Geographical distribution of present day Poaceae as evidence for the origin of African floras

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ABSTRACT

The major tribes and sub-families of grasses occupy worldwide latitudinal belts, which can be related to an evolutionary sequence of climatic adaptations. However, genera tend to be confined to individual continents, suggesting that grasses do not easily cross the oceans, and that the worldwide distribution of the family may have been achieved when the continents were closer together. Species distributions are likewise strongly influenced by the effect of climatic adaptation and continental isolation, but they show a number of aberrations. These are probably a legacy of climatic disturbance during the Pleistocene.

RÉSUMÉ

LA RÉPARTITION GÉOGRAPHIQUE DES POACÉES ACTUELLES EN TANT QU'ARGUMENT A L'APPUI DE L'ORIGINE DES FLORES AFRICAINES

Les principales tribus et sous-familles des graminées occupent à une échelle mondiale des zonations latitudinales qui peuvent être apparentées à une séquence évolutionnaire d'adaptations climatiques. Cependant, les genres ont tendance à être confinés à des continents isolés, ce qui laisse supposer que les graminées ne traversent pas facilement les océans et que la répartition générale de la famille dans le monde peut s'être accomplie quand les continents étaient plus rapprochés les uns des autres. Les répartitions d'espèces sont de la même façon fortement influencées par l'effet de l'adaptation climatique et de l'isolement continental, mais elles montrent un certain nombre d'aberrations. Celles-ci sont probablement un héritage de la perturbation climatique pendant le Pléistocène.

Direct evidence of past floras can only be obtained from the geological record, but it is often so scanty as to be of little help. However, present day floras are the children of the past, and contain at least some clues to their ancestry. These clues are of two kinds.

The first relates to present day distributions. Distribution maps for individual species are often instructive, but one should be wary of reading too much significance into them. This is partly because of the probabilistic element in plant dispersal. A single anomalously distributed species points only to an event so unlikely that we may never discover what it was. Ten or twenty similar distributions raise our expectations of more prosaic causal factors, and offer some hope of deducing what they might have been. The other reason for interpreting individual distributions with caution is that, by ignoring the less distinctive patterns enjoyed by the majority of species, they leave too much unsaid. I have therefore approached the problem of plant distribution by seeking first of all to understand the commonplace, using large statistically robust samples.

The second kind of clue comes from phylogeny. At its simplest, this amounts to an initial presumption that tribes evolved before genera and genera before species, offering the possibility that successive levels of the taxonomic hierarchy will afford us a sequence of glimpses into the past. Inevitably these glimpses will be grossly distorted by subsequent history, but it is nevertheless possible to glean something from them.

Of course, neither of these clues can be pursued with any confidence if they are obscured by taxonomic uncertainty. It is fortunate that, largely because of their economic importance, our taxonomic understanding of the grasses has developed to a point at which we can apply these methods with a reasonable hope that taxonomic doubt will not be a limiting factor. Let us then look at the distribution of the grasses to see what can be deduced from it.

The family

The factors contributing to the world-wide success of the grasses are fairly well-known, but it is much more difficult to assess their relative importance. A glance at the map in Cross (1980) shows that species counts are low in deserts, and it is a matter of common observation that they are also low in the shade of forests. Grasses do best in the region of seasonal rainfall between forest and desert, and it seems that their emergence as a dominant vegetation type was primarily a matter of climatic adaptation to this zone on the forest fringe. These adaptations can be seen in their life-form with its basal tillering, incorporation of the leaf-sheath into the mechanical system thus permitting the development of intercalary meristems, and the further modification of leaf-sheaths to replace the floral envelope. Undoubtedly this was associated with more subtle physiological adaptations, implied by such features as the narrow erect leaf-blades and peculiar stomata.

The second major factor was that of fire, which seems, in the African savanna at least, to have been a regular feature of the natural environment (Komarek, 1972). Grasses burn readily in the dry season, but are themselves tolerant of fires severe enough to eliminate many other life-forms, and so we have an ecosystem in which the grasses provide the fuel which ensures their own survival.

Thirdly, we have the emergence of grass-eating herbivores, and a further development of the

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ecosystem into one in which the grasses attract and sustain a degree of predation sufficient to cripple their competitors.

The final factor is man, who has joined the ecosystem and exploited it for the subsistence of himself and his livestock. In so doing, he has vastly extended its range by felling the trees which previously excluded it. Indeed, he has so confused matters that we can now only guess at what the natural grassland climate really was.

There is much that is obscure in the early history of the grasses, but the first critical step seems to have been the emergence of a life-form which was outstandingly adaptable to the environment of the forest fringe, and to subsequent events in the ecosystem that developed there. It conferred a competitive advantage sufficient for the family to occupy and to maintain its hold upon open habitats throughout the world.

Sub-families and tribes

The distribution of the major infra-familial taxa have been mapped by Hartley (1958a, 1958b, 1973), Hartley & Slater (1960) and Cross (1980), whose findings may be summarized as follows:

> Andropogoneae, Paniceae, Chloridoideae, Bambusoideae — tropical. Arundinoideae — subtropical and warm temperate zones of southern hemisphere. Pooideae — north temperate.

To understand this distribution it is necessary to take a quick look at the taxonomy of the family (Clayton, 1981). The most primitive grasses, as judged by their inflorescence structure, are the Bambusoideae, whose nearest neighbours among the Angiosperms seem to be Flagellariaceae. Since both are rain-forest groups, it is reasonable to infer that grasses arose in or near the forest. This would seem to be contradicted by their anemophilous pollination, but actually the Bambusoideae, as defined by certain anatomical peculiarities, contain three groups which can be interpreted as follows:

Bamboos. Grasses which became secondarily woody, and entered the forest to compete with trees.

Bamboo allies. A collection of broad-leaved shade-loving curios, which seem to represent the end products of unsuccessful lines that have taken refuge in the forest. Their bizarre variations give some inkling of the diversity which may once have existed before the family acquired its characteristic life-form.

Oryzeae. Although now specializing in aquatic habitats, they give some hint of the kind of open environment adjacent to forest in which the grasses might have arisen.

The next step was the Arundinoideae; true grasses of the open savanna, which are primitive in the sense that their anatomy represents the lowest common denominator of subsequent sub-families.

There then arose two divergent lines; the Chloridoideae which are evidently derived from Arundinoideae, and the Panicoideae, the derivation

of which is less obvious and still somewhat controversial. They herald a new development — the evolution of Kranz anatomy and C4 metabolism. This makes photosynthesis more efficient in high temperatures and high light intensities, so it is no surprise to find that these are now the principal tropical sub-families. Nor that the Arundinoideae have been unable to compete with them, and have found a refuge in the southern subtropics.

The final step was a comparatively slight anatomical deviation from Arundinoideae. But it was evidently accompanied by a more profound physiological adaptation to cold climates, enabling the Pooideae to become the predominant sub-family of the north temperate zone.

We find, therefore, a history of physiological adaptations, whose net result has been to align the sub-families along world-wide climatic latitudinal belts. They pay little heed to ocean barriers, and even at subtribal level one is hard pressed to distinguish between continental floras.

Genera

Patterns of generic distribution may be found by dividing the world into a number of geographical units, recording each genus as present or absent in each unit, and sorting the resulting data matrix by cluster analysis. Each cluster is then displayed by transferring the presence counts of its constituent genera onto a map, and drawing in contours. The results can be summarized as follows (Clayton, 1975):

87 widespread genera

450 genera divided into seven major clusters, each of continental size

98 genera shared between geographically adjacent clusters. They link the clusters into two chains, underlining the difference already observed between tropical sub-families and the temperate Pooideae.

Evidently genera are not good travellers, two thirds of them being confined to single continents; yet we have already seen that the tribes are rather uniformly dispersed. To resolve the apparent paradox, we must look into the matter of dating.

The first positive record of grasses comes from pollen in the Palaeocene. It is followed, in the Oligocene, by fossil spikelets of *Stipa*, and by the first appearance of high-crowned teeth among fossil mammals. The high-crowned tooth strongly indicates a shift from browsing to grazing since it is an adaptation to abrasive food, such as grass whose leaf epidermis contains grains of silica. We thus have evidence that by the Oligocene grassland was an established vegetation type, containing at least one extant genus (Clayton, 1981).

Now the continents parted company in the latter part of the Cretaceous, but had not drifted very far apart by the beginning of the Tertiary. For example, Africa and America were probably some 800 km apart in the Palaeocene, moving gradually towards their present separation of 2 500 km (Raven, 1979; Raven & Axelrod, 1974). We therefore have no

need to embark upon an inconclusive discussion of the feasibility of transoceanic dispersal, for the grasses evolved at a time when sea gaps were much less formidable obstacles, and I believe it was then that the tribes attained their world-wide distribution. Thereafter, genera continued to evolve, but intercontinental exchange became increasingly difficult as the gaps widened, and so generic distributions gradually assumed their present aspect of continental isolation.

Another point to emerge is that, at least by the measure of generic diversity, Africa contains the greatest of all the grassland ecosystems.

Species

Species can be analysed in much the same way as genera by scoring them as present or absent in quadrats of country size, and then applying cluster analysis. It is sometimes supposed that each species would have its own environmental optimum, resulting in a mosaic-like distribution pattern. This may be true on a local scale, but on a wider scale species are found to be rather strongly clustered, an effect which probably stems from entrainment with the dominant, climatically determined life-form. Individual members of a cluster may vary considerably in their environmental amplitude, so that the cluster has no sharp boundaries, but fades away gradually at the edges, and is best mapped by a form of contouring. This effect may well be exaggerated in the case of grasses, which display a great capacity for infiltrating the seral stages of communities from which they would otherwise be excluded. Certainly the grass flora of a given area is usually composed of species from several overlapping clusters or phytochoria.

When mapped out, smaller clusters tend to be nested within larger ones, a phenomenon which affords a natural basis for their classification; they have been described and mapped by Clayton & Cope (1980). The largest clusters of all are termed Kingdoms, of which there are probably five (the doubts concern South America, whose taxonomy is still very confused). Evidently this category reflects the continental isolation that we have already seen among genera.

The African grass flora is almost entirely Palaeo-tropical, but there are a few exceptions. Thus the Pan-temperate Kingdom extends to North Africa, and is represented south of the Sahara by a number of weedy introductions. There are also about 40 pan-tropical weeds of uncertain domicile, and a trace of Neo-tropical species; most of the latter are clearly introduced weeds, leaving about a dozen whose status is still arguable.

The Palaeo-tropical Kingdom may be divided into two Subkingdoms, evidently representing a lesser degree of continental isolation. The Deccan-Malaysian Subkingdom need not greatly concern us, apart from noting a sprinkling of records along the East African coast which are almost certainly the consequence of coastwise trading; the few records in West Africa are even more obviously associated with the hinterland of ports. The other half of the Palaeo-tropical Kingdom is the Afro-Arabian Sub-kingdom. This is the only purely notional unit which it has been found necessary to introduce, there being no grasses whose distribution matches its limits. However, its recognition serves to emphasize that African grass species are essentially African in origin.

The Afro-Arabian Subkingdom contains six Regions. With the possible exception of Madagascar, these Regions coincide with major climatically determined vegetation belts. They are in equilibrium with the environment, and their members have occupied all the territory available to them. Whatever migratory episodes they have suffered in the past, the regional species are those which have successfully adjusted their distribution to conform with current climatic patterns.

Domains within Regions are rather more interesting. Thus we find that within the Guineo-Congolan Region there are separate Guinean and Congolan Domains. There seems to be no obvious climatic reason why they should be thus confined, and the existence of separate species pools is probably attributable to difficulty in dispersing across the uplands of the Cameroon mountain range.

The Sudano-Zambezian Region contains Sudanian and Afro-oriental Subregions, corresponding to environmental differences sometimes informally summarized by the terms Lowland and Upland Africa. It is not so much a matter of absolute climatic differences or a major barrier at the junction of the Subregions, but rather that suitable habitats are sparser on the opposite side, making migration more difficult. The Subregional species are those which have not yet achieved it.

The Afro-oriental Subregion contains three Domains — Ethiopian, Zambezian and Transvaal. It may be that local climatic differences could account for the existence of three separate species pools within the savanna, but there is another possibility. The Saharo-Sindian Region dips southward to Tanzania and then reappears as an outlier in South West Africa, implying the former existence of an arid corridor between these now disjunct areas. The corridor would have surrounded the Ethiopian Domain and driven between the Zambezian and Transvaal Domains, permitting their floras to evolve in isolation. Although the Domains are now connected by continuous savanna, a unified species pool has not yet been fully restored.

Endemics

I have presented a model which relates African species pools to the major climatic zones through entrainment with the dominant vegetation type. They are sometimes subdivided when free dispersal is hindered by the filter effect of physical obstacles. They are occasionally distorted by an unresolved legacy of past climatic change. I have so far said little about the other main driving force of chorology, which is speciation.

This is a subject on which it is easy to theorize, but difficult to acquire factual evidence. One of the traditional approaches to the problem is through

endemism, and attempts to distinguish between centres of origin and refugia. The frequency of one-country endemics has been mapped by Clayton & Cope (1980), revealing classical centres in Fouta-Djallon and Ethiopia, but elsewhere the pattern is very confused. The highest counts occur in South Africa, Madagascar, Peninsular India, South East Asia and Australia, where isolation is clearly an important factor. Otherwise they are strongly correlated with mountain topography (the pediplain of the Congo-Zambezi watershed is an unexplained exception), and form long chains rather than discrete centres. In short, the concept of endemic centres, at least in its simple form, is shown to be somewhat naive and not particularly helpful. The geography of speciation remains an open question, but I would suggest that the striking difference between the mountains and the plains lies not so much with active speciation in the former, as with ruthless extinction in the latter.

The Afro-montane Region

There remains the matter of the Afro-montane flora, which presents a number of unusual and fascinating problems. Its grasses may be defined as those whose distribution lies mainly above 2 000 m, or as those which belong to the sub-family Pooideae; both definitions give substantially the same species list. They can be divided into four elements (Clayton, 1976):

1. A small element from the Pan-temperate Kingdom and its subdivisions. Most are widespread weedy species almost certainly introduced with agriculture. A very few are more characteristic of moorland than ruderal habitats, hinting at the possibility of a direct migratory route (birds?) between the moorlands of Europe and Africa.

2. The 'Afro-montane' species with a lower altitudinal limit of around 2 000 m, which show a quite surprising degree of uniformity on widely separated mountains. They have attracted much debate, the consensus of opinion being that dispersal was facilitated by 'stepping stones', during a period of cooler climates when suitable habitats developed on a number of lower peaks.

3. The 'Afro-alpine' species with a lower altitude limit of around 3 000 m, which show a quite different pattern of distribution, being either endemic to a single mountain, or sharing apparently random pairs of adjacent mountains. It seems that this element is the result of speciation to occupy the empty alpine environment created by the uplift of the great volcanoes and the Ruwenzori fault block; and that there has been no assured migratory route between peaks, but some random dispersal dependent on chance events.

4. A small South African element, being a northward extension of another montane flora of pooid grasses centred on the Drakensberg range.

We have already seen that the Pooideae probably arose in Eurasia, and it is tempting to relate their arrival in Africa to the Plio-Pleistocene creation of the great volcanoes on which they are now so prominent. But the concept of opportunistic migration from Europe does not altogether account for the presence of a second pooid flora in South Africa. It is difficult to estimate altitudes in Miocene Africa due to the extensive upwarping that occurred towards the end of this period, but there is evidence that a number of the older mountain blocks which we see today (particularly the Ethiopian massif) then stood at about 2 000 m. I believe that the pooid immigration was to these mountains, sufficiently long ago for two separate indigenous floras to differentiate. They are essentially native floras of long standing, and it would be misleading to think of them as Pan-temperate outliers.

The montane flora is obviously a distinct ecological entity, but its treatment as a separate Afro-montane chorological Region raises philosophical problems. It would seem to imply that the floras of adjacent ecological habitats could be independently distributed. There is no evidence that this is true of, say, swamps and dry land in Africa. Nor does it seem applicable to the montane flora of tropical Asia, where mountains occur as ranges rather than inselbergs. Is it, in fact, true of African mountains? If isochores are plotted for the Afro-montane grasses, they are found to be very similar to those of the Ethiopian Domain, implying that adjacent lowland and montane floras have not achieved any significant degree of independent migration.

Of course, at generic level, the lowland and montane floras are very different. Should we take account of generic chorology, with its very different time scale, when defining floristic elements, and if so where will this lead us? The montane grasses of the Old World tropics are certainly a special case, but treating them as Regional phytochoria seems to raise more problems than it solves.

I have presented a picture of how the grasses achieved their present distribution in Africa. It is essentially a fairly simple picture, for the use of large samples has averaged out idiosyncracies of ecological preferences, habitat distribution, community competition and dispersal probability. I am very conscious that gaps in the factual evidence have been bridged by speculation, and that the results pertain to only a single family. I look forward to seeing their generality tested by similar analyses of other families.

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