FLORA AND VEGETATION OF MADAGASCAR

by

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Introduction

Madagascar, which covers an area of about 590,000 km² (230,000 square miles), is about 1,500 km (940 miles) long and extends from 11°57′ to 25°32′ latitude south, forming what is really a small continent. The diversity of types of climate and edaphic conditions means that there are very varied ecological environments and practically the only type missing is very high mountains, as the highest point on the island, the Tsaratanana mountain mass, is only 2,876 metres above sea level.

The relief and the winds prevailing on the island determine the distribution of the major plant formations: the narrow coastal plains of the east and the steep rise of the Pre-Cambrian basement, the high plateaux, constantly exposed to the trade winds, receive abundant rainfall (more than 1,500 mm). The dense rain forest still occupies a large area there. Towards the west, from an average height of 800 metres, the land slopes more gradually towards the coastal plains. Here, the trade winds bring almost no rain and gradually become hot and dry, increasing the aridity of these regions. They are, however, subject to the monsoon regime during the summer in the southern hemisphere, an influence that dwindles sharply towards the south. Consequently, there is a double rainfall gradient, as the quantity of rain and length of the rainy season decline from east to west on the one hand, and from north to south in the western regions on the other. The extreme south of Madagascar receives only very irregular rainfall amounting to 300 mm or less, and the dry season lasts at least 10 months.

This double gradient obviously results in the existence of increasingly xerophilous types of vegetation: dense dry forests, more or less deciduous or sclerophyllous, and finally with a bush with *Euphorbia* and *Didiereaceae* in the South.

In the west and south, the climatic drought is often intensified by the edaphic conditions, sandy or limestone soils on which the vegetation exhibits xeromorphic adaptations that are sometimes spectacular.

Although these forest types, with the distribution already mentioned, represent climax forms of the vegetation, they often only occupy limited areas, sometimes only isolated patches.

Over considerable areas, these forests have been replaced and as a result of brush fires and human interference almost entirely graminaceous formations are maintained. The forests, cleared for agricultural purposes

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and devastated by fire, are giving way to more or less deteriorated secondary formations, the '*savoka*'.

This state of affairs is all the more regrettable in view of the fact that Madagascar, with its variety of ecological environments and its ancient geographical isolation, has a flora of an exceptional richness (about 10,000 species of *Angiosperms*) and with a very high degree of specific endemism, often exceeding 80 % in the case of groups belonging to the original vegetation of the island.

It is therefore to be expected that the Malagasy flora and vegetation will be an exceptionally interesting subject of study from all aspects, floristic, biogeographical, ecological, phyto-sociological, etc.

Much research has already been done and mention should be made of H. PERRIER DE LA BATHIE and H. HUMBERT, who have undoubtedly made the largest contribution towards increasing our knowledge. A map of the plant cover and ecological conditions on a scale of 1:1,000,000 has been published[1] and of the 200 or so families of vascular plants found in Madagascar, more than 130 have already been dealt with in 'Flore de Madagascar et des Comores', published by the Museum d'Histoire Naturelle, Paris, France.

The Ecological Environment

Climate, soils and geology have all been studied elsewhere and only the data required for an understanding of the plant distribution will be found here.

BIOCLIMATES AND PHYTO-GEOGRAPHICAL DIVISIONS

Although the extreme south of Madagascar is below the Tropic of Capricorn, the Malagasy climate is entirely tropical, mainly due to the fact that the rain falls almost exclusively in the hottest season.

The temperature is fairly uniform throughout the island in the low-altitude coastal regions: annual mean from 23 to 27°, average for the coldest month 20 to 23°, annual range varying from 3° in the north of the island to 7.5° in the dry southern regions. On the other hand, the temperature variations caused by altitude are large, the average lapse-rate being about 0.6° for every 100 m change in level. In some of the regions of the high plateaux, at an altitude of about 1,000 m, it freezes for a few days every year, and the cold may be considered an important ecological factor for the vegetation, even though it comes at a time when the plant life is resting because of the drought.

We have already mentioned the main factors responsible for the rainfall distribution. The action of the trade winds on the east coast gives a

1 HUMBERT and COURS DARNE, 1965.

rainfall exceeding 1,500 mm and possibly exceeding 3 m, without any ecologically dry month, and with high temperatures; these features indicate a climate of the sub-equatorial type.

The tropical nature emerges with the appearance of a dry season, the length of which increases towards the west and towards the south.

On the eastern slope of the plateaux, the rainfall still exceeds 1,500 mm with a dry season of 1 to 4 months and a main temperature in the coldest month of between 10 and 15 °C.

On the western slopes, the dry season is longer, up to 5 or 6 months, with rainfall that may be less than 1,500 mm. However, it should be noted that the saturation deficit is particularly low in the dry season because of the frequency of fogs caused by the dominant action of the trade winds at that time.

On the western plains, the dry season lasts 7 to 8 months, at least in the southernmost regions, with rainfall of about 1,500 mm in the north but only 500 to 1,000 mm further south.

Finally, the very dry climates in the extreme south are difficult to define precisely, partly because of the lack of data but mainly because of the extreme irregularity of the rainfall, always stormy and very localised. Some regions may not have any precipitation for twelve to eighteen months, which is obviously a predominant limiting factor.

Also, very little information is available on the climate of the regions more than 2,000 metres in altitude.

Some rainfall-temperature diagrams are given below as an example (Figure 1).

The diagram for Maroantsetra, on the eastern coast, clearly shows the absence of a dry season, which is first seen at Moramanga, on the first foothills of the plateaux. It becomes longer from Tananarive to Morondava (west coast) and then Beloha, in the south, and at Faux-Cap, in the extreme south, the whole year is virtually dry.

The bioclimates of Madagascar can be established by taking account of a number of factors that appear determinant: overall rainfall, number of dry months, mean temperature of the coldest month. These can be seen in the legend to the following vegetation map of Madagascar. We give here a simplified outline of the bioclimatic map, prepared solely on the basis of rainfall quantity and distribution (except for the high altitude areas). This map could be made more informative by inclusion of the temperature factor (Figure 2).

These bioclimatic distinctions fit in well with the conventional phytogeographical divisions of the island by H. Humbert. Based mainly on climatic factors, they correspond to a plant community of the climax type.

These divisions are as follows, and they are illustrated by the map in Figure 3 (Humbert, 1954, 1960).

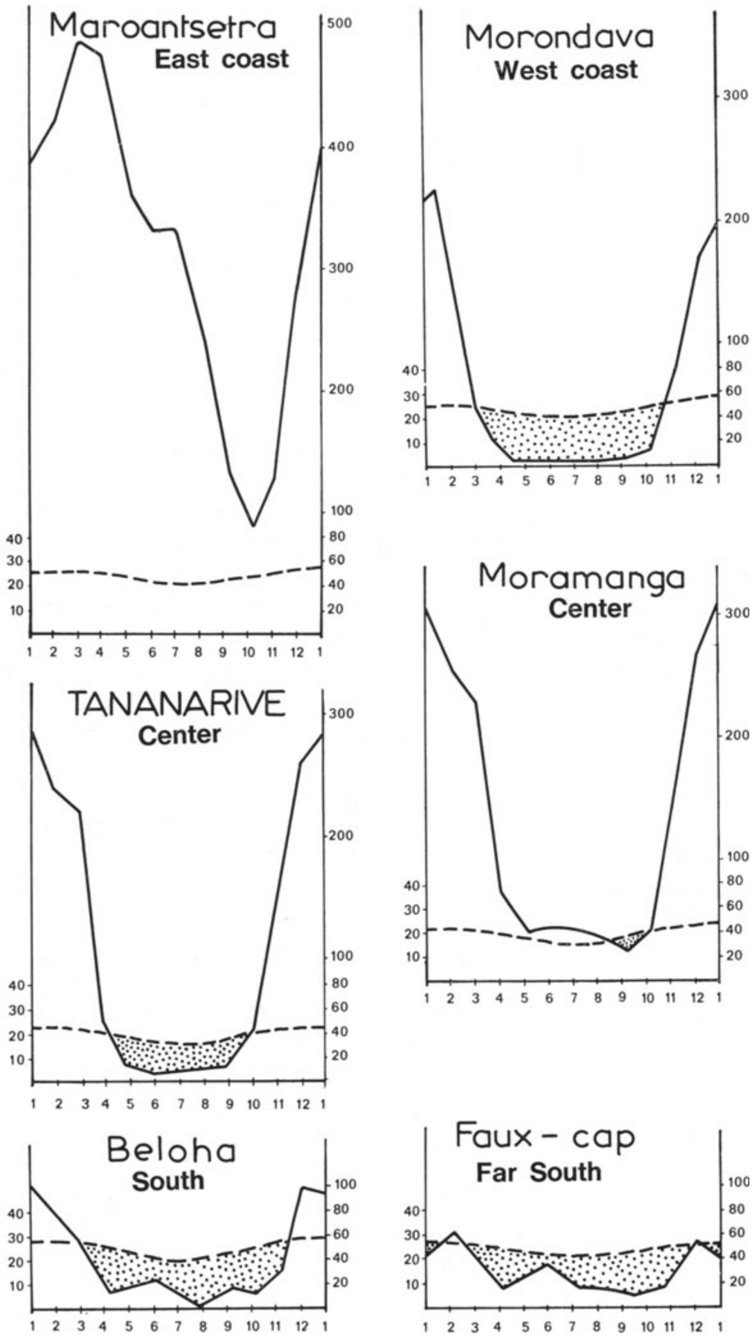

Fig. 1. Rainfall-temperature diagrams.

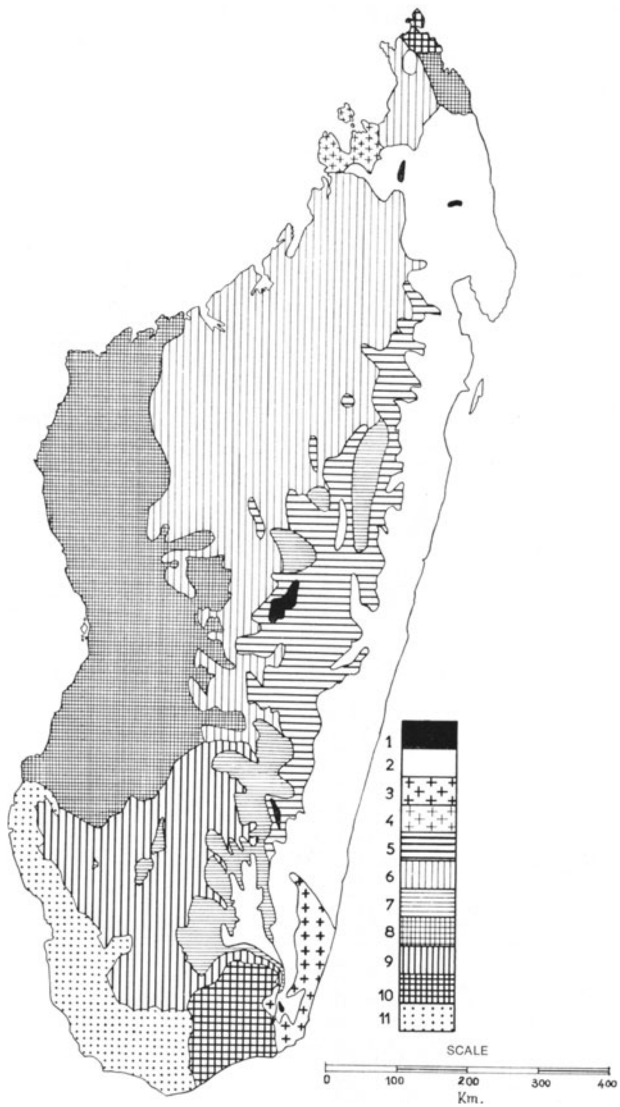

Fig. 2. Bioclimates of Madagascar (Simplified outline according to HUMBERT and COURS DARNE 1965).

1. High-altitude bioclimates. Rainfall exceeding 2,000 mm. No dry months. t (temperature of coldest month) between 0 and 10 °C.
2. Rainfall exceeding 2,000 mm. No dry months. t almost always above 15°.
3. Rainfall between 1,500 and 2,000 mm. No dry months. t exceeding 15°.
4. Rainfall exceeding 2,000 mm. 3–4 months dry season. t above 20°.
5. Rainfall between 1,500 and 2,000 mm. From 1 to 4 months dry season. t between 10 and 15°.
6. Rainfall between 1,500 and 2,000 mm. 5 to 6 months dry season. t above 20°.
7. Rainfall between 1,000 and 1,500 mm. 5 to 6 months dry season. t between 10 and 20°.
8. Rainfall between 1,000 and 1,500 mm. 7 to 8 months dry season. t above 20°.
9. Rainfall between 600 and 1,000 mm. 7 to 8 months dry season. t above 15°.
10. Rainfall between 400 and 600 mm. 7 to 8 months dry season. t between 15 and 20°.
11. Rainfall below 400 mm. 9 to 11 months dry season. t between 15 and 20°.

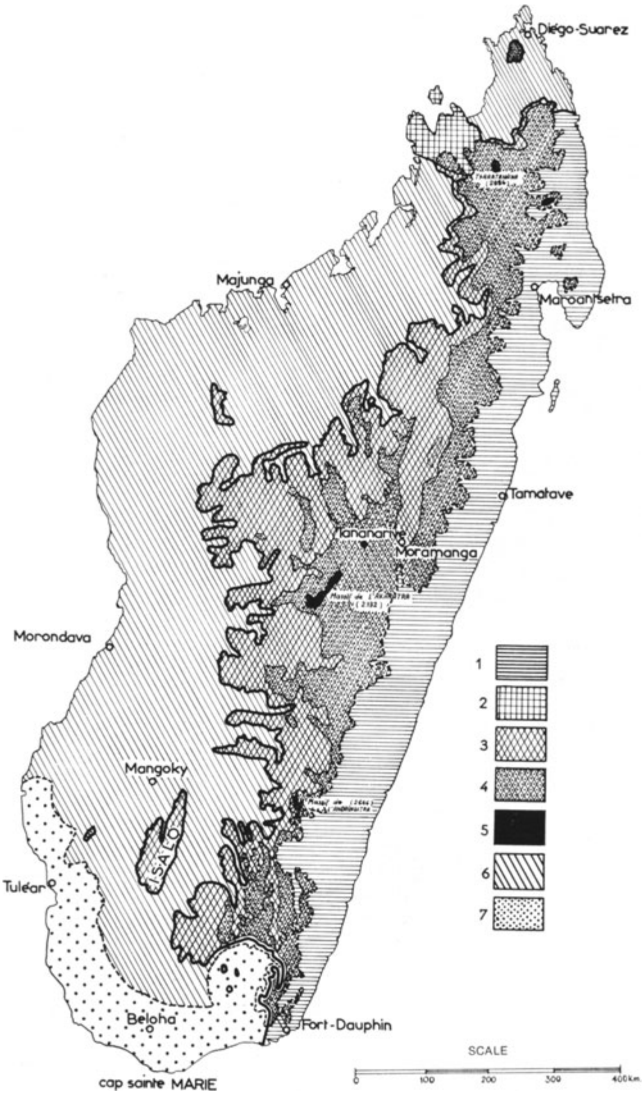

Fig. 3. Madagascar. Phytogeographical divisions (according to HUMBERT) 1955. 1. East area; 2. Sambirano area; 3. Centre area (western slopes); 4. Centre area; 5. Area of the high mountains; 6. West area; 7. South area.

Madagascar is divided into two phyto-geographical Regions that are very distinct, both in their vegetation and in their climate.

These are the eastern Malagasy Region and the western Malagasy Region, each being divided into a number of Domains and Sectors.

Without going into detail, we will merely point out the main characteristics of these sub-divisions.

1. Eastern Malagasy Region

East Domain: Eastern coast up to an altitude of 800 m; annual rainfall from 2 to 4 metres, three-fifths of it falling in the hot season, humidity and temperature always high, no dry season. The climax is the dense rainforest.

Sambirano Domain: This is an extension of the above area running as far as the west coast. Little difference in the climate and types of vegetation.

Centre Domain: This includes the central plateau region, the mountains and the west and east slopes above an average height of 800 m. The rainfall is about 1,500 mm, falling almost entirely in the hot season. The dry season may extend to several months, but it is very much moderated by fog and condensation which greatly reduce its aridity.

Towards the east, where the trade winds still make their effect clearly felt, the climax is once again a rainforest, but lower and with a large number of epiphytes. Towards the west, where the trade winds are hotter and drier, the climax is only a low forest of an accentuated sclerophyllous nature.

The High Mountains Domain, above 2,000 m, probably receives large quantities of precipitation. But the vegetation is exposed to wide variations in the degree of humidity, insolation and temperature. The climax is variable: low rain-forest with an abundance of epiphytes and grassy undergrowth, sclerophyllous forest with trees laden with mosses and lichens, and wooded country characterised by bushes of ericoid appearance.

The idea of a phytogeographical Domain restricted to a single altitude is nevertheless open to debate. Even though there are clear physiognomical and biological similarities between the plant formations of the various massifs, the floral differences are quite clear-cut, and the altitude-conditioned formations might preferably be considered to belong to specific levels of the phyto-geographical units in which these massifs are situated.

2. The western Malagasy Region

The West Domain, below 800 m approximately. The rainfall decreases gradually from north to south (from 1,500 to 500 mm approximately) and the dry season, with a high atmospheric aridity, lasts 6 to 8 months. The climax consists of varied types of dense forests, dry and deciduous. The extreme north of Madagascar, beyond Sambirano, belongs to this Domain.

The South Domain is marked by an increasing aridity: rainfall of about

Plate 1. Forest with mosses and herbaceous undergrowth. Andringitra massif (altitude: about 2,000 m.).

300 to 500 mm, very irregular, long, often extremely long, periods of drought. The climax consists of deciduous forest, wooded country formations or dense bush, with numerous highly adapted aphyllous, prickly or succulent species.

SOILS

The Malagasy soils are extremely varied because of the parent rock and the climatic influences that governed pedogenesis: ferralitic soils in the east in particular, tropical ferruginous soils or lithosols on various rocks in the west. Their influence on the type of vegetation is far from negligible, so that although the conventional concept of climatic climax prevails generally, edaphic climaxes cannot be ignored.

In the west especially, where the water supply is often the main limiting factor for the vegetation, the soil may have a decisive effect on the nature of the climax. The most striking example is the vegetation on the mountains or limestone plateaux of the Karst type, which form a very arid environment from the edaphic aspect: the vegetation is then strongly oriented towards extremely accentuated forms of xerophytic adaptation.

THE INFLUENCE OF MAN

It is not possible to discuss the Malagasy vegetation without devoting considerable time to the direct or indirect action exerted by man. The climax forest vegetation today only occupies limited areas, and has often been replaced by open formations, wholly herbaceous or with sparse shrubs: man is certainly responsible for at least a very large part of this.

Many authors have tried to show 'how the original indigenous Malagasy vegetation has disappeared and how, from the day man set foot on the island, the forest that completely covered it has gradually given way to grassland, savanna and savoka, various types of a substitute vegetation that now occupies almost nine-tenths of the area of the island' (HUMBERT, 1927).

The map in Figure 4 shows the extent of the herbaceous formations compared to the forest.

All these herbaceous areas are burnt almost every year. Extensive stock raising is important in Madagascar with more than 10 million heads of zebus. As grass productivity is much higher in the rainy season than in the dry season, the area grazed during the rains is small in relation to that required in the dry season. The only way the stock farmer can get rid of the uneaten grass on the pasture lands is by burning it. He cannot control the fire, which spreads well beyond the areas that really need burning.

The fire attacks the edges of the forest, so that the still wooded areas are being regularly depleted. Man is also destroying the forest to grow

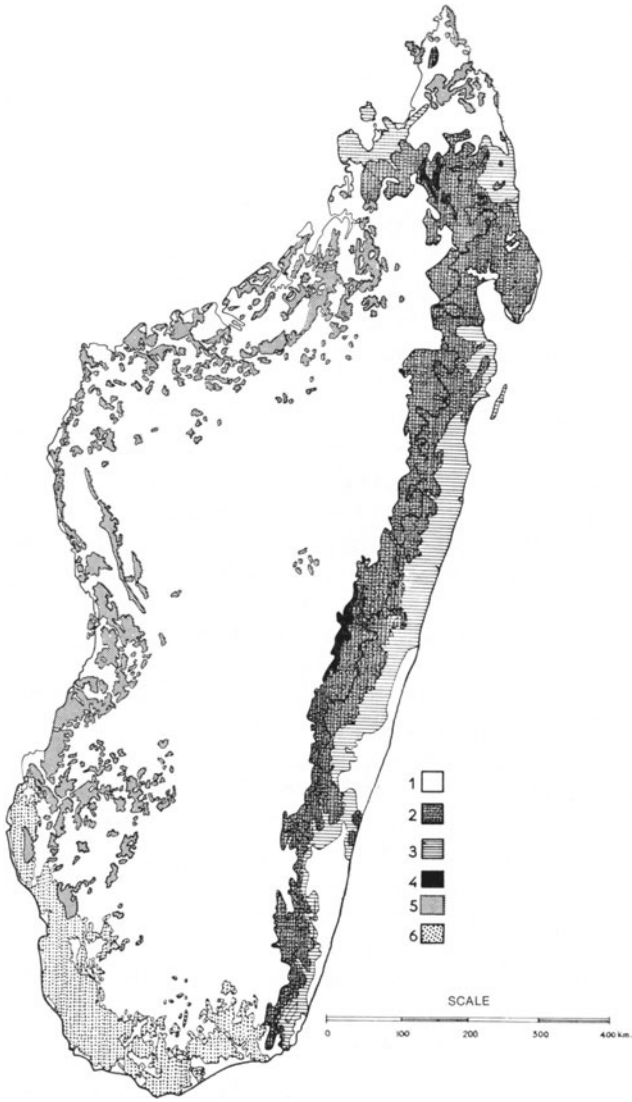

Fig. 4. The forest formations in Madagascar (according to HUMBERT and COURS DARNE) 1965.
1. Savanna and steppes; 2. Dense rain forest; 3. Savoka; 4. Mountain forest; 5. Sclerophyllous and deciduous forest; 6. Xerophyllous thickets.

food crops. This is the practice of *Tavy:* the forest is partly cut down and burned. The crops (rice, maize, manioc, etc.) are planted and after the harvest the fallow land is invaded by heliophilous, herbaceous and then ligneous plants. Gradually the secondary forest, the savoka, becomes established and after ten years or so it may be used once again. But each time it is cleared, the forest vegetation becomes weaker and eventually an essentially graminaceous formation will occupy the land. Considerable areas are being destroyed in this way.

This rapid crop rotation is essential because of the fragility, not to say poverty, of the forest soils. The heat and humidity conditions prevailing in the undergrowth are very favourable to an intense microbial life. Consequently, the organic debris falling to the ground (leaves, dead branches), instead of being slowly transformed into humus, is rapidly decomposed by the micro-organisms to the mineral stage. Thus the fertilising elements are made available to the roots very rapidly. The luxuriance of the tropical forest is due to a very rapid turnover of a limited nutritive stock rather than to greater richness of the soil. When the clearing of the forest interrupts this cycle, the fertilising elements are soon washed away by the rain or removed with the harvest and the soil very rapidly becomes impoverished.

This itinerant agriculture could only be stabilised by applications of manure and mineral fertilisers that are an impracticable proposition in the present economic situation.

There is no doubt at all that at the present time man is contributing to the recession of the forest and the establishment and maintenance of large areas of herbaceous formations.

Practically all authors consider man to bear the full responsibility for the disappearance of the forest in Madagascar. Can this theory be unreservedly accepted? We shall revert to this point after a study of the vegetation has enabled us to demonstrate a number of facts that have perhaps not always been given sufficient attention in the research done to date.

Flora and Vegetation

The vegetation of any country, and more particularly in Madagascar, is the result of a whole collection of ecological factors, as we have seen.

The origin of the flora is, however, much more remote. An existing flora is the culmination of all the preceding floras. This evolution is controlled by all the genetic phenomena of speciation: mutation, hybridisation, etc. and also by all the climatic and geographical vicissitudes undergone by the region concerned. Madagascar, a very large island, with varied ecological conditions, geographically isolated for a very long time and having enjoyed relative climatic stability, is therefore of exceptional interest.

THE FLORA

We have already mentioned the very great richness of the Madagascan flora and its high degree of endemism. More should be said about this.

1. The facts

Our existing knowledge of the Madagascan flora gives us a fairly accurate idea of its endemism and its affinities (H. Perrier de la Bathie, 1936; H. Humbert, 1959). The figures quoted below are taken from these two authors. Instead of considering this flora as a whole, it is more interesting to draw a number of distinctions. First between the eastern and western Regions, with their very different ecological conditions, and considering biological conditions and plant formations.

The eastern Region, with about 500 genera and 5,500 species of its own, is much richer than the western Region, with only 200 genera and 1,800 species. Some 600 species are common to the two Regions. However, endemism is much more pronounced in the western Region (38 % generic endemism and 89 % specific endemism) than in the eastern Region (22 % generic endemism and 82 % specific endemism). Among the common species, there are 9 % endemic genera and 47 % endemic species. These figures only cover indigenous species and not plants introduced into the island. The latter have completely different biological characteristics. Many are annuals (more than 50 %, compared to 3 % in the indigenous flora) and they are mainly herbaceous plants (more than five-sixths). Some have been deliberately introduced by man and of the others, most have an effective dissemination capacity, adhesive fruits, light seeds, etc. This flora is found almost exclusively in environments modified by man and has not penetrated into the original forest formations.

The characteristics of the original flora are very different: more than 80 % of the species are woodland plants and endemism is most marked in the forest formations and among the woody plants:

Percentage of specific endemism in the different formations:

Littoral	21 %
Marsh	56 %
Rocky outcrops	82 %
Forest or bush formations	89 %

Percentage of specific endemism in the different biological types:

Annual grasses	58 %
Perennial grasses	85 %
Shrubs	94 %
Trees	94 %

Resuming the study of regional endemism, we find that the most marked originality is in the South Domain (generic and specific endemism 48 and 95 %), followed by the West (41 and 90 %), then by the East (37 and 90 %) and lastly by the Sambirano (23 and 89 %) and Centre (21 and 89 %) Domains.

There are several families endemic to the island, the most remarkable being the *Didiereaceae*, found in the dry southern regions.

As Madagascar is an island, it is interesting to consider the possible origins and affinities of its flora: did it evolve where it is by diversification from a very ancient foundation? If not, what was the possible extent of introductions from adjacent territories?

A first important fact to be noted is the antiquity of the Malagasy flora. In the Cretaceous, when the Angiosperms spread so widely, tropical conditions prevailed over almost the entire island. The families existing at this time were therefore gradually driven back into the regions that are hot at the present time, following climatic incidents occurring during the Tertiary and Quaternary periods.

Most of these ancient families are today represented in Madagascar in the form of a pantropical element, accounting for more than 40 % of the flora, which seems to show that the climatic conditions have been subject to little variation there since the most ancient times.

However, there are undoubtedly close relationships with the flora of other continents and these indicate that there may have been continental links between Madagascar and these regions.

Eliminating species that may have been transported recently, it is possible to demonstrate affinities with Africa (excluding southern Africa) bearing on about 27 % of the flora. The affinities between many African and Malagasy species appear to show that this African influence is relatively recent.

The eastern element, with Indo-Malaysian affinities, represents only 7 % of the flora. In addition, as these affinities are found mainly at genera level, any eastern connections are certainly older than the links with Africa.

The southern hemisphere affinities (South Africa, South America, Oceania) are even less numerous. The few species and the common genera usually have marked archaic characteristics. They are distributed throughout the island, whereas the eastern element is found mainly on the eastern slopes and the African element on the west side of Madagascar It may therefore be concluded that this southern flora is extremely ancient.

2. The explanations

The geological history of Madagascar and details of the biology of certain plants can throw some light on the facts set out above.

Geological history of Madagascar

We have already mentioned the possibility of land links between Madagascar and other continents. There are geological arguments that might confirm these hypotheses, although in Madagascar palaeobotanical information is very rare (Bourreau, 1949).

It is thought that the Mozambique Channel first opened up in the

Permian period, but it may have been affected subsequently by numerous variations, especially in the Cretaceous period, as a result of the huge fractures and volcanic eruptions that took place at that time. The opening up of this channel was not therefore final at the very first, and the general regressive nature of the Upper Miocene could indicate that a continental link still existed between Madagascar and Africa at that time. Various arguments, based in particular on the existence of the dwarf hippopotamus in Africa and Madagascar, indicate that there were discontinuous links in the form of lagoons and strings of islands at the end of the Pliocene period. After this, Madagascar's isolation became final.

Only the extinct floras of the Primary and Triassic periods have left interesting fossils: 'Gondwanaland' flora of the Permian and Lower Trias times, with *Gangamopteris*, *Glossopteris*, *Ginkgophyllum*, *Voltzia*, etc. and silicified trunks of conifers from Triassic time, *Araucarioxylon*, *Cedroxylon*, etc.

The history of Madagascar can therefore be divided into three periods:

1. Ancient period, prior to Upper Cretaceous, with extensive continental links to the southern continent and probably other tropical continents. The establishment of the basic elements of the flora, especially those with pantropical, southern and oriental affinities, would date from this time.

2. In the Tertiary period, the links may have continued, in a more or less permanent fashion, with Africa only, which accounts for the importance of the African floristic affinities. Some pantropical elements may also have been able to reach Madagascar at that time through Africa.

3. Finally, a long period of isolation dating from the Pliocene. The flora was then enriched by new elements brought either from the East by the ocean currents or from Africa by the winds and migrating birds. More recently, man has been responsible, deliberately or accidentally, for a large number of introductions.

Biological arguments

It should first be noted that the same significance cannot always be attributed to an endemic species: some species may be considered as relics of ancient floras that are largely extinct. They have long since lost any possibility of evolving and are today isolated in the modern flora. Systematic relations can sometimes be established with very widely distributed groups, which show how very old they are. These are *palaeo-endemic* species.

The *neoendemic* species are linked to ancient types by continuous series of intermediaries, showing the maintenance of the capacity to evolve in these groups. This capacity may have been 'reactivated' in a more or less recent age as a result of climatic or geological accidents that suddenly modify the environmental conditions. Microendemism, very marked in some Malagasy genera represented by species that are strictly limited to one mountain mass or another, indicates that the differentiation of new species is continuing today: some species of *Helichrysum*, *Senecio*, Cyperaceae, etc., although they have easily-transported seeds, are limited to very small areas, which clearly demonstrates their recent appearance.

We have already mentioned the existence of certain floristic affinities with other regions of the world: Africa (mountain ranges of the East and Southern Africa in particular), Indo-Malaysia, etc. Do these affinities result from ancient continental links, or are they due to the transport of diaspores by currents, winds or birds? Have the endemic species emerged merely from the transformation of an ancient flora in study or do they result from the differentiation of species introduced more or less recently?

Both hypothesis are probable: species introduced very recently by man (*Pavonia*, *Sida*, *Cyperus*, etc.) have already given rise to a number of endemic species or varieties. On the other hand, plants with heavy diaspores that lose their germinating capacity very rapidly and are very demanding ecologically were only able to move over land, and very slowly. Many Malagasy species belong to genera or families that were already represented in the Cretaceous floras. These floras, of a markedly tropical nature, at that time occupied the land up to high latitudes, whence they have since disappeared as a consequence of climatic upheavals. This is a reliable indication of the ancient nature of the Malagasy flora, which has been able to continue its existence because of climatic conditions that have varied little over the ages. And the existence in Madagascar, among these ancient species, of plants with non-transportable diaspores implies the existence of extensive continental links in these ancient times.

We must not rule out the possibility of transport by natural agents other than man, although the importance of this factor has often been exaggerated.

Transport by sea, on the currents of the Indian Ocean, is certain. The human population of Madagascar also arrived by this route, bringing with it numerous cultivated plants, including rice.

Some introductions are recent: for example, *Triumfetta procumbens*, establishment of which was noted on the east coast in about 1920. Littoral species have remaind identical to what they are in their country of origin: *Casuarina equisetifolia*, *Heritiera littoralis*, for example, whose fruits are dispersed by sea. In other cases, possibly indicative of more ancient introduction, the littoral species has given rise to a number of endemic plants more or less widely distributed throughout the island.

The *Barringtonia* genus, for example, alongside two species of oriental origin, is also represented by an endemic species close to one of them. *Calophyllum inophyllum*, an introduced littoral species, has given rise to four endemic species. There are also littoral species with affinities with plants in India or Malaysia, which are today endemic to Madagascar, while the introduced foreign species has disappeared: *Cycas thouarsii*, *Nepenthes madagascariensis*, for example. In such cases, it is permissible to wonder whether transport by sea can still be accepted. As HUMBERT pointed out (1959), it is 'rather difficult to understand why, on the one hand, *Cycas*, *Nepenthes* and *Ceriops*, endemic to the eastern coast . . . should have derived from ancestors brought by the currents at an indeterminate age and why, on the other hand, if the currents served as a vehicle at that time, they should not still be playing this role by bringing in their congenera which should behave like the species now distributed without variations over the different shores of the Indian Ocean. Should we not rather envisage a continuity of shoreline broken at the end of the Cretaceous period, resulting in segregation and parallel evolution?'

The question of transport by the wind or by birds can be debated in the same way.

It is certain that cosmopolitan plants from marshes or moist places must have been brought by aquatic birds in the form of seeds stuck by the mud to their claws or feathers.

Many varieties with holarctic affinities are to be found both in Madagascar and on the great mountain massifs of Africa; it is a debatable point whether this distribution is due to transport or whether it should be considered as evidence of former climatic conditions.

Here again, some species have remained identical in Madagascar and in Africa *(Cardamine africana*, *Viola abyssinica*, *Antherotoma naudinii)*. In other genera Malagasy endemics have appeared while the species originally introduced has continued *(Stellaria*, *Alchemilla*, *Epilobium*, etc.*)* or has disappeared *(Cerastium*, *Plantago*, *Salix*, *Anagalis*, etc.*)*.

Regarding the family of Compositae, H. HUMBERT (1959) has made comments showing that the importance of transport by the wind should not be overestimated. The genera *Helichrysum*, *Vernonia*, *Senecio* have diaspores that appear to be perfectly well suited to transport by wind. They are represented in Madagascar by numerous species, with between 90 and 100% specific endemism. Foreign introduction of seed, even if rare, would certainly have reduced the extent of this endemism. Consequently one is forced to accept a parallel evolution, in Madagascar and elsewhere, without connections, of separate lines, from ancestral types that occupied geographically continuous territories.

The family of the Ebenaceae, for example, comprises 97 species in Madagascar which belong to the primitive flora of the different regions of the island. All are well established and seem to be derived from a common generic type. This may be of Eastern origin, and successive adaptations have enabled it to spread to all the different ecological regions of the island (H. PERRIER DE LA BATHIE, 1951).

The Malagasy flora is accordlingly of remarkable originality, and for botanists it is an extraordinary subject of study. The inventory of the flora is largely completed today, but much research still remains to be done, especially with modern methods of systematic in order to clarify the affinities of the various Malagasy taxonomic units with each other and with those of other regions of the world. One field in particular has been explored very little: palynology and palaeopalynology, which could probably throw light on many points in the botanical history of Madagascar.

The Vegetation

The diversity of ecological conditions and the richness of the flora account for the very varied and sometimes extremely original aspects of the Malagasy vegetation. The forest in the east is obviously very little different, from the physiognomical aspect, from other similar formations in the tropical world, and its interest lies chiefly in the original nature of its flora. On the other hand, the presence of certain plants, morphologically very well adapted, gives the vegetation of the dry stations a very special appearance: the rock formations with *Aloe*, *Pachypodium*, Crassulaceae, succulent Compositae, etc., and the southern thickets with Didiereaceae, aphyllous Euphorbias, etc., are very curious botanical landscapes.

Between these two extremes, all types of intermediate formations may of course be found.

Many of these plant formations have disappeared or are now only found in rare patches giving only a faint idea of what the original vegetation might have been. This is the case in particular in the Centre and West regions, where the climax vegetation has generally been destroyed.

It is beyond the scope of this paper to give a detailed description of all these types of vegetation. In any case, it would frequently be no more than a physiognomic and floristic description of fairly limited interest. The phytosociological study of the Malagasy vegetation has in fact barely been touched upon. It is difficult, with the knowledge we have at present, to define precisely the climaxes and their ecological requirements. Only a few studies have tackled the question of the dynamics of plant groups. The precise nature of the equilibrium that may exist between forest formations and open graminaceous formations has not been defined.

The definition of Malagasy bioclimates, of which we have already spoken, has however made it possible to define a certain number of climax types. Starting from these types, one can observe in each case *series of vegetation* representing the various plant formations, more or less degraded, that are derived from them: forest, secondary growth, savanna, for example. The different terms of these series, which do not have the value of phyto-sociological groups, have common ecological conditions.

The map of the vegetation of Madagascar (Humbert and Cours Darne, 1965) is based on these principles. The different series are defined on it by the least deteriorated plant formation that can be observed there at the present time.

The geographical distribution of the different terms of a series today only represents a transitional stage: under the effect of human interference, the degraded types of vegetation are generally increasing to the detriment of the original types.

The speed of this deterioration naturally depends on the intensity of human interference, but it is also dependent on the vigour of the plant formations: there is no doubt that, because of the climatic conditions, the eastern forest is much more robust than the western forest, which is much more susceptible to fire. Conversely, woody plants will find it much easier to colonise herbaceous formations in the West than in the Centre, for floristic reasons, to which we shall revert later, and for pedological reasons. The soils of the high plateaux, made very ferralitic and severely eroded by the climatic conditions to which they are exposed, have become unsuitable for any type of woody vegetation. In the West, however the degradation is in general not so far advanced, and some soils have retained a structure that in theory would allow the establishment of woody vegetation.

It now remains for us to give a brief description of the different types of vegetation and first the woody formations that can be defined, as was done in the legend of the vegetation map, by a certain number of typical species, genera or families, without going so far as to attribute a precise plant-sociological value to these characteristics. In these forests, there is great floristic variety, but the species there are very dispersed, which makes it extremely difficult, without detailed research, to distinguish plant associations in the forest.

We shall then try to clarify the significance of the herb formations in the different areas of the island.

I. THE WOODY FORMATIONS

In the eastern Region, which is the most humid and is broadly limited on the eastern side of the island by the height of 800 metres, different types of forest give way to each other. Their physiognomy and floristic composition will be determined by the variation in climatic conditions, especially height, rather than by the edaphic conditions.

The low-altitude dense rain forest (from 0 to 800 metres) (series with *Myristicaceae* and *Anthostema*). In the *Eastern Domain*, this extends almost the full length of the island, but its width does not exceed a few tens of kilometres. Where it has not been destroyed by clearing, it takes the form of an high forest, with the conventional stratification of the rain forest: highest stratum from 25 to 30 metres, mixed with lianes (Bamboos, Apocynaceae, Menispermaceae) and having a remarkably uniform appearance despite the floristic variety of its components. The foliage is very uniform, with limbs of medium dimensions, generally long and acuminate; the flowers are small and not easily visible, with a few rare exceptions. From the ground it is difficult to distinguish the woody species and the lianes and there are great problems to be overcome in collecting botanical specimens. Of the most widely represented families, the Euphorbiaceae, Rubiaceae, Araliaceae, Sapindaceae, Anacardiaceae, etc., mention can be made of some typical genera: *Cynometra* (Cesalpiniaceae); *Ocotea*, *Ravensara* (Lauraceae); *Diospyros* (Ebenaceae); *Dilobeia*, a monospecific endemic genus of Proteaceae, with Indo-Malaysian affinities; numerous species of palms. The heliophilous lianes flourish at the tops of the trees or on the natural or artificial borders of the forest, where they form a sort of 'scar tissue' that is difficult to penetrate.

The floristic composition of the middle stratum is different, with families such as Ochnaceae, Erythroxylaceae, Myrsinaceae, Violaceae, Flacourtiaceae, Tilliaceae, etc., with shade-tolerant foliage and much larger limbs.

The bottom stratum is very discontinuous, with very frequently a bare cover of dead leaves and branches on the ground. Elsewhere can be found, either isolated or in small populations, ferns, dwarf palms and shrubs or herbaceous plants generally of the Rubiaceae, Acanthaceae, Gesneriaceae, Balsaminaceae, etc. families.

Epiphytes, ferns and orchids in particular, are frequently found in the different strata.

In the *Sambirano* Domain (series with *Chlaenaceae*, *Myristicaceae*, *Anthostema*), the physiognomy of the forest remains very much the same, but with a slightly different floristic composition and in particular fairly numerous Chlaenaceae.

The floristic richness of these forests is an obvious indication of their very great age: the development of this flora, most of whose genera were already represented in the Cretaceous flora, has only been possible because of the continuation of very homogeneous climatic conditions in these regions.

We have already pointed out how this forest, which appears so strong, was in fact living in a closed cycle and was actually very fragile.

Indeed, it has very often been replaced by secondary formations, known as '*savoka*' in Madagascar, resulting from its destruction in order to grow temporary crops: mainly rice, maize, beans, manioc, etc.

The vegetation of this savoka is very dense and impenetrable, composed of a few heliphilous species.

Among the most typical of these, introduced species such as the *Citrus* or *Psidium* (guava tree) may be mentioned, as well as the following:

Bambusa *(Ochlandra capitata)*;

Graminaceae *(Arundo madagascariensis)*;

Zingiberaceae *(Aframomum angustifolium)*;

Solanaceae *(Solanum auriculatum)*;

Hypericaceae *(Haronga madagascariensis)*;

Compositae *(Psiadia sp.)*; Ericaceae *(Philippia sp.)*;

Ferns *(Pteridium aquilinum, Lycopodium clavatum)*.

One of the most typical species is a member of the Strelitziaceae

(Ravenala madagascariensis). This can be found in the original forest, but it shows remarkable adaptations to life in the savoka, where it can form large populations. Its underground seedling is perfectly protected against fire and its very hard seeds can exist for many years in the forest humus until the land is cleared and they receive the light necessary for germination.

The medium-altitude dense rain forest (800–1,300 metres) (series with *Tambourissa* and *Weinmannia*), situated in the eastern part of the Centre Domain, still has a high annual rainfall, with a fairly marked dry season and more accentuated temperature minima. However, it has largely disappeared and now only exists in isolated patches and a narrow fringe along the edge of the East area.

This is a dense formation, almost entirely evergreen, and also with a very large number of species, but not as strong as the eastern forest: a single stratum from 20 to 25 metres high, above an undergrowth with more plentiful shrubs and herbaceous plants.

In the top stratum, *Tambourissa*, *Weinmannia*, *Symphonia*, *Dalbergia*, *Vernonia*, etc. are among the best represented genera.

In the undergrowth, arborescent ferns *(Cyathea)*, shade graminaceous plants, Acanthaceae, Labiae, Balsaminaceae, Gesneriaceae, etc. Also in the undergrowth there are species belonging to genera mainly found in temperate countries: *Plantago*, *Cardamine*, *Alchemilla*, *Rubus*, *Sanicula*, etc. Epiphytes are abundant, not only orchids (in particular the *Bulbophyllum* genus which has more than 150 species in Madagascar), ferns, Cactaceae *(Rhipsalis)*, Piperaceae and Crassulaceae, but also mosses and lichens that may cover the branches of trees completely.

These characteristics – the substantial extent of the herbaceous undergrowth and the development of mossy vegetation – become more and more marked at higher altitudes and fully justify the name of 'Mossy and herbaceous undergrowth forest', which has been given to this formation in the mountain massifs.

The high-altitude 'lichen forest' replaces the mossy forest, usually at a height of between 1,300 and 2,000 metres, when the edaphic conditions no longer allow the latter to develop. This is a sclerophyllous forest with small-leaved and very twisted trees 10 to 12 metres high, where branches are covered with epiphytes. On a coating of moss there are ferns, orchids, Piperaceae and Usnea hanging in long strands. Many of these species are also found in the thick stratum of mosses and lichens covering the ground (consisting mainly of Hypnaceae, *Sphagnum* and *Cladonia* on the rocky substrata).

There are numerous species typical of this forest: *Dicorypha viticoides*, *Tina isoneura*, *Rhus taratana*; and one member of the Chloranthaceae family, the only one found in Madagascar, related to a New-Caledonian genus: *Ascarinopsis coursii*.

The best represented families are the Compositae, Rubiaceae, Lauraceae, Araliaceae, Ericaceae, etc. Mention should also be made of the presence of Gymnosperms *(Podocarpus)* and bamboos that may in places form pure populations, such as *Arundinaria marojejyensis*.

This forest has often been destroyed and only patches of it still remain. It is very susceptible to fire: generally situated on shallow rocky soils, it dries out rapidly after a few days of sun and wind and becomes very inflammable. Fire can spread easily through the thick layer of humus, mosses and lichens carpeting the ground. The forest is then replaced by bush consisting mainly of Ericaceae and *Helichrysum*.

The Domain of the high mountains, over 2,000 metres, is formed of a number of isolated masses: the Tsaratanana (2,886 m) and the Marojejy (2,137 m) in the north, the Ankaratra (2,643 m) in the centre, and the Andringitra (2,659 m) in the south-east. These summits, which often emerge from the cloud ceiling, are subjected to great variations in humidity, sunshine and temperature, with severe frosts during the winter (—15 °C in June on the Andringitra). Although the lichen or moss forest may extend above 2,000 m if the edaphic or microclimatic conditions are suitable, the most general form found there is bush or herbaceous vegetation greatly adapted to these severe ecological conditions.

This 'ericoid bush' type vegetation forms a wooded landscape rather like a Mediterranean *maquis*, with numerous microphyllous species with an ericoid habit (Ericaceae: *Philippia, Vaccinium*; Compositae: *Helichrysum, Stoebe*). Some small trees mostly belonging to the lichen forest are found here too: *Agauria* (Ericaceae), *Cussonia* (Araliaceae), *Faurea* (Proteaceae), *Podocarpus*, etc. Climbers and herbaceous plants are not very numerous and of the epiphytes only mosses and lichens still survive.

The rocky outcrops are occupied here and there by a low herbaceous and chamephytic vegetation, which is remarkable for the numerous instances of adaptation to xerophytism on the part of the plants found there. Such places are virtually devoid of soil and are frequently subject to intense radiation from the sun. This formation, which has traditionally been given the uncomplimentary name of 'xerophyte turf', is not in fact confined to high altitude regions. It is found in all rocky locations, from sea level to the tops of the highest mountains, with a very clearly defined distribution of the various species according to altitude. It is best developed in the central regions, at heights between 1,000 and 1,500 metres. Among the most interesting biological types, the following may be mentioned: crassulescent species (stems: *Pachypodium, Euphorbia, Cynanchum*; leaves: *Kalanchoe, Aloe, Senecio*); reviviscent species *(Myrothamnus, Selaginella)* or *Xerophyta* (Veloziaceae) which are distinguished by the presence of a sheath around the stem formed by old leaf bases in which large numbers of casual roots develop. Many of these plants disappear as altitude increases, and on the tops of the highest mountains practically nothing is to be found except *Xerophyta* and a few species of *Senecio* and *Kalanchoe*.

Finally, at high altitudes it is also possible to find a mountain type of prairie, the flora of which includes various plants of holarctic affinity, such as the following genera, for example: *Linum*, *Geranium*, *Alchemilla*, *Sedum*, *Galium*, *Lysimachia*, *Anagallis*, *Stachys*, *Epilobium*, *Poa*, *Festuca*, *Bromus* and *Brachypodium*.

In wetter locations, this prairie may resemble a peat bog, with *Sphagnum*, *Xyris*, Eriocaulaceae and *Drosera*. In these peaty depressions the presence of a Malagasy representative of the South African and Australian family of Restionaceae *(Restio madagascariensis)* may also be noted.

The *sclerophyllous forest* with *Uapaca bojeri* and *Chlaenaceae* is considered to be typical of the stage of the western slopes in the Centre Domain. It should therefore occupy the western slope of this area up to a height of 800 metres, i.e. regions with a drier and hotter climate than the rest of this area, but still with extreme minimum temperatures. However, it is now only found in isolated patches, often very deteriorated, and rather having the appearance of a densely wooded savanna because the originally shrubby undergrowth has been replaced by a carpet of heliophilous grasses.

The top stratum, 10–12 metres high, consists essentially of *Uapaca bojeri*, a remarkably fire-resistant variety because of its thick bark and its sprouting capacity. It is accompanied by a number of Chlaenaceae and other trees, amongst which mention may be made of *Asteropeia* sp. (Theaceae), *Agauria salicifolia* (Ericaceae), *Cussonia bojeri* (Araliaceae), *Brachylaena microphylla* (Compositae), etc.

Shrubby undergrowth consisting mainly of *Philippia*, *Vaccinium*, Compositae *(Helichrysum)*, Rubiaceae, etc.

This forest is very susceptible to fire which can easily penetrate the undergrowth from the forest borders. It then disappears or, as we have already mentioned, takes on the appearance of wooded savanna because of the resistance to fire of certain woody species. These degraded forms are nowadays localised in areas of rocky outcrops, which form a refuge against fire because of the relative sparseness of the carpet of grass in such localities.

In the valleys remains of a more mesophilous forest can still be found, with a very rich flora including palm trees *(Chrysalidocarpus* sp.*)* and species belonging to the Eastern flora.

The original vegetation in the *West Domain*, to which we now come, still consists of forests, but very different from those we have considered so far. Their main feature is the existence of a rest period in the dry season, during which most of the trees lose their leaves. As the dry season grows longer, we shall see the emergence in increasing numbers of plants that are highly adapted to drought: aphyllous Euphorbias, *Pachypodium*, *Adenia*, *Vitaceae* with swollen trunks for water storage.

In these regions, where water is the vital limiting factor, the influence of the soil is predominant and will determine the existence of many edaphic climaxes.

Plate 2. Western slopes, Centre area. Degraded residual sclerophyllous forest *(Asteropeia densiflora)*.

Plate 3. Dense dry deciduous forest of the West area.

These forests form the *Dalbergia*, *Commiphora* and *Hildegardia* series.

Several types can be distinguished depending on the nature of the soil.

On laterite clays, the soils are relatively well provided with humus. The organic matter does not deteriorate so fast as in the east because the micro-organisms, inhibited by the water shortage, are less active. The forest is thin, about fifteen metres high or sometimes more, with a large number of species: *Dalbergia*, *Stereospermum*, *Xylia*, *Cordyla*, are among the representative genera. Lianas are very abundant, with many Asclepiadaceae; shrubby undergrowth consisting mainly of Rubiaceae, Compositae and leguminous plants. Epiphytes have virtually disappeared, with only a few orchids having leaf structures highly adapted to the drought.

These formations are found mainly in the north and north-west of the Domain.

On sandy soils the forests are still the most extensive, and their type varies according to the water supply. On the fairly humid soils, they are little different from the forest on clay and can be characterised by the frequency of *Tamarindus indica*, whose fruit is eaten and sold in the markets. Further south, in more arid conditions, these forests take on a special physiognomy because of the presence of Baobabs *(Adansonia)* and large aphyllous arborescent Euphorbias with the habit of *Araucaria (E. enterophora)* and Didiereaceae *(Didierea madagascariensis)*.

The flora of the forests on *limestone plateaux* contains many special species, in particular leguminous plants *(Albizzia, Acacia, Poinciania)*, Anacardiaceae *(Protorhus)*, Sapotaceae *(Sideroxylon)*, etc. The undergrowth is thick with lianes (Asclepiadaceae, Passifloraceae, Ampelidaceae) and shrubs. It is on the rocky escarpments of these plateaux that the 'Flame Tree' *Poinciania regia* is found, a very fine ornamental species that is cultivated in gardens throughout the tropical world.

In some regions, for example, the karst mountain mass of Ankarana, the vegetation is greatly modified by the aridity of the soil and takes on an appearance similar to that found in the South Domain. On this very fissured limestone, the soil is very shallow or even non-existent and the roots go down deeply into the interstices in the rock: fleshy stems or leaves, reduction in or disappearance of the leaves, and presence of spines give the vegetation a very curious appearance, and some of the species belong to the flora of the South. The most spectacular are the *Aloe*, some euphorbias and aphyllous *Cynanchum*, Ampelidaceae *(Cyphostemma)* and Passifloraceae *(Adenia)* with stems that are grossly swollen at the base, *Pachypodium* with a spiny trunk that is bottle-shaped.

These dense dry forests nowadays occupy large areas on the limestone slopes (Plateaux of Ankarana, Kelifely, Antsingy and Mahafaly) and on the sandy soils along the coast below a height of 300 metres. Elsewhere in this area the forest has frequently disappeared, doubtless because of less favourable edaphic conditions which have reduced its resistance to fire and land-clearing. On hydromorphic soils *Medemia nobilis* palm trees

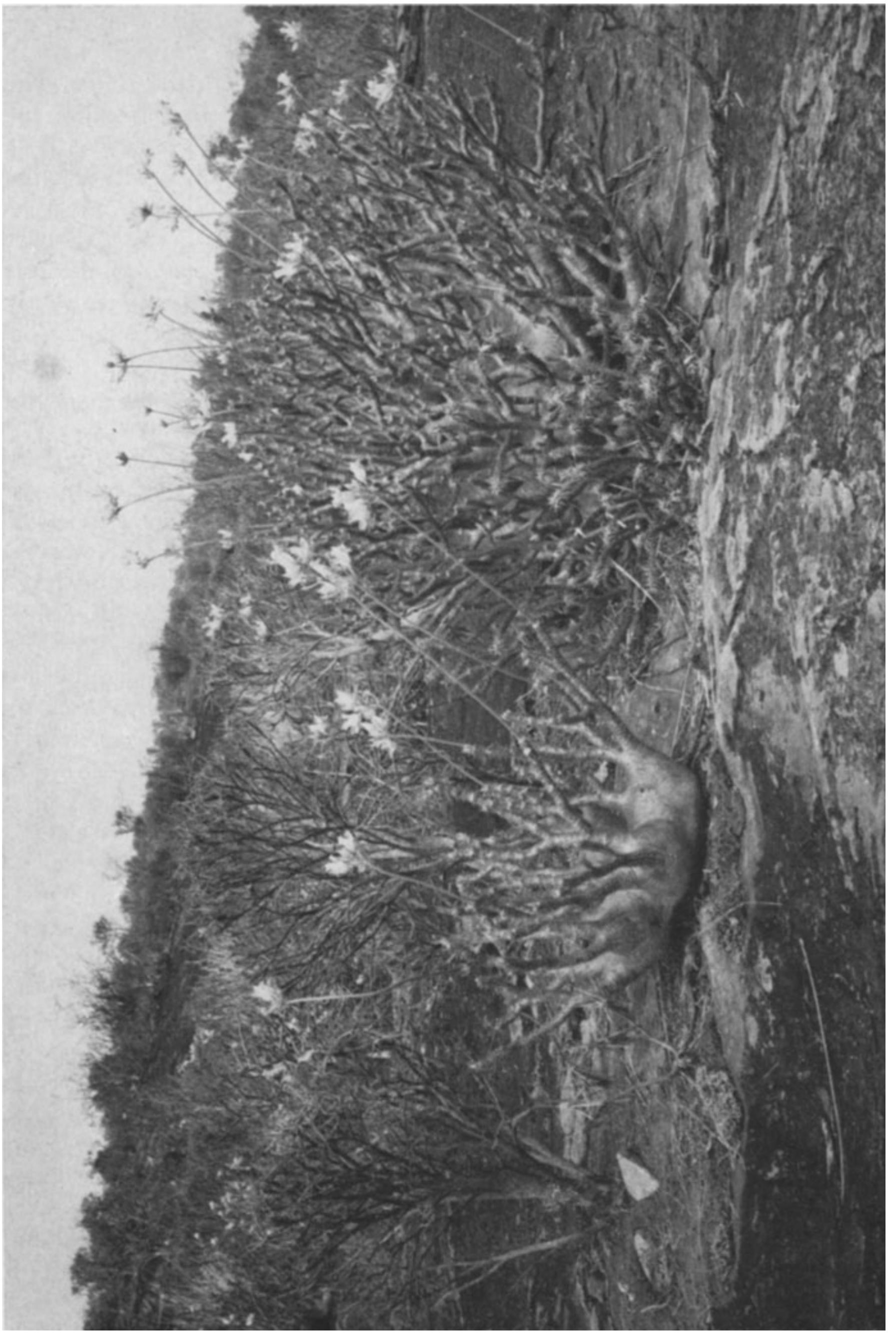

Plate 4. Xerophilous rock vegetation: *Pachypodium rosulatum* (in flower) and *Xerophyta dasilyroïdes:* Centre area (altitude: about 1,500 m.).

often remain to provide evidence of a forest which is nowadays very degraded.

Because of the erosion caused by the denudation of the western slopes, the rivers in the west carry large quantities of alluvial materials. Because of this, the port of Majunga is practically condemned and the Betsiboka has deposited vast alluvial areas, the 'Baiboa', upstream of its estuary. This is applicable throughout the area, but these alluvial deposits, highly cultivated, have only rarely retained vestiges of their original vegetation. This consisted of a very strong forest *(Canarium, Kahya, Terminalia, Ficus, Treculia)*. Palms are also found in these formations: *Medemia nobiles* associated with *Ficus sakalavarum* or *Raphia ruffia*, in flooded areas, whether the flooding is temporary or permanent.

The series with *Didiereaceae* and *euphorbias* in the South Domain

The main feature of the climate in the south is the low rainfall and also the extreme irregularity of the precipitation, which may fall at various times in the year, as there are not two clear-cut seasons. Because of the drought, the soils on limestone, sands or metamorphic rocks are not very developed pedologically and are often skeletal. Consequently, except along the water courses, the vegetation has pronounced xerophilous features and a very special physiognomy. It is in this area that the endemism of the flora is most marked, which is evidence of its great age and the long persistence of similar ecological conditions.

The vegetation of the South area has been defined by H. PERRIER DE LA BATHIE and H. HUMBERT as a thicket characterised by the presence of the Didiereaceae family and aphyllous bushy species belonging to the genus *Euphorbia*. There is in fact a certain amount of confusion in this definition between the concepts of flora and plant geography. Actually, in this Domain, as it is traditionally defined, thicket is to be found, as well as deciduous forest formations which clearly belong to the West Domain. In addition these forest formations may include Didiereaceae and Euphorbias *(Didierea madagascariensis, Alluaudia ascendens, Euphorbia enterophora)* among their flora. The boundary between these two formations, forest and thicket, really depends very largely on edaphic factors, since the forest can penetrate into the climatically driest regions if the edaphic conditions are favourable, and vice versa. The thicket proper, in the strict sense of the term, is very restricted and is in fact generally limited to a narrow coastal strip with a maximum width of a few tens of kilometres only. This strip corresponds closely with the areas of lowest rainfall recorded in Madagascar. Nevertheless the thicket represents an important vegetal biomass, much more important than that of the steppes of the western Sahara in Africa, which nevertheless receive an equivalent amount of rain. This can no doubt be explained by the different annual distribution of rainfall, by the greater atmospheric humidity along the

Plate 5. Rock vegetation in the Isalo massif: *Pachypodium rosulatum* and an aphyllous papilionacean, *Mundulea phylloxylon.*

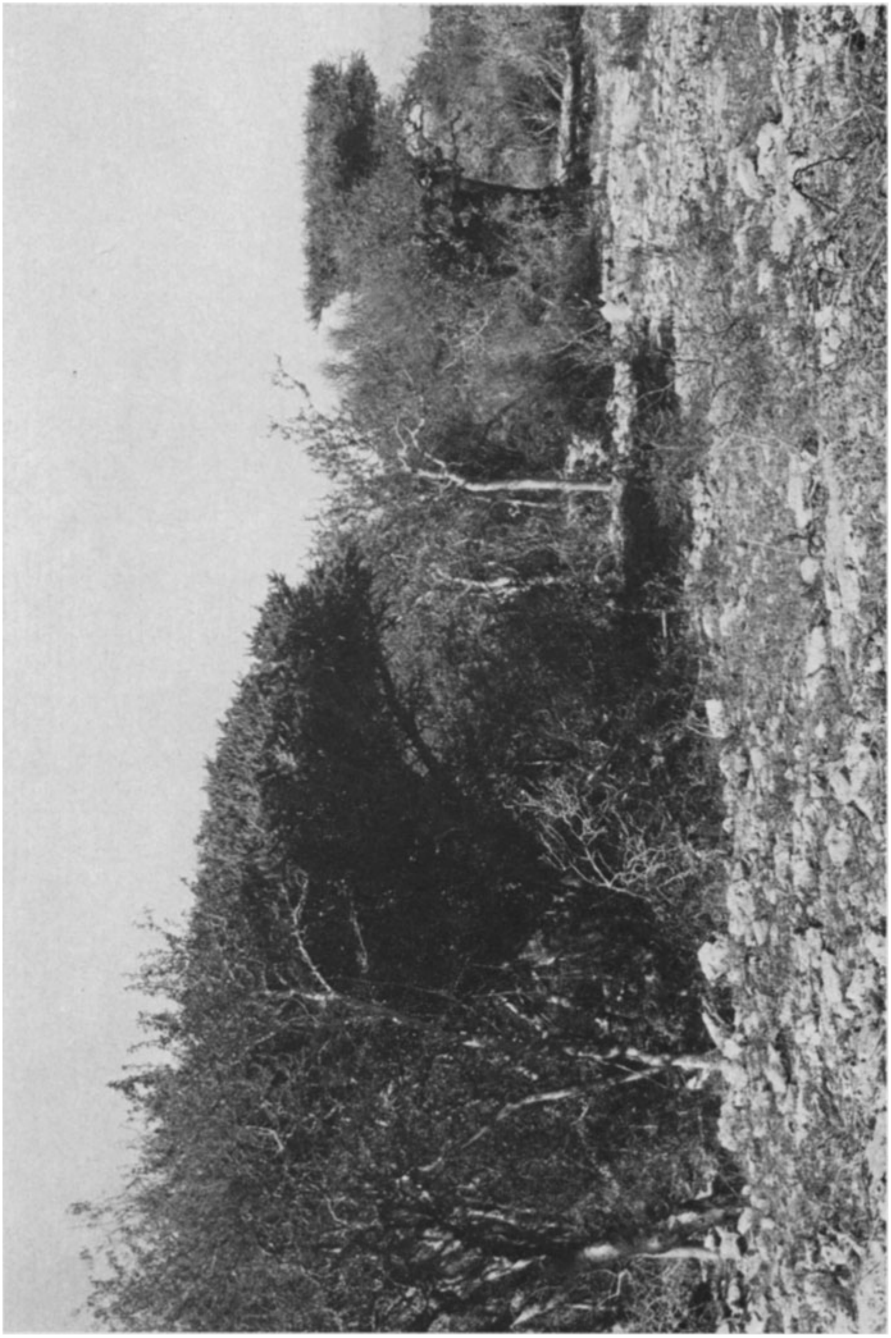

Plate 6. Bush in the South area with *Alluaudia comosa:* near Tuléar.

Plate 7. Bush in the South area with *Alluaudia montagnacii* and *Adansonia fony;* Mahafaly limestone plateau, coastal region to the south of Tuléar.

Plate 8. Bush in the South area with *Alluaudia montagnacii* and *Didierea trollii* (more ramified, centre). Coastal regions to the south of Tuléar.

Plate 9. Didierea madagascariensis, in flower, in the bush near Tuléar.


Plate 10. Euphorbia stenoclada, in degraded bush, Tuléar region.

Malagasy coast and by the remarkable biological adaptations of the plants of the thicket.

The appearance of the Malagasy thicket is also markedly distinguished by the presence of the endemic family of Didiereaceae and the genus *Euphorbia*.

The former has four genera and about twelve species, all confined to the south. Some of them show a remarkable convergence of forms with the Cactaceae, so that there is sometimes a very strong analogy of landscape between the thicket of southern Madagascar and some American formations such as the Brazilian 'Caatinga'. Some Didiereaceae, too, bear some resemblance to the Fouquieriaceae of the Californian deserts.

The arborescent aphyllous euphorbias, with fleshy and sometimes spiny branches (like *E. stenoclada*), also play an important part in the constitution of the plant life in the south. The other arborescent species are relatively rare: *Adansonia*, *Moringa*, with bottle-shaped swollen trunks, *Dicoma*, *Ficus*, etc.

The flora consists mainly of bush species forming a dense thicket that is difficult to penetrate. Many have only very small leaves or sometimes none at all; many are spiny. The leaves are very frequently borne on short and very thin branches. Some very prolific families are represented in the thicket: Mimosaceae, Tilliaceae, Euphorbiaceae, Acanthaceae, Rubiaceae, Anacardiaceae, Combretaceae, etc.

There is no continuous herbaceous carpet over the ground: with a few graminaceous plants, Velloziaceae and reviviscent *Selaginella* are mingled

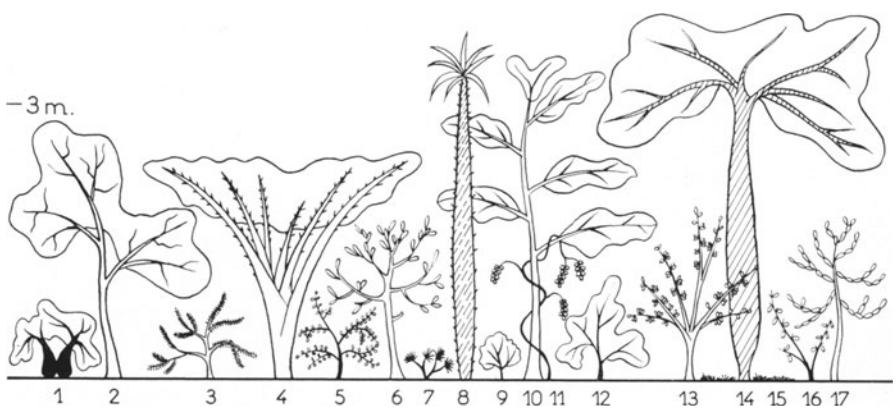

Fig. 5. Thicket of *Alluaudia comosa*, diagram: 1, *Commiphora monstruosa;* 2, *Cassia meridionalis;* 3, *Bauhinia grandidieri;* 4, *Alluaudia comosa;* 5, *Rhigozum madagascariensis;* 6, *Euphorbia leucodendron;* 7, *Xerophyta dasylirioïdes;* 8, *Pachypodium lamerei;* 9, *Blepharis calcitrapa;* 10, *Terminalia subserrata;* 11, *Xerosicyos danguyi;* 12, *Croton* sp.*;* 13, *Megistostegium perrieri;* 14, *Delonix adansonioïdes;* 15, *Selaginella nivea;* 16, *Alluaudiopsis fiherenensis;* 17, *Euphorbia oncoclada.*

Fig. 6. Bush thicket of *Alluaudia procera;* diagram: 1, *Albizzia tulearensis;* 2, *Diospyros latispathulata;* 3, *Alluaudia procera;* 4, *Selaginella nivea;* 5, *Cyphostemma laza;* 6, *Pachypodium geayi;* 7, *Croton* sp.*;* 8, *Alluaudia dumosa;* 9, *Gyrocarpus americanus;* 10, *Aloe divaricata;* 11, *Euphorbia* sp.*;* 12, *Alluaudia humbertii;* 13, *Xerosicyos danguyi;* 14, *Maerua nuda.*

some very low, often fleshy plants: *Aloe, Kalanchoe, Senecio,* etc. Some lianas, Asclepiadaceae, often aphyllous, *Cissus, Adenia,* etc. and very curious Cucurbitaceae with thick, fleshy leaves and capsular fruits, belonging to the genus *Xerosicyos.*

Figures 5 and 6 give, in diagrammatic form, an idea of the principal biological forms that can be found in the thicket.

This bush vegetation has a general greyish colouration largely due to the presence of aphyllous euphorbias. After rain, many plants rapidly produce an abundance of flowers, sometimes very large and often brightly coloured (leguminous plants, Acanthaceae, *Uncarina,* Capparidaceae, etc.).

Relatively speaking, this type of vegetation is less deteriorated than the other climax formations on the island particularly on limestone lithosols which are unsuitable for agriculture. It is also not affected by fire: there is very little grassy carpet, and an abundance of aphyllous, microphyllous or fleshy plants; fire cannot gain a foothold on it. Consequently the deteriorated areas close up again quickly, but often with different species from those found in the original formation. It is a paradox to find in Madagascar that the least deteriorated original plant formation is precisely the one in the driest regions that would be expected to be the most fragile.

Without going into detail on the *littoral vegetation*, mention should be made of the large mangrove areas (about 200,000 hectares), mainly along the western coast where conditions are more favourable for its establishment. The Madagascan mangrove has one endemic species: *Ceriops boiviniana* (Rhizophoraceae), together with *Rhizophora mucronata*, *Bruguiera gymnorhiza*, *Avicennia marina*, *Sonneratia alba*, *Lumnitzera racemosa* and *Xylocarpus moluccensis*, which are species belonging to the mangroves of the Pacific.

II. THE GRASS FORMATIONS

Although they cover considerable areas in Madagascar, the study of them has been very much neglected because the richness of the forest formations has appealed so much to biologists. These grass areas take the form of vast monotonous expanses, bare or with a few shrubs. Their very poor flora varies little: it consists largely of pantropic plants or introduced species. All these formations are generally considered as secondary and recent, resulting directly from the action of man; the isolated areas of forest are considered as relics of the original formations that have now partly disappeared.

In other regions, especially Africa, certain research work (Koechlin, 1961; Aubeville, 1962) has shown that the savanna, the establishment of which had traditionally been attributed to man, could in fact have had much more ancient origins: not only man, but palaeoclimatic events, possibly preceding his interference, could be blamed.

Does the same apply to Madagascar? It is still difficult to come to a conclusion on this point. We shall nevertheless try to put forward some hypothesis on the basis of a general study of the various aspects of this graminaceous vegetation.

The herbaceous formations of Madagascar may be of different types.

First of all there are true savannas, which may or may not contain shrubs. The grasses are hemicryptophytes, with striped cauline blades, which form a dense carpet. These savannas cover a large part of the West Domain.

Steppes similar to the formations in the southern Sahara, with *Aristida* and *Cenchrus*, are to be found in the extreme south but cover only limited areas.

In the Centre and the East the herbaceous formations have a definite steppe-like appearance, with grasses with narrow basilar blades, the tufts of which form quite a bright carpet. But these are quick-growing species, and the determinism of this formation is edaphic rather than climatic: it grows on soil which is very degraded and impoverished and has an extremely compact surface. We are a long way from the conditions of the

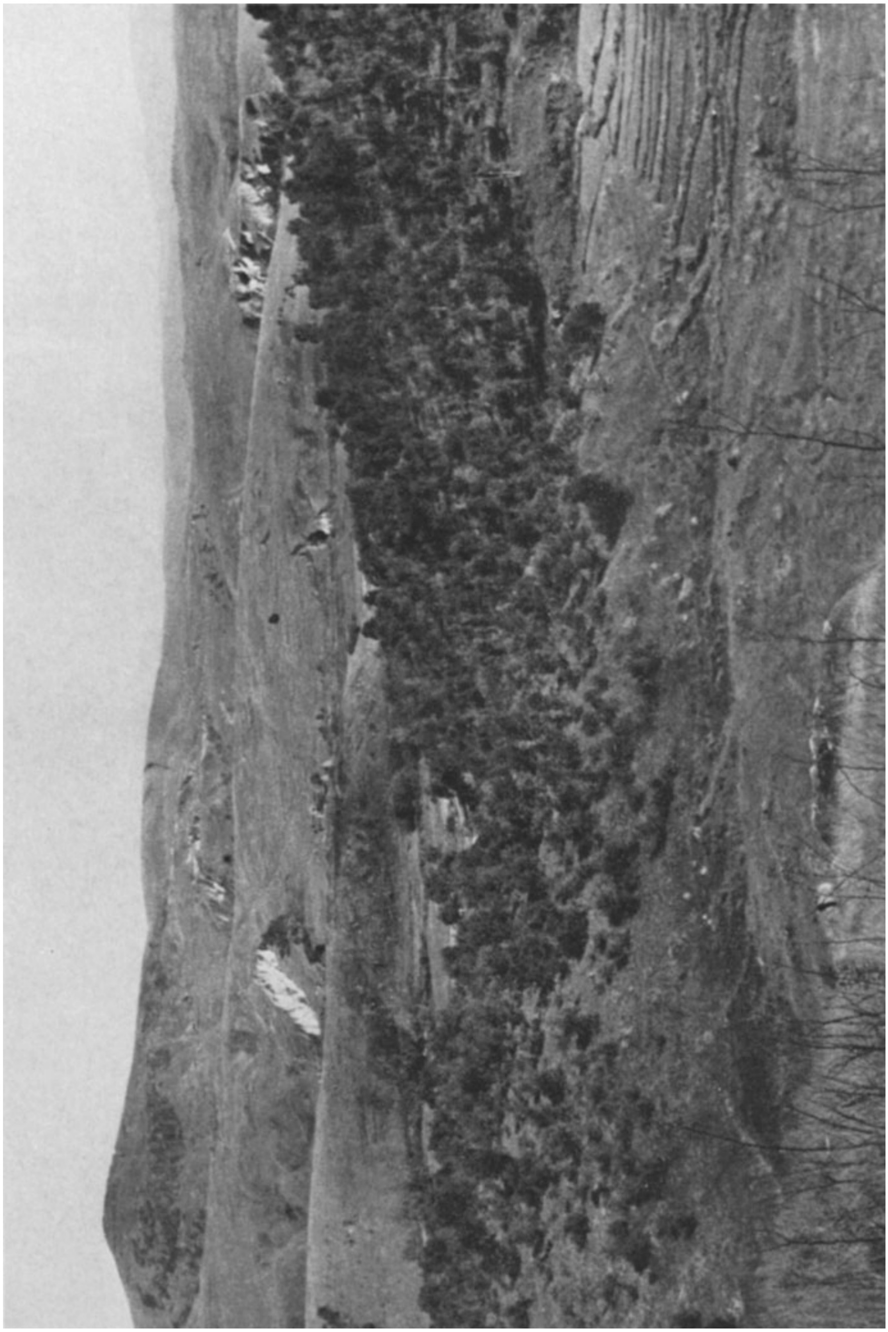

Plate 11. Landscape of high plateaux near Tananarive: pseudo-steppe with *Aristida*, 'lavaka' erosion and re-afforestation with *Eucalyptus*.

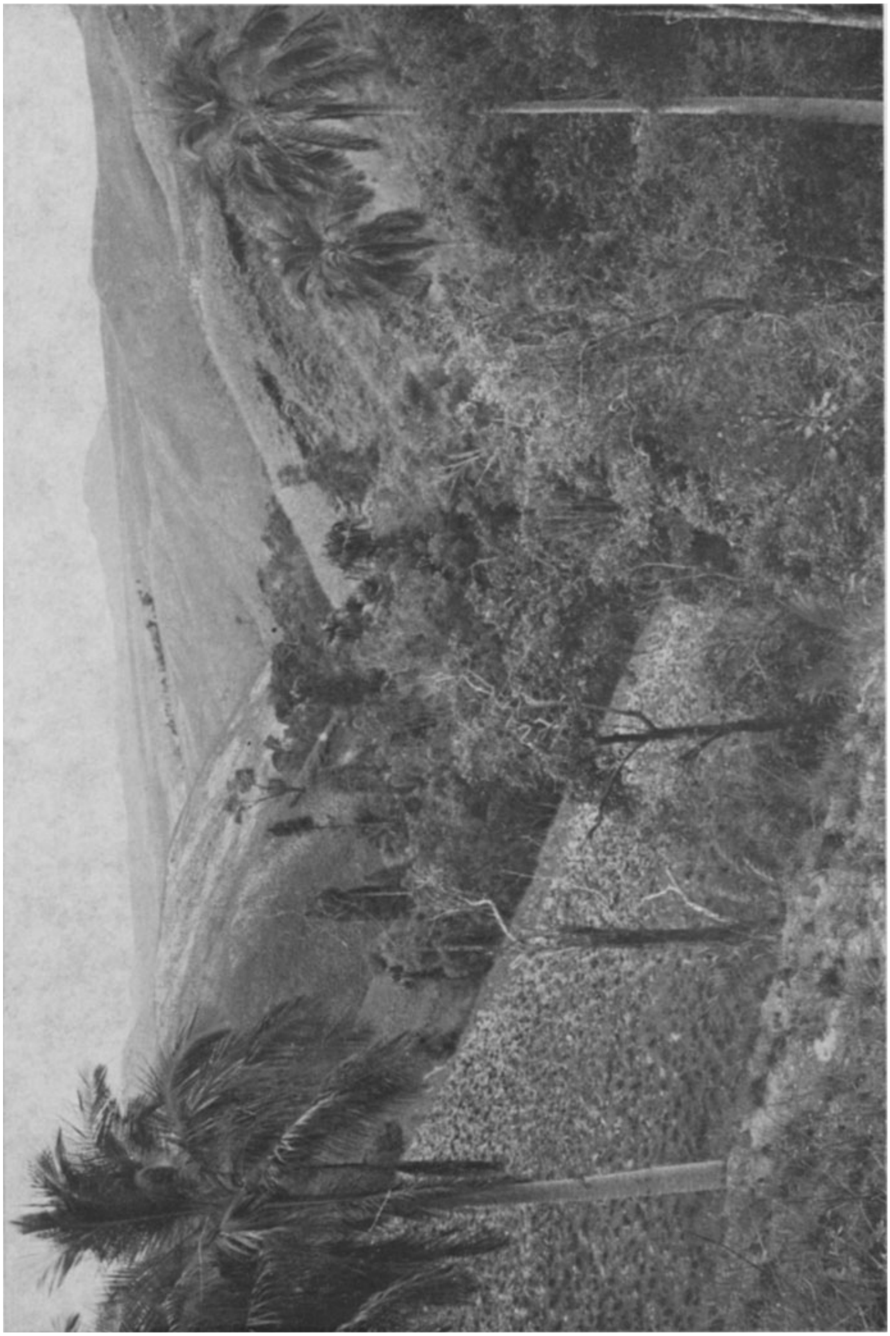

Plate 12. Destruction of the forest in the Centre area (western slopes) and its replacement by grassland; the palm tree is a *Chrysalidocarpus* sp.

true south Sahara steppe, and so, to avoid confusion, we prefer to use the term 'pseudo-steppe' here. This has already been proposed as a description of the very similar formations in the Congo (J. L. TROCHAIN and J. KOECHLIN, 1958).

In the East and Sambirano Domains, apart from a definite forest climax, *Aristida* pseudo-steppes cover large areas on the hills behind the coast, which are bare or dotted with *Ravenala* or guava trees. These pseudo-steppes are clearly spreading. They are the result of the destruction of the forest by 'tavy' practices, of an excessively rapid re-use of the fallow land, and finally of repeated burning. They are to be found on very eroded and impoverished ferrallitic soils which seem to have suffered degradation on such a scale that the natural re-afforestation of such places is no longer possible, in spite of the climax. Under other pedological conditions, on the other hand, the fallow forest land remains in a vigorous state and resists the establishment of grasses.

In these humid areas, man's exploitation of the vegetation remains very extensive, and the areas of forest changed to secondary growth or replaced by grassy vegetation are increasing all the time.

In the Centre Domain, apart from hollows and very occasional patches of forest, the grassy pseudo-steppe with *Aristida rufescens* forms the dominant component of the botanical landscape. Here too it covers eroded hills whose compact and impoverished soils are frequently deeply gashed by 'lavaka' types of erosion. The *Aristida* is accompanied by a few graminaceous species (*Ctenium*, *Trachypogon*, *Elionurus*, and *Loudetia* in certain regions) and by some rare Dicotyledons. *Imperata cylindrica*, *Hyparrhenia rufa* and *Heteropogon contortus*, species more demanding in their requirements, occur in less eroded localities in soils with a higher humus content.

There too the *Aristida* pseudo-steppe, the constituents of which have been ruthlessly selected by fire, seems to be the ultimate and doubtless irreversible stage of the evolution of the vegetation. These soils are in fact so degraded that it is doubtful if natural re-afforestation would be possible.

The whole of the West of Madagascar is basically the region of the more or less shrubby savannas with *Heteropogon contortus*.

The shrubby flora is very sparse; it includes some palms (*Hyphaene shatan*) and, on hydromorphic soils, *Medemia nobilis* and *Borassus madagascariensis*, as well as shrubs, some of which (*Ziziphus mauritianus*, *Sclerocarya caffra*) have been introduced while others (*Stereospermum variabile*, *Dicoma incana*, *Acridocarpus excelsus*, *Gymnosporia linearis*, etc.) are endemic.

It is remarkable that this woody flora should be formed in savannas located in an area with a relatively arid climate, whereas it is absent in savannas whose climax is of a more humid forest type.

This could be explained as being due to the drier climate, which limits the development of the herbaceous stratum, and to the violence of the fires: this argument does not apply in Madagascar where, on the contrary, the herbaceous carpet is more developed in the savannas of the West than

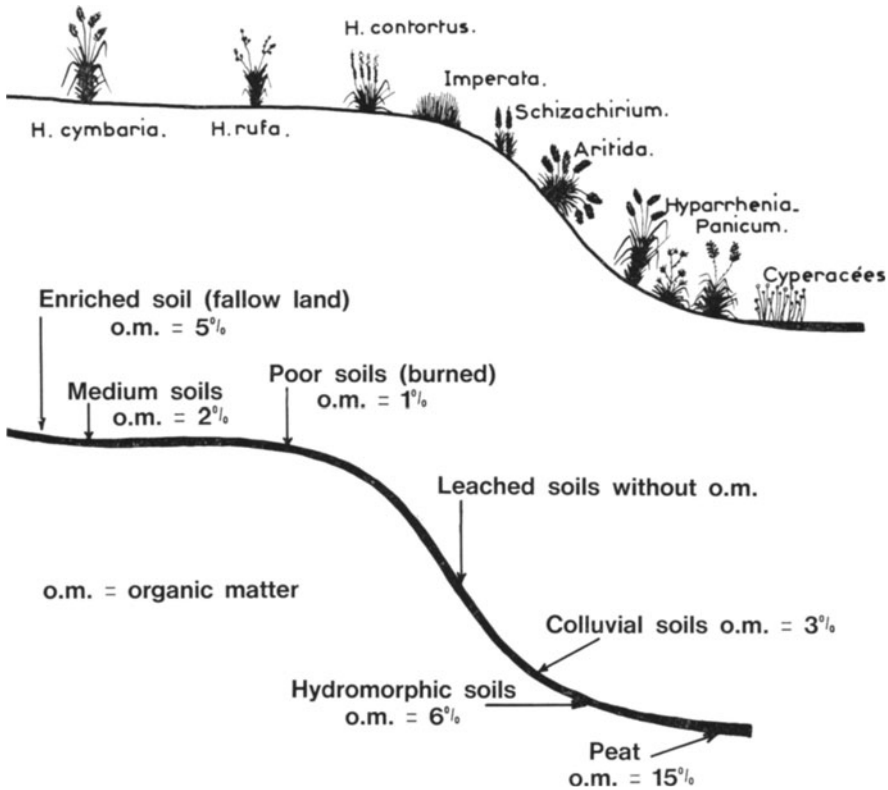

Fig. 7. Vegetation and soil catena in the mid-west of Madagascar (according to GRANIER 1967).

in the pseudo-steppes of the Centre Domain. On the other hand, there is a biological explanation: in the dry, deciduous and relatively open forests of the West, the trees are naturally exposed to conditions which are already very arid. It can be visualised that a species might quite easily emerge from the forest and adapt itself to life in the savanna, provided that it is able to withstand fire. On the other hand, ecological conditions differ so much between a savanna and a dense rain-forest that it is difficult to see how a species from these forests could live in the savanna. This is a general phenomenon: the shrubby flora of the African savannas in areas having a long dry season is extremely rich. On the other hand, the savannas of subequatorial regions are purely herbaceous or contain only a very small number of woody species. The same differences occur in Brazil between the Campos cerrados of Central Brazil and the Campos Limpos of the Rio Branco region (AUBREVILLE, 1961).

The herbaceous carpet is generally well developed, relatively dense and

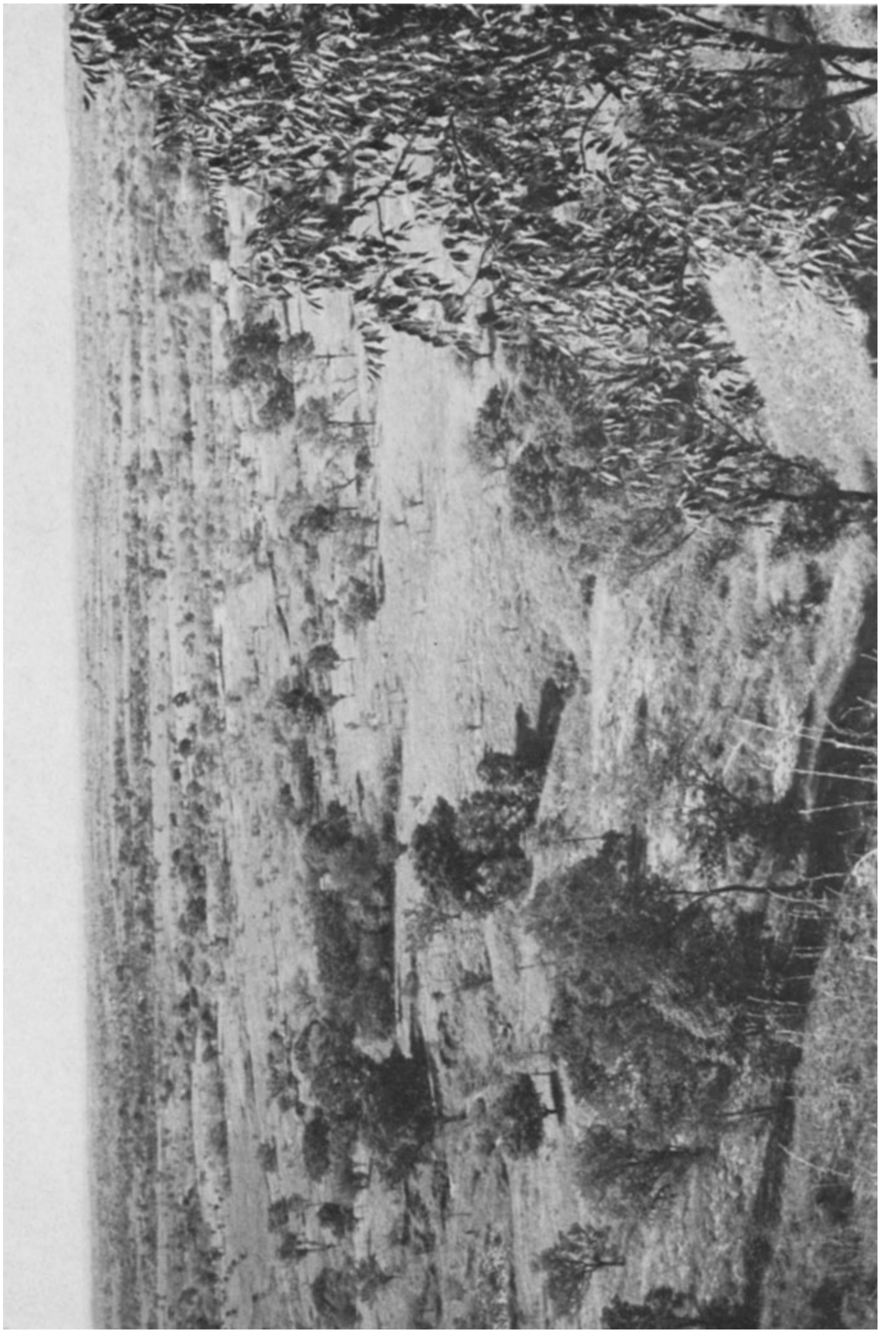

Plate 13. Shrubby savanna in the West area.

Plate 14. Shrubby savanna with *Medemia nobilis* in the West area.

high, with *Heteropogon contortus* as the predominant species in average ecological conditions. *Imperata cylindrica*, *Hyparrhenia dissoluta*, *H. cymbaria* and *H. rufa* are found in the deepest and most moist soils; *Aristida rufescens*, *Loudetia stipoides* and *Chrysopogon montanus* appear on the eroded slopes and in the poorest soils. The dynamics of the vegetation of these savannas are almost entirely conditioned by a certain number of factors: fire, grazing, agriculture and erosion.

With regard first of all to the balance of the boundaries between the forest and the savanna, it may be noted that the forest-areas are nowadays confined to certain edaphic localities (sand, limestone) which seem to them to be particularly suitable, and these boundaries are virtually stabilised. Fire may attack the forests, but it is usually a forest-type vegetation, albeit degraded, that grows again after the fire. Similarly, in most instances it is forest-type fallow land that returns after clearing. If therefore the savannas of the West are to be regarded as recent secondary formations, it must be admitted that the destruction of the forest took place under climatic conditions different from those prevailing today, or else that the forests that have disappeared were of another, more fragile type.

At the same time, fire maintains an almost completely stable balance between the different plant constituents of these savannas, a balance which can be destroyed by the overintense effects of certain factors such as grazing, cultivation or erosion.

Grazing will cause above all harmful exploitation of certain highly appreciated graminaceous species *(Imperata*, *Hyparrhenia*, *Heteropogon)*, and this will favour the development of less desirable species *(Aristida)*. Subsequently over-grazing, degradation of the soil by agriculture, and erosion are further factors which will lead to a reduction of the density of the herbaceous carpet and at the same time of the intensity of the fires. The real nature of the climax may then be demonstrated by increased development of the shrubby flora and by the establishment in the savanna of heliophilous forest elements. This evolutionary tendency is clearly shown by the spread through the savannas of species of shrubs such as *Stereospermum variabile* or *Ziziphus mauritianus* and by the establishment of woody species such as *Sarcobotrya strigosa*, *Acacia farnesiana*, *Haronga madagascariensis*, etc.; areas denuded by erosion are colonised by dense populations of *Terminalia seyrigii*.

Finally, in the South Domain, graminaceous formations take up only a very small amount of space, in areas where the thicket has been eliminated by clearing and intensive grazing has subsequently prevented the woody vegetation from returning. It is generally a question here of steppes with *Cenchrus ciliaris*, *Aristida congesta*, *Panicum voeltzkowii* and *Eragrostis* spp. as their principal constituents.

In conclusion, what significance should be given to these herbaceous formations in Madagascar?

It is clear that their homogeneity, the sparseness of their flora and the affinities of the latter all point to a recent secondary origin. Indeed, before our very eyes the degradation of primitive formations by human action still continues on a considerable scale, especially as these attacks affect areas that are getting smaller all the time.

It should not be forgotten, however, that the arrival of man in Madagascar is of recent date: round about the 4th century A.D. (H. Deschamps, 1965), and that the population was for a long time quite small (6,562,041 inhabitants in 1966, compared with only 2,550,000 in 1900) and is very unevenly distributed. Even today, vast areas in the West are almost totally uninhabited and have no doubt always been so. In spite of this, in a country where the climax is of a forest type throughout, woody formations, whether degraded or not, occupy only about 28% of the total area (A. Guichon, 1960). It may be wondered, therefore, how these men, with their rudimentary tools, and whose agricultural or pastoral interests are often very limited, could have cleared such extensive areas. In addition, the forest formations remaining today seem to be in balance with the climate, and in any case, the burning of them is not possible without preliminary felling (this does not apply to certain formations in the West and at high altitudes, however).

Nevertheless, certain facts may possibly explain the rapid and violent destruction of the forests. Firstly, as in all islands, the endemic flora is extremely fragile: as it has evolved from a small number of original components, the species, which have generally become closely associated with very specialised environments, have not been subjected to as rigorous a process of selection as that on the great continental landmasses. Accordingly, these species put up a poor resistance to competition from introduced pantropical species which are much more aggressive.

Furthermore, in Madagascar there is practically no secondary forest flora such as is found, for example, in Africa with such dynamic woody species as the umbrella tree *(Musanga cecropioides)*, the *Macaranga*, *Anthocleista*, etc., or even such herbaceous plants as the Zingiberaceae and Marantaceae. This is no doubt due to the fact that forest degradations are of too recent a date in Madagascar for such a flora to be able to volve. When a Malagasy forest was destroyed, there was thus nothing capable of taking its place and preparing the way for its re-formation. These empty spaces were thus easily overrun by introduced plants, particularly grasses.

Some of the formations that have now disappeared, such as the sclerophyllous forest and the dry forests of the West, were no doubt relatively fragile and burnt easily. It is also quite possible that climatic conditions, which were rather drier than they are today, contributed to this destruction. It is nevertheless difficult to give an opinion on the exact nature of the plant formations that may have been destroyed in this way.

Many Malagasy landscapes, particularly on the high plateaux, are much marked by an abundance of 'lavaka'-type erosions. Some of these lavaka are active and provide evidence of intensive erosion at the present time. On the other hand, others have ceased to be active and have been recolonised by vegetation; it has been possible to date some of these forms later than the arrival of man in Madagascar (M. PETIT and F. BOURGEAT, 1965).

It is accepted that the lavakas cannot be hollowed out in the forests but only in open formations. We are thus obliged to admit that such formations existed before the arrival of man. They are clearly different from the present-day savannas or pseudo-steppes, but they may have formed easy targets for the fires lit by the first human inhabitants.

Conclusions

We have only been able to give a brief sketch here of the flora and vegetation of Madagascar. Many problems still have to be solved in this field: although the exploration of the flora is well advanced, much remains to be done in the areas of plant biology and phytosociology. However, we think we have sufficiently emphasised the great interest of this country. The continuation of tropical climatic conditions since very remote times, a situation at the meeting point of several floristic worlds, existing or extinct, and the phenomena of species evolution over long periods in an isolated environment account for the richness and originality of this flora.

The diversity of climatic and edaphic conditions and gradations of variation that are often extremely sudden, are also conditions that have favoured an intense intra-insular micro-endemism and the diversification of numerous plant formations, which are often remarkable for the forms of biological adaptation taken by many of their species. But as nearly everywhere else in the tropical world, the interference of man has greatly modified the distribution of plant formations and the composition of the flora. Some species, collected by the first botanists to explore Madagascar, have never been found again because the plant formations that contained them have disappeared.

Madagascar thus possesses an inheritance of inestimable value, but one which is gravely threatened. A great effort towards safeguarding it has already been made by the creation of nature reserves in many areas. But the struggle must be intensified to protect this natural heritage which is so rich, and to increase very quickly the means available to perfect our knowledge of it.

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