems to be responsible, since there is no evidence of the ridges or slopes being more subject to fog than the gullies. Wind is not involved, because wind-pruning, which is distinct when it occurs, was seen only at certain sites on the steep north-facing slopes from Portland Gap toward Blue Mountain Peak and on knife-edge ridges in HIGH ALTITUDE forest.

Shreve emphasized the favorable water supply in the gullies, and we accept that there is a more favorable supply than on ridges and slopes; however, we do not consider water supply to be a limiting factor for trees and shrubs on the slopes or ridges after the seedling stage. Furthermore, the characteristic GULLY species do not appear in the VERY WET RIDGE forest on Mt. Horeb, where instead we see different wetness indicators, such as *Cephaelis elata* and *Selaginella denudata*.

The penetration of lower altitude species to their highest limits in gullies is very commonly observed on tropical mountains. It is also seen in the North Temperate Zone, where it can be related, at least in some cases, to the incidence of flushed soils in the gullies and leached soils on the ridges (Gorham, 1953). More generally, many species in Europe are restricted to more fertile sites at the northernmost edge of their range (see, for example, McVean & Ratcliffe, 1962; Stalfelt, 1972), and many species can be established artificially if the soil is limed and N, P, and K are added (cf. Miles, 1974). Superficially, the situation in Jamaica appears to parallel this classical leaching situation — some species are confined to the flushed sites, others are much more frequent and taller on them, and yet others show a response in performance but not obviously in frequency.

One field observation strongly suggests a role for nutrient supply. On the slopes of John Crow Peak at about 1500 meters, below the limestone but above the last small gap in the ridge, the forest is much taller than the widely distributed WET SLOPE forest described above (p. 333) and buttresses 0.5 meters tall are common; the pH of the topsoil is 4.7 to 4.8. Unfortunately we have no information on the tree species present. The most obvious explanation for the occurrence of this forest is that it benefits in some way from the leaching of the limestone above it.

The foliar analyses for "core" species at different sites (TABLE 5) yield some evidence to support the hypothesis that nutrient supply is more favorable in gullies than on slopes and ridges with mull humus. K levels are higher in gully material of both *Alchornea* and *Clethra*, but there are no consistent differences in N or P. Tropical forest soils seem generally to differ from temperate forest soils in showing not only plentiful mineralization of nitrogen but also abundant production of nitrate at very acid sites (pH 4.0–4.5, see Cunningham, 1962; De Rham, 1971), and we should perhaps not expect a significant difference between GULLY and SLOPE soils in this respect. However, the MULL RIDGE soils are significantly more acid yet (pH 3.5–4.0), and apparently nothing is known of the mineralization characteristics of such soils. The lack of apparent difference in P status may result from a very poor supply at all sites (owing to the various soil parent materials all being deficient in that element), or it may result from the mycorrhizas of the mature trees being so effective in uptake that any soil differences are hidden. Clearly much more research is needed on this problem. This should involve more extensive foliar analyses, tests on the mineralization of nitrogen in the soil, bioassays of the various soils with seedlings, and fertilizer experiments with adult plants *in situ*. Some work along these lines has been carried out by one of us (E. V. J. T.) and, after analysis, will be reported elsewhere.

The idea that mineral supply might limit the distribution of forest types on wet tropical mountains was put forward before (Grubb, 1971) as a possible explanation of the "Massenerhebung" effect, the occurrence of given forest types at lower altitudes on smaller, outlying mountains. At that time the implication was that the species of LOWLAND, LOWER MONTANE, and UPPER MONTANE forests are successively better adapted to poor mineral supply. Alternative partial explanations of the "Massenerhebung" effect have since been put forward (Grubb, 1974; Grubb & Stevens, in press). The present suggestion does not imply that LOWLAND, LOWER MONTANE, and UPPER MONTANE species necessarily have different mineral requirements according to some absolute standard, but that at the upper limits of their distributions there may be an interaction between mineral supply and climatic factors such that mineral supply (determined by topography) can become the chief limiting factor.

The next species group to be considered is that confined to MULL RIDGE and WET SLOPE forests (TABLE 2). By analogy with what is established for vegetation in other parts of the world, we suggest that some aspect of competition keeps several of these species out of the gullies, where they would probably grow very well if all other plants were removed. Their upper limit is not obviously related to topography, and some function of temperature is likely to be limiting — possibly leaf temperature rather than air temperature, since fog is definitely more frequent in the HIGH ALTITUDE forest from which they are absent. The same temperature limitation applies to three of the six "core" species and many of the DRY SLOPE species (TABLE 2).

Of particular interest is the failure of the MULL RIDGE and WET SLOPE species (TABLE 2) on the mor humus soils and the distinctly poorer performance of the "core" and MOR RIDGE species there. Some idea of the complexity of the chemical factors likely to be limiting growth on the mor humus can be gained by reviewing the work done on growth of crops on very acid lowland peat in Indonesia and Malaya. As a general rule it is necessary not only to add large amounts of lime to raise the pH to a value greater than 4.5, but also to add nitrogen, phosphorus, potassium, and copper (Polak, 1948). A few crops will grow in unlimed peat, e.g., pineapple, which responds to N, K, and Cu (Allen & Coulter, 1957; Parbery & Venkatachalam, 1964), and tapioca, which responds to N, P, and S, but not to K (Lim, Chin, & Bolle-Jones, 1973). There is also variety in the responses of crops that grow only after liming. Wet padi has an overwhelming requirement for P (Allen & Coulter, 1957); sweet potatoes need additional N and K, but do not respond when P alone is added (Chew, 1970); and tomatoes need not only N, P, and K, but also Bo (Joseph, Serrat, & Williams, 1970).

By analogy with the above results, we may suggest that the failure of MULL RIDGE and WET SLOPE species on mor results from the low pH as such. The fact that the pH is so low (< 3.5) suggests that the exchange sites are mostly saturated with hydrogen, since aluminum, when present, is an effective buffer to pH ca. 4.2 (cf. Jackson, 1963). Thus the undoubted toxicity of aluminum ions for many plants invading soils of pH < 4.8 (cf. Grime & Hodgson, 1969) is unlikely to be relevant here. Rather, the high concentrations of hydrogen ions are likely to be toxic as such; many plant cells are damaged in the laboratory at pH < 4 and are unable to absorb mineral nutrients (Arnon & Johnson, 1942). Clearly, experiments with seedlings of MULL RIDGE and WET SLOPE species are needed. Even if the pH were raised to the range of 3.5–4.0, that found in the MULL RIDGE soils, there might prove to be a variety of nutrient deficiencies, depending on the species tested.

We have, from foliar analysis, some evidence of the mineral nutrients possibly limiting growth of the "core" and MOR RIDGE species, which can by definition tolerate the extraordinarily high hydrogen ion concentrations of the mor humus. The foliar analyses of *Alchornea* and *Clethra* (TABLE 5) show very low levels of K, and the small amount of K circulating in the forest has been amply confirmed by one of us (E. V. J. T.) through other lines of investigation. Effective limitation of plant growth by shortage of potassium on acid peats in the Northern Hemisphere has been reported by Heikurainen (1964), Tamm (1964), and Goodman and Perkins (1968a, b), but it seems that no case of parallel limitation on mor has been reported. The failure of uptake of K in *Alchornea* and *Clethra* may be a result of hydrogen ion toxicity. It is notable that foliar Na levels are actually higher and, unless the exchangeable Na in the soil is unusually high, this suggests that the reduced K uptake is not explicable simply in terms of a low "K potential," i.e. low ratio of the chemical activity of K to the chemical activity of other cations. Such an effect would apply to Na as well as to K. It is perhaps surprising that the foliar levels of Ca and Mg are not particularly low in the *Alchornea* and *Clethra* from mor humus, but it was similarly found that the foliar levels of these elements are no lower in the trees of UPPER MONTANE rain forest on very acid peat in Malaya than in trees of LOWLAND rain forest on a deep latosol (Grubb, 1974).

There is no evidence for a poorer supply of P for either species analyzed, but there is some indication of a lower level of N in *Alchornea*. In the Temperate Zones one usually finds a shortage of mineralized nitrogen, especially nitrate, in mor humus (see results from widely separated areas reported by Pearsall, 1952; Handley, 1954; Zöttl, 1960; Ellenberg, 1964; Lemée, 1967; Lamb, 1975), but there are records of appreciable nitrification, at least at certain times of year, in various types of mor at pH 2.6–4.0 (Romell & Heiberg, 1931), in peat at pH < 4 (Klötzli, 1969), and in certain unusually acid mulls of pH 3.7–4.0 (Davy & Taylor, 1974; Runge, 1974). Samples of mor and acid peat from the lowland tropics contain appreciable amounts of ammonium, but generally low to very low levels of nitrate (Ellenberg, 1954; Richards, 1965). However, relatively high levels of nitrate were recorded from lowland peat in Malaya by Parbery and Venkatachalam (1964). Unfortunately it appears that no experiments on mineralization of nitrogen in such soils in the laboratory have been reported. While the soils will possibly nitrify readily, all of the nitrate may be taken up immediately by the plants or be very rapidly leached.

In some highly organic soils Cu and Zn can be so effectively adsorbed or chelated by the soil that they become limiting factors for plant growth (Polak, 1948; Allen & Coulter, 1957; Wallace, 1961; Kanapathy, 1972; Stalfelt, 1972); the analyses of *Alchornea* and *Clethra*, however, yield no evidence for their implication in the present situation. Possibly Bo is in short supply (cf. Joseph *et al.*, 1970).

At present we have no evidence that any chemical factor other than potassium shortage is implicated in the poor growth of the plants on the mor. However, it is likely that the very high concentration of hydrogen ions has a generalized effect in reducing the performance of even the plants that can tolerate it sufficiently well enough to survive. Much more analytical and experimental work is needed, and there may well be appreciable differences between species of forest trees, as there are between crop plants.

The HIGH ALTITUDE species are few in number (cf. TABLE 2). The more or less strict confinement of most of them to high altitude sites strongly suggests that downward penetration is controlled primarily by temperature, although a requirement for continuously favorable water relations may possibly be involved.

The DRY SLOPE species seem to be absent from the WET SLOPE and MULL RIDGE forests, mainly as a result of competition; the few individuals of several DRY SLOPE species that are present appear to be very well grown. They do not seem to need drier conditions to grow well. This interpretation is supported by the occurrence of several DRY SLOPE species in HIGH ALTITUDE forest (cf. p. 340), where there is certainly more rainfall and more fog, but fewer species and possibly less "competition pressure." The most extreme example of a "competition-intolerant" species is *Bocconia frutescens*, whose major natural habitats are probably landslips and river gravels. It was seen on one fairly fresh landslip at 1470 meters with *Clibadium terebinthinaceum*, *Hedyosmum nutans*, *Trema floridanum*, and the rare *Tovaria diffusa*, as well as with *Lobelia assurgens*, *L. caudata*, and *Pityrogramma tartarea*. *Hedyosmum nutans* also invades DRY SLOPE and MULL RIDGE forest occasionally. Care must be exercised in discussing "competition intolerance" in species like *Bocconia frutescens*. It may easily outgrow plants of other species of the same age, but it is a poor competitor over its whole life cycle, presumably dying young and invading established vegetation only with difficulty.

In summary, it is clear that the montane forests of Jamaica show great variety within a small area and provide fine opportunities for the investigation of critical factors limiting the distribution of particular species groups. More sophisticated observations will help us formulate the hypotheses more clearly, but the prime need now is for experimental studies.

ACKNOWLEDGMENTS

The work carried out in Jamaica by E. V. J. T. was wholly financed by a Science Research Council Overseas Research Studentship. The visit by P. J. G. was financed by the University of Cambridge Travel Fund and the Brooks Fund of the Cambridge Botany School.

We owe an outstanding debt to Dr. C. D. Adams, who identified almost all of our angiosperm material, read the manuscript most critically, and contributed many ideas. Dr. Adams and Prof. G. H. Sidrak kindly supervised the work of E. V. J. T. during the period from December, 1973, to March, 1975. Mr. G. R. Proctor identified all of our ferns and some of the Rubiaceae. The Director of the Public Gardens generously allowed the Cinchona Botanic Garden House to be used as a routine base for field work. Dr. H. Waters provided frequent assistance with photographic work. Rosamund Tanner helped with field work and laboratory work from June to September, 1974. Messrs. J. B. Dickie and G. Frampton provided invaluable support during the field work in the John Crow Mountains. Drs. P. F. Stevens and T. C. Whitmore provided constructive criticism of the manuscript.

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