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## The dispersal of forest tree species in Uganda during the Upper Pleistocene

A. C. HAMILTON

### SUMMARY

The evidence relating to the history of lowland forest in Uganda during the Upper Pleistocene is reviewed. On the basis of present-day patterns of distribution of forest species and of pollen diagrams, a hypothesis of forest movement is put forward.

### RÉSUMÉ

L'auteur esquisse l'état de la connaissance scientifique de l'histoire de la forêt à basse altitude pendant le Pléistocène supérieur en Uganda. D'après la distribution actuelle des espèces forestières et les diagrammes polliniques, il présente une hypothèse sur l'évolution de la forêt.

Uganda has experienced great changes in climate during the Upper Pleistocene. The distribution of vegetation types as a whole and of species within vegetation types have undoubtedly been greatly affected by these vicissitudes. In this paper the evidence relating to the history of lowland forest within the country during the past 15 000 years is briefly reviewed.

Forest today covers about four percent of the land surface of Uganda (Langdale-Brown & al., 1964). The area of forest must, however, have been considerably greater before the arrival of iron-working agriculturalists during the last 2000 years (Posnansky, 1967; Soper, 1969). It has been estimated that forest forms the natural vegetation in those areas which experience two rainy seasons a year and have a mean annual rainfall of over 1140 mm and in those areas with only a single rainy season and a mean annual rainfall of at least 1520 mm (Langdale-Brown & al., 1964). Judging by the distribution of forest remnants and climatic data, the main areas of natural forest cover are considered to be a belt about 50 km wide around the northern shore of Lake Victoria, a strip running down the eastern shoulder of the Rift Valley, extending in places into the Rift itself, and the higher mountains.

A quantitative analysis of the vertical distribution of forest trees in Uganda has indicated that, when the country is considered as a whole, floristic composition changes gradually with increasing altitude (Hamilton, 1975). It would therefore appear that no clear-cut boundaries can be drawn between either highland and lowland forests or between highland and lowland forest species. For the purpose of the present

paper, lowland forest species are taken to be those which occur predominantly below an altitude of 2000 m.

Combinations of flora-areas	{	1	2	3	4	1	1	1	2	2	3	1	1	2	1
						2	3	4	3	4	4	2	2	3	2
												3	4	4	3
															4
Number of species recorded . . . . .		0	46	0	10	7	0	0	3	87	0	1	43	39	56

Table 1. — The number of lowland forest tree species in Uganda (from Hamilton, 1974) recorded from different combinations of flora-areas as used for the *Flora of Tropical East Africa* (Turrill & al., 1952-).

The horizontal distribution of lowland forest tree species in Uganda is best considered in relation to the four flora-areas (Fig. 1) into which the country has been divided for the *Flora of Tropical East Africa* (Turrill & al., 1952-). Judging by available records, lowland forest species show a clear-cut pattern of distribution in Uganda (Table 1), with forests becoming increasingly impoverished in terms of numbers of species from west to east and from south to north across the country (Hamilton, 1974). It is, for instance, noteworthy (1) that virtually all species found in Flora-area one are also found in Flora-area two, (2) that virtually all species found in Flora-area three are also found in both Flora-areas two and four, and (3) that there are many species found in Flora-area one which are absent from Flora-area, three, and *vice versa*. It is suggested that present-day patterns of species distribution are a product, not only of present-day environmental conditions, but also of forest history. It is postulated that lowland forest has spread from Flora-area two into Flora-area one, from Flora-area four into Flora-area three, and probably from Flora-area four into Flora-area two. This hypothesis of forest movement is illustrated on Figure 1.

Two pollen diagrams give dates for the spread of lowland forest across Uganda. Analysis of a sediment core from Pilkington Bay in Lake Victoria near Jinja shows that forest first appeared in the area at about 12 000 years B. P. (Kendall, 1969). Long-distance pollen in a diagram from Lake Mahoma, lying in a kettle hole on Ruwenzori, indicates that an approximately similar date marks the appearance or expansion of lowland forest on the plateau which surrounds the range (Livingstone, 1967; Hamilton, 1972). This forest expansion at 12 000 B. P. is attributable to climatic change. There is evidence, not only from Uganda, but also from other regions of East Africa, that a long dry period extending back to at least 25 000 years B. P. was succeeded at about 12 000 B.P. by much moister conditions (Butzer & al., 1972; van Zinderen Bakker & Coetzee, 1972).

Published pollen diagrams do not show the localities of the refugia where lowland forest was able to persist during the arid period which preceded 12 000 B.P. and, to estimate the sites of these, it is necessary at present to rely on distributional evidence, both botanical (Hamilton, 1974) and zoological (Kingdon, 1971). Judging by species richness, it is thought that the main Central African lowland forest refuge area lay in Eastern Zaire, probably extending into Uganda in the Impenetrable-Kayonza Forest region. A minor refugium may have been present at Sango Bay on the Lake Victoria shore, but, if present, this was probably neither large in area nor rich in species.

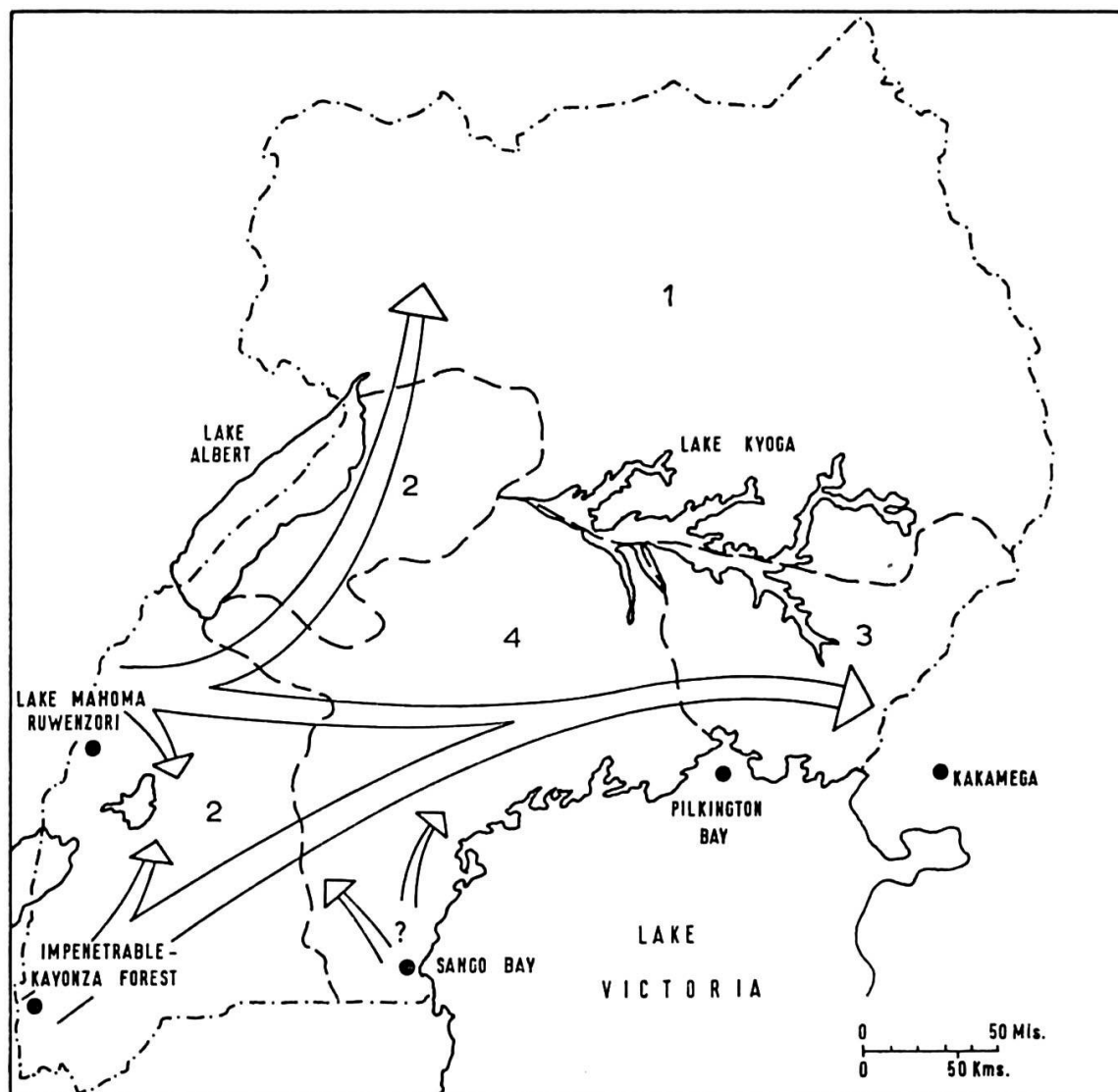


Fig. 1. — Map of Uganda showing the four flora-areas as used for the *Flora of Tropical East Africa* (Turrill & al., 1952-) and the postulated directions of lowland forest spread across the country after 12 000 years B.P.

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