MORTON, J.K. 1972.

In VALENTINE, D.H. (ed.)

Taxonomy, phytogeography and evolution.
Academic Press, London, p. 221-236.

14 | Phytogeography of the West African Mountains

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INTRODUCTION

Mountains, like oceanic islands, have long been a focal point of interest to biogeographers. They provide a window into nature's laboratory, through which we can see the processes and products of evolution. Here evolutionary forces are concentrated and focused onto a smaller number of biota in simpler communities. Environmental extremes, such as temperature, wind, radiation, rainfall and drought operate on small isolated populations of plants and animals, often with an abundance of open habitats, where competition is at a minimum; for those same extremes of environment reduce the inflow of competitors from lower altitudes. Under such conditions evolution is accelerated, and the origin and survival of new biotypes is encouraged. Here too the effects of genetic drift are sometimes apparent. Chance survival of characters may occur in small populations when these characters are not subject to strong selective pressures. Hence mountains provide an excellent open-air laboratory in which to study evolution. This is, no doubt, one of the reasons why they have attracted the attention of so many biologists. However, a further reason, I am sure, is the beauty and grandeur of many mountains, and the peculiar fascination which they hold for so many of us.

The African mountains are remarkable because many of them lie on or near the equator, so that tropical and arctic conditions occur in close association, with tropical forest and savanna at the foot and arctic ice-fields and tundra at the top of the higher peaks.

LOCATION OF HIGH GROUND

Figure 1 shows the location of the higher land in Africa and of the alpine peaks. Land over 10,000 ft is restricted to a few more or less isolated
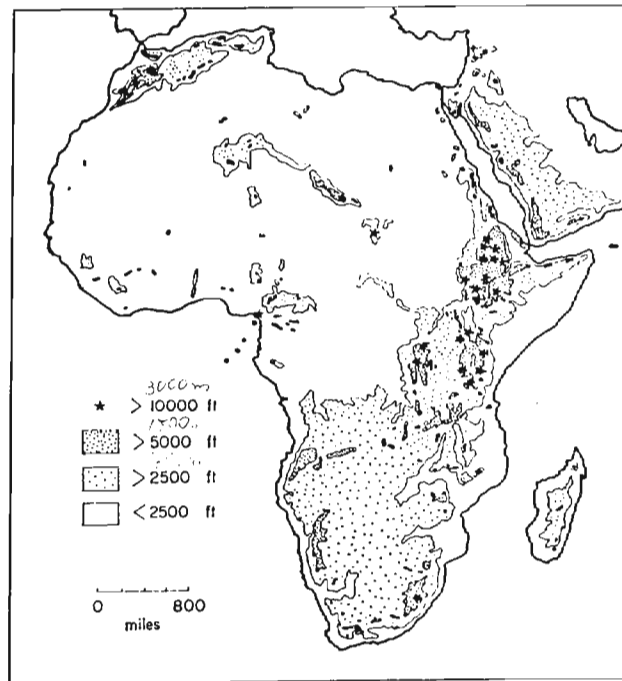
FIG. 1. Areas of high land in Africa.

FIG. 2. High land in West Africa.

peaks, mainly in the East African and Ethiopian regions. These peaks are the home of what Hedberg (1959) appropriately terms the afro-alpine flora. Mountains of lower elevation are much more frequent and many peaks, plateaux and massifs occur between 5000 and 10,000 ft. These are the home of montane floras and faunas, and present much of great interest to the biologist. At lower elevations the effects of altitude are also apparent in the floristic composition, if not in the physiognomy of the vegetation.

In West Africa (Fig. 2) the areas of higher land are fewer, lower and more distantly spaced, but each holds a characteristic association of montane species. Lower hills also occur which, in a few cases, hold remarkable assemblages of plants normally found at higher altitude. Such areas are of major importance to the biogeographer, for in times of changing climate they could form stepping stones for the migration of plants and animals, or refugia for the remnants of former floras and faunas. They emphasize that altitude is not the only factor determining the occurrence of montane species. Other factors, both environmental and historical, can partially compensate for it.
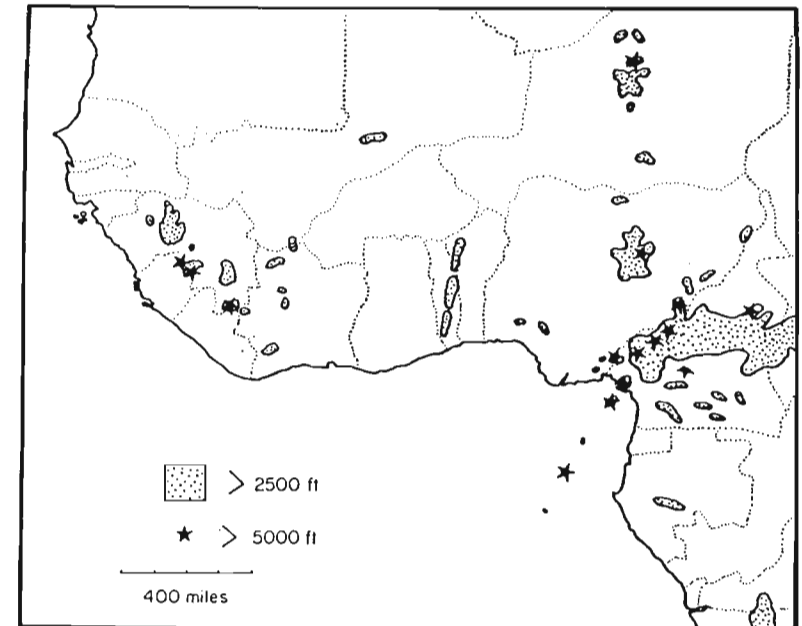
STATISTICS OF THE WEST AFRICAN FLORA

West Africa has a flora of some 7500 species. It has been the subject of intensive study over the last 20 years with the preparation of the revised edition of the Flora of West Tropical Africa. As a result our knowledge of the taxonomy, nomenclature and distribution of the vascular plants of this region is probably more complete than that of any other major region in tropical Africa—perhaps even in the tropical world. The following analysis deals only with the dicotyledons (the revision of the monocotyledons is not yet published) and covers both mainland West Africa and the offshore islands of Principé, S. Tomé and Annobon (data from Hepper and Keay, 1954, 1963; Exell, 1944, 1956). Out of 5091 species of dicotyledons 718 (14%) are montane. I have defined montane species as those predominantly or exclusively associated with land over 2500 ft. Land of this elevation is markedly disjunct in West Africa and can be grouped into 4 major systems.

(1) The Cameroons system—i.e. Cameroons Mt., Fernando Po (only 40 miles offshore), the Adamaoua and Mandara ranges extending inland

to near Lake Chad; the Bauchi plateau, and isolated peaks in southern Nigeria—Oban and the Idanre Hills.

(2) The Togoland system—the Togoland Hills and Atakora Mts.

(3) The Guinean system including the Nimba and Loma Mts, Tingi Hills and the Fouta Djalon, etc.

(4) The oceanic islands of Principé and S. Tomé (Annobon is too low to have a montane flora).

Within the montane flora of West Africa 47% of the species are confined to West Africa—i.e. are West African endemics; 53% are species which also occur outside West Africa, mainly on the mountains of East and Central Africa, i.e. are widespread species.

ENDEMISM

Most of the endemics are confined to only one of the four mountain systems which I have described; only 15% occur on two or more systems. The Cameroons system is by far the richest in endemics with 48%. The Guinean system has 20%. The islands have 15% and the Togoland system only 2%.

The high incidence of endemism (47%) in the mountains of West Africa is remarkable and is an indication both of the active evolution which has occurred, and is still occurring, in these mountains, and also of the considerable degree of isolation to which this flora has been subject. Many of these endemics are species of apparently recent origin with close relatives either in the montane vegetation or in the lowland forest and savanna.

As shown in Table I, several genera and families have been particularly successful in exploiting the opportunities afforded by these mountains and islands, thereby filling the ecological niches with new species.

Equally remarkable is the dearth of endemics in most of the larger mainly tropical families which make up a major part of the lowland forest floras. The numbers of endemic species in these families are as follows: Annonaceae 3; Menispermaceae 3; Woody Papilionaceae 3; Caesalpiniaceae 0; Mimosaceae 0; Moraceae 1; Meliaceae 3; Connaraceae 1.

A comparison of endemics in the mainland mountains with those of the islands (Table II) provides an explanation of these data.

The significance of these figures lies, not in the dearth of montane savanna endemics on the islands (this is to be expected, for there is no montane savanna on them), but in the high percentage of such endemics

TABLE I. Endemic montane species in W. Africa.

	No. of montane species in West Africa	No. of these which are endemics	Habitat, etc.
Dissotis	17	15	forest edge, rocks, grassland
Impatiens	17	13	mainly forest
Vernonia	38	14	forest edge and grass
Lobelia	12	6	mainly grassland
Plectranthus	12	7	forest and grassland
Solenostemon	8	7	grassland
Begonia	7	7	6 from islands
Compositae	138	47	—
Melastomataceae	33	30	—
Acanthaceae	24	18	—
Herbaceous Papilionaceae	67	20	—
Rubiaceae	57	29	14 from islands

TABLE II. Habitat and location of endemic montane species.

	Forest	Savanna (inc. woodland and rocky scrub)
Mainland	71 (26%)	201 (74%)
Islands	48 (95%)	2 (5%)

on the mainland montane savannas. There is no lack of montane forest on the mainland, and in fact its area probably exceeds that covered by montane savanna; but only one third as many endemics have evolved in it as in the savanna. The reasons for these differences become clear when we consider the past history of these mountains and islands. As Exell (1944, 1956) observed, the islands of S. Tomé, Principé and Annobon have been isolated from the mainland since their volcanic origin during the Tertiary. Their present flora must have arisen from chance arrivals across the ocean from mainland Africa. S. Tomé (the largest of the islands, with the major area of montane habitat) lies 250 miles from Fernando Po and from the Niger Delta, and 150 miles from the Gabon coast. With such distances, and with the large expanse of coastline formed by the arc

of the mainland from which migrants could originate, the ocean does not form a complete barrier to plant dispersal—rather it is an effective means of ensuring that some dispersal occurs. Anyone who has lived on the coast of Africa near the mouths of some of the major rivers, is familiar with the considerable quantities of plant material which are brought down into the sea. This ranges from whole trees and branches, complete with epiphytes, to bulbs, rootstocks, fruits and seeds. These are distributed along the coast, often carried considerable distances by tides and currents. That most of this living material perishes in the salt water is undoubtedly true, but it is equally obvious from the plants which begin to grow on the shoreline and in small lagoons etc, that many survive. Hence I am of the opinion that distances across the sea of 150 or 250 miles are insufficient to form a complete barrier to plant migration. It is by such ocean transport, of the normal forest flora of the coast of the Gulf of Guinea, that these islands were colonized. Their flora is almost wholly derived from that of the lowland forests. Most of the endemics are closely related to, and presumably evolved from, these immigrants from the mainland. The high proportion of forest endemics in the mountains of these islands is merely a reflection of the natural vacuum that existed on these islands after their volcanic origin and of the forest habitat which dominates them. Chance arrivals would find a wide range of niches in which to grow, with rich volcanic ash and abundant rain. Under these favorable conditions, with a lack of competition and with small isolated populations, rapid evolution would be likely to occur. Thus these islands became populated by species from the lowland forests of the mainland and by endemics which evolved from them and were able to colonize the montane habitats. The montane flora of these islands consists of 84 species (dicotyledons only) of which 50 are endemic. The other 34 occur on the mainland, having either migrated to or from the islands. All except 3 have obvious possible means of dispersal over the distances involved. Fourteen have seeds or fruits eaten by birds or bats; 10 have sticky or small seeds which could become attached to birds; 3 have efficient wind-borne fruits (with pappus); and 4 have large floating fruits which may have been water-borne at a time when vegetation belts were lower than they are today.

In contrast to the islands, the montane forests of the mainland have not shown the same degree of speciation because they have always presented a closed system, which has usually been continuous with the lowland forests. Any changes in climate which occurred would merely elevate or depress the upper limit of the forest. Hence no ecological vacuum

existed in which accelerated speciation would be favoured, and as a result few montane forest endemics have evolved.

The montane grasslands, on the other hand, present a situation comparable to that on the islands. They were colonized by species from the lowland savanna and by migrants from other mountain systems. Changes in climate, both temperature and rainfall, caused advances of the forest, and most of the areas of montane grassland were probably greatly reduced or eliminated, except on the high alpine peaks of the Cameroons. However, cliffs and rock outcrops formed refugia in which dense forest could never grow, regardless of climate. Here many montane grassland species survived, though doubtless many others became extinct. Such refugia within the limits of the present range of forest can be seen today in many parts of West Africa, e.g. the Nkawkaw Scarp in Ghana, the Idanre Hills of Nigeria, the hills of Bafodia and the Freetown Peninsula in Sierra Leone. Further oscillations in climate caused recession of the forest, leaving considerable areas on the mountain tops suited for grassland species, but with relatively few such species available to colonize them. A partial ecological vacuum was created, similar to that on the islands after their volcanic origin. In this vacuum rapid speciation occurred. New types arose from species which moved into the montane savanna habitat from the refugia, the surrounding forest and from further afield, and adapted to it.

This I believe to be the explanation for the high endemism in the montane grassland floras of the mainland and the montane forest flora of the islands. Both have been areas of evolutionary opportunity. Speciation was stimulated by the creation of ecological vacua which could not be filled from surrounding sources. In the case of the mainland mountains, climatic changes were the cause, through a shift in the limits of the forest; in the case of the islands it was their volcanic origin, de novo out of the sea.

The process of speciation on the mountains of the mainland can be likened to an evolutionary pump. Climatic changes drive the pump. The piston is the forest which advances and retreats on the mountain sides. The montane grasslands on the summits are thus alternatively compressed and allowed to expand. New types of plants evolve to fill the expanded grassland habitats. The next stroke of the pump will not destroy all these new types. In many cases it will merely compress them and bring them into close proximity in the refugia. This will stimulate the production of more variation through hybridization which will provide the raw material for another spurt of evolution during the next expansion of the grassland habitats when the piston again descends.

WIDESPREAD SPECIES AND DISJUNCTION

The remaining 53% of the montane flora of West Africa consists of widespread species, i.e. those which also occur in areas outside West Africa, and in almost all cases on the mountains of East and Central Africa. They represent but a small proportion of the total montane flora of tropical Africa. Hooker (1864) in the first account of the flora of Cameroons Mountain pointed out that it was but an impoverished version of the flora of the other high mountains of Africa. It is often assumed, no doubt correctly, that most of these plants migrated into West Africa, though I am sure some also migrated in the other direction to enrich the floras of East and Central Africa. Analysis of these widespread species shows that 36% only get as far as the Bauchi Plateau and interior part of the Cameroons system (southwards to the Bamenda Highlands); 29% penetrate to Cameroons Mountain and Fernando Po; 9% have reached the islands of the Gulf of Guinea; 2% occur on the Togoland system, but not further west; and 20% extend to the Guinean system.

A further 4% have reached the Guinean system but are absent from the intervening mountains of West Africa, i.e. they either made a long distance hop from East or Central Africa to the Guinean system, or they migrated across the intervening area and then died out (or collectors have yet to find them!).

ADAPTATIONS TO THE AFRICAN MONTANE ENVIRONMENT

What characteristics have enabled plants to migrate into montane habitats in Africa and to speciate there? Information is fragmentary, but several aspects warrant comment, particularly those related to daylength, reproductive biology and polyploidy.

1. Daylength

Many of the afro-alpine species (which occur on the high peaks of the East African mountains and the Cameroons) belong to genera, and in some cases species, mainly found in the northern hemisphere, where they flower under the long day conditions of the northern summers. Of 54 species of afro-alpine plants which I have successfully grown to flowering and which belong to these high latitude genera, all appear to be daylength neutral—none are short-day species. This is in marked contrast to many of the species belonging to lowland tropical genera, which are short-day plants. It would appear that species which migrated from the Northern

regions into afro-alpine habitats have not undergone any basic change in the physiology of flowering; they have not become short-day plants. Thus it may be presumed that they were pre-adapted to the daylength conditions of the African mountains.

2. Reproductive Biology

Most of the African montane species which I have grown in cultivation have proved to be self-compatible and in many cases self-pollinating. This applies to all the species of the genera (Table III) which I have been able to study.

TABLE III. Self-compatible genera of the montane flora.

Family	Genus*
Gramineae	*Poa, Agrostis, Aira, Deschampsia, Pennisetum*
Cyperaceae	*Carex, Cyperus*
Juncaceae	*Luzula*
Caryophyllaceae	*Uebelinia, Stellaria, Cerastium, Sagina, Silene*
Labiatae	*Satureja, Salvia,* and most species of *Solenostemon* and *Plectranthus*
Compositae	*Crassocephalum, Dichrocephala, Laggara, Aspilia, Crepis, Sonchus,* many species of *Helichrysum* and *Vernonia*
Rubiaceae	*Galium, Anthospermum*
Umbelliferae	*Sanicula, Caucalis, Cryptotaenia, Pimpinella*
Geraniaceae	*Geranium*
Rosaceae	*Rubus, Alchemilla*
Papilionaceae	*Trifolium, Indigofera, Desmodium,* and at least some species of *Crotalaria* and *Vigna*
Urticaceae	*Parietaria*

* *Note:* It is possible that a few of these species may be apomicts.

In marked contrast is the large-flowered genus *Dissotis*, which has speciated so freely in the West African mountains and produced many endemics. These are mostly insect pollinated and in many cases self-incompatible. Few members of the montane flora are obligate inbreeders and most have retained an unspecialized reproductive biology—a valuable adaptation for species migrating into new areas.

3. Polyploidy

Polyploidy has also played a role in the evolution of these montane floras. Several years ago (Morton, 1966) I reported that the incidence of polyploidy in the flowering plants of Cameroons Mountain was 49%, almost the same as that in the East African mountains (45%). This is in marked contrast to the lower percentage (26%) found in the flora of West Africa as a whole. The association of polyploidy with montane habitats is well seen in a number of species which occur in both the lowlands and the mountains (Table IV).

TABLE IV. Intraspecific polyploidy and the montane habitat.

Name	Somatic chromosome number
Platostoma africanum P. Beauv.	14, 28, 42
Crassocephalum crepidioides (Benth.) S. Moore	20, 40
Commelina benghalensis L.	22, 44, 66
Commelina diffusa Burm. f.	30, 60
Aneilema beniniense (P. Beauv.) Kunth	52, 78
Aneilema umbrosum (Vahl) Kunth	20, 40, *ca* 100
Crinum ornatum (Ait.) Bury	22, 44, 88
Eupatorium africanum Oliv. and Hiern.	22, 44
Hyptis lanceolata Poir.	32, 64

TABLE V. Interspecific polyploidy and the montane habitat.

Species	Somatic chromosome no.	Species	Somatic chromosome no.
Rubus fellatae A. Char., R. pinnatus Willd.	28	*R. exsuccus* Steud.	42
Vernonia undulata Oliv. & Hiern.	18	*V. blumioides* Hook. f.	36
Achyrospermum oblongifolium Bak.	28	*A. africanum* Hook. f.	84
Microglossa volubilis DC.	18	*M. densiflora* Hook. f.	36
Cardamine africana L., C. hirsuta L.	16	*C. trichocarpa* Hochst.	32
Geranium simense Hochst. ex. A. Rich.	28	*G. ocellatum* Cambess.	56

Many of the polyploids of Table IV are probably incipient new species and several which are morphologically distinct have been given infraspecific recognition. Cases involving distinct but related species are also frequent (Table V).

Hence it is clear that polyploidy has been a significant factor in the evolution of the montane floras.

THE SIGNIFICANCE OF DISJUNCTION

Fifty-three per cent of the montane species of West Africa also occur outside this region and as a result have a markedly disjunct distribution.
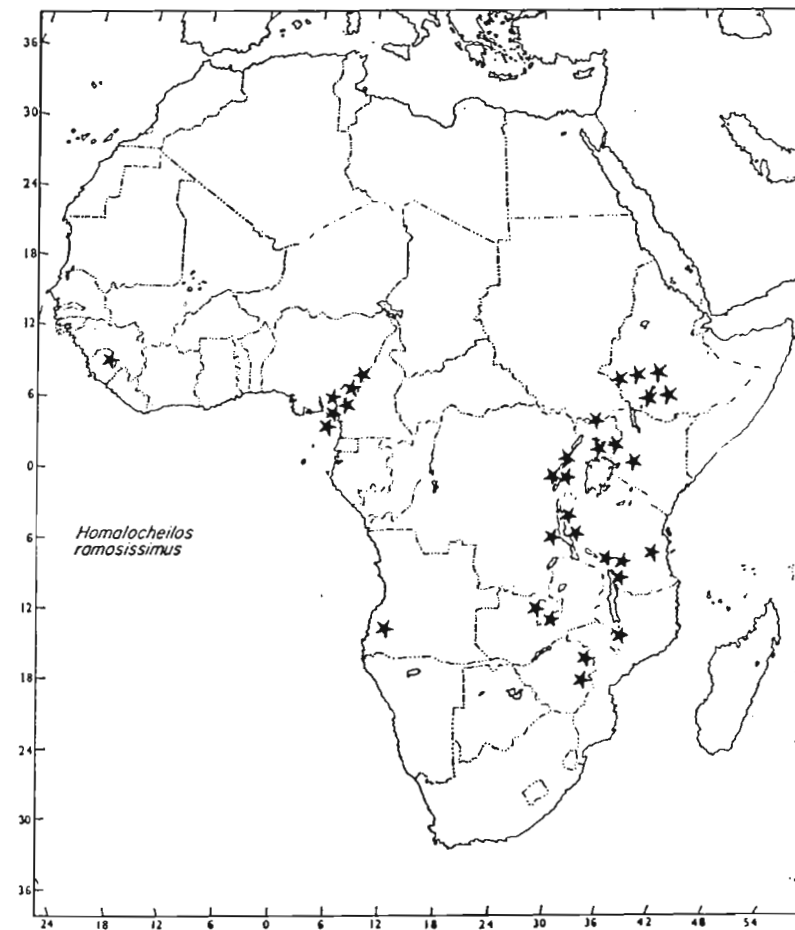

FIG. 3. Distribution of *Homolocheilos ramosissimus*, showing a typical pattern of disjunction.

Homalocheilos ramosissimus (Hook.f.) J. K. Morton (Fig. 3) is a typical example. Many of their stations are separated by considerable distances. I have previously suggested (Morton, 1961) that these disjunctions could only be explained on the basis of past climatic changes in Africa, which would have extended the areas occupied by montane species, though not necessarily making them continuous. Data on present day altitudinal ranges of many of the montane species suggests that a lowering of vegetation belts of up to 3000 ft (i.e. equivalent to a drop in temperature in the region of 4° to 6°C) must have occurred in relatively recent times. (Most of the montane species have diverged but little in their disjunct populations and hence have probably not been isolated for very long.)

Why postulate climatic change? Could not long-distance dispersal account for these disjunctions? That some long-distance dispersal has occurred I do not doubt. The small seeds of such plants as *Drosera* and *Radiola* could become attached to the feet or feathers of birds, which might carry them appreciable distances. Similarly the spores of ferns and the minute seeds of orchids would appear to be well adapted to long distance dispersal in the upper atmosphere. However, many heavy-seeded plants have no conceivable means of traversing great distances across the land, where flotation on ocean currents cannot be involved—e.g. *Crossandra massaica* Mildbr. and *Ochna ovata* F. Hoffm., both of which are confined in West Africa to the Shai Hills of Ghana but occur in east or central Africa— a disjunction of over 2000 miles. To discount wholly climatic change we must be able to show that such plants have a means of dispersal across the distances involved. In many cases no such means exist. An analysis of dispersal adaptations in the flora of one of the mountain groups in West Africa, the Loma Mountains and Tingi Hills (Table VI), gives some indication of how insufficient are theories of long-distance dispersal in accounting for present-day distributions patterns. These mountains have 183 montane species of flowering plants (including monocotyledons).

It appears that less than half of this flora has any apparent possible means of traversing appreciable distances, and even amongst these it is doubtful whether many could travel from one side of the continent to the other— distances of 1000 to 2000 miles. However, given climate change, these distances would be greatly reduced. Upland areas lying between the main mountain systems could support montane communities and become stepping stones for the spread of the montane flora. In West Africa, lowering of vegetation belts by about 2000 ft would create a situation in which montane communities were rarely if ever more than 100 miles apart,

TABLE VI. Dispersal of seeds in 183 montane species
of the Loma Mountains and Tingi Hills

Mode of seed dispersal	Percentage of flora
Small seeds, possibly suited for dispersal by wind or on the feet and feathers of birds	22
Succulent fruits; or seeds eaten by birds or bats	12
With effective means of wind dispersal (e.g. pappus)	6
Total adapted to some form of long-distance dispersal	40
With sticky seeds or fruits, suited for dispersal by mammals	9
Inefficient means of wind dispersal suited for local transport only	6
Explosive mechanisms	6
Adapted for dispersal by ants	2
Total adapted for local dispersal	23
With large seeds or fruits with no apparent means of dispersal	37

well within the range of dispersal by roving animals, birds and wind; the constipated duck or elephant then becomes a real factor in plant dispersal! A lowering of vegetation belts by 2000 to 3000 ft in the area separating the Cameroons system and the mountains of East and Central Africa would have a similar effect and a series of short hops would be all that was necessary to get the present montane flora across the continent. It should be noted that even today, few of the afro-alpine species of the Cameroons are confined to the summit peaks. Most can be found as low as 6000 ft and in many cases much lower. The afro-alpine element does not extend west of the Cameroons system.

In West Africa many upland areas exist between the main mountain systems, e.g. Idanre and Ado in Nigeria, the Shai, Atewa and Banda Hills and the Gambaga Scarp in Ghana, the Gbengbe and Kuru Hills in Sierra Leone. Most of these already hold a small and presumably relict montane flora, indicating that they have functioned as such stepping stones for migration under former climates which were more favourable to montane species. A corridor of high land connects the mountains of Central and

East Africa with the Cameroons system, and out of this, smaller peaks rise which would have formed the links in a chain of montane communities across the continent.

That climatic changes of the size envisaged have occurred has been demonstrated in recent years by many workers in a variety of fields. The evidence has been ably collated by Coetzee and Zinderen Bakker (1970) and Zinderen Bakker (1969), and reviewed by Hedberg (1969). It comes from numerous studies on fossil pollen in many parts of Africa; from fossil snow lines and glacial drift on the high mountains of East Africa; from fossil evidence of frost activity at low altitudes in North and southern Africa; from lake deposits in the Sahara; and from studies on other groups of organisms including birds (Moreau, 1966), butterflies (Carcasson, 1964) and the tropical forest (Aubréville, 1949). As observed by Livingstone (1967) and Hedberg (1969), some of the data from pollen analysis and glacial phenomena may be interpreted in terms of either a depression in temperature or a change in rainfall and humidity. However, much of the other evidence clearly indicates a lowering of temperature. The evidence from these sources indicates that 2 major cool periods existed, together with a third more moderate period. These extended between 50,000–43,000 years ago, 30,000–12,000 years ago and 5500–4700 years ago. The depression in temperature involved in the first two has been variously estimated at 4° and 9°C in tropical Africa, greater in North Africa. The more recent cool spell was apparently less severe, but it too would have an effect on plant distribution. The last major change in Africa, that between 30,000 and 12,000 years ago, was contemporaneous with the Würm glacial advance of Europe (which is equated with the Wisconsin of North America) and has been termed the Mount Kenya Hypothermal (Zinderen Bakker, 1969).

Though both Exell (1944, 1956) and Hedberg (1969) tend to discount climatic change as a factor in the distribution of the African flora, they worked on very specialized floras, Exell on oceanic islands and Hedberg on the alpine flora of the high mountains. In both cases long-distance dispersal must have played a major role in producing the present day floras, though the distances involved range only from about 100 to 300 miles. In the case of the East African mountains it could have been less under different climatic conditions. It would be wrong to extrapolate from the peculiar and very specialized problems of these island and high alpine floras, to the whole of the African upland floras. Biogeographers are frequently guilty of such extrapolations; hence we have those who

would explain all distributions in terms of, on the one hand long distance dispersal, or on the other of climatic change and land bridges. If there is any consistency in Nature it is in her diversity—diversity both in form, function and process—and this is no less true of distribution methods.

CONCLUSIONS

It is my belief, on the basis of the evidence presented here, that the present-day distribution of the montane floras of Africa is the result of:

(1) Climatic change which has created major advances and recessions of the montane (and lowland) vegetation.

(2) Dispersal, most of it over relatively short distances at periods of maximum extent of the montane vegetation, when most of the distances involved would have been in the region of 50 to 100 miles—well within the capacity for dispersal by wind, birds and wandering animals. Longer distance dispersal has also doubtless occurred, particularly of species with minute seeds which might be carried by wind and migrating birds. In the case of the oceanic islands dispersal by the sea has been the major factor.

(3) Rapid speciation in (a) the montane habitats resulting from a type of "evolutionary pump" operated by climatic change; (b) the forested islands where an ecological vacuum was created by their volcanic origin in the Gulf of Guinea.

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