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Late Pleistocene and Holocene History at Mubwindi Swamp, Southwest Uganda

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Deposits beneath Mubwindi Swamp provide a partial record of vegetation history since at least 43,000 yr ago. We studied pollen from two cores and obtained nine radiocarbon ages from one of these cores and three radiocarbon ages from the other. Pollen deposited before and soon after the last glacial maximum represents vegetation very different from the modern vegetation of the Mubwindi Swamp catchment. Although species now associated with higher altitudes were dominant some elements of moist lower montane forest persisted, possibly because of favorable soils or topography. The pollen data provides evidence for a late glacial montane forest refuge near Mubwindi Swamp. Moist lower montane forest became much more widespread soon after the glacial maximum. The only irrefutably Holocene sediments from Mubwindi Swamp date to the past 2500 yr. During this time a combination of climatic and human-induced changes in vegetation can be seen in the pollen records.

INTRODUCTION

The Rukiga highlands in the southwestern corner of Uganda (Fig. 1) contain steeply sloping ridges separated by deeply incised valleys. Many of the valleys are poorly drained and, because of the generally high levels of effective precipitation and relatively cool temperatures, contain deep accumulations of organic-rich sediments. Plant fossils preserved within such sediments at four sites have previously provided the basis for reconstruction of the region's vegetation history. Radiocarbon ages have been obtained for Muchoya Swamp (2260 m) and Ahakagyezi Swamp (1830 m) (Taylor, 1990, 1992, 1993). Evidence from the other two sites, Butongo and Katenga swamps (Morrison and Hamilton, 1974), has not been dated directly. This situation has limited attempts to produce a regionwide reconstruction of vegetation history, which has been hindered further by Muchoya and Ahakagyezi swamps being located close to the upper and lower altitudinal limits of the Rukiga highlands, respectively, while having catchments that have been heavily modified by forest clearance and agriculture.

We studied radiocarbon-dated fossil pollen from a fifth site in the Rukiga highlands, Mubwindi Swamp. The catchment for the swamp lies at an altitude intermediate between those of Muchoya and Ahakagyezi swamps and presently supports dense stands of moist lower montane forest which forms part of Bwindi (formally Impenetrable) Forest National Park. The pollen and radiocarbon data are used in conjunction with results from modern pollen and vegetation studies to establish the vegetation history of the Mubwindi Swamp catchment, and to provide a link to some of the dated changes in vegetation around Muchoya and Ahakagyezi swamps. The data provide a test of the theory that Bwindi Forest was close to the site of a forest refuge during past cold and dry climatic periods, as has been proposed by some researchers (e.g., Butynski, 1984; Hamilton, 1974, 1975, 1982).

The Study Area and Site

The Rukiga highlands lie within 1° 20′ of the equator and experience two dry seasons each year, from December to January and from June to August. Heavy mists often form during the mornings and after rain, particularly within the deeper valleys. Although there are no data available, it seems reasonable to assume that present-day temperature lapse rates in the Rukiga highlands do not differ greatly from the typical value for central and eastern Africa, 6.5°C per kilometer (Kenworthy, 1966).

In the absence of human activity, vegetation in montane areas in east and central Africa can be divided into three major altitudinal zones; the Afro-Alpine Belt (>3500 m), the Ericaceaous Belt (3500–2600 m), and the Montane Forest Belt (3300–1700 m) (Hedberg, 1951). There is considerable altitudinal overlap between the different types of vegeta-

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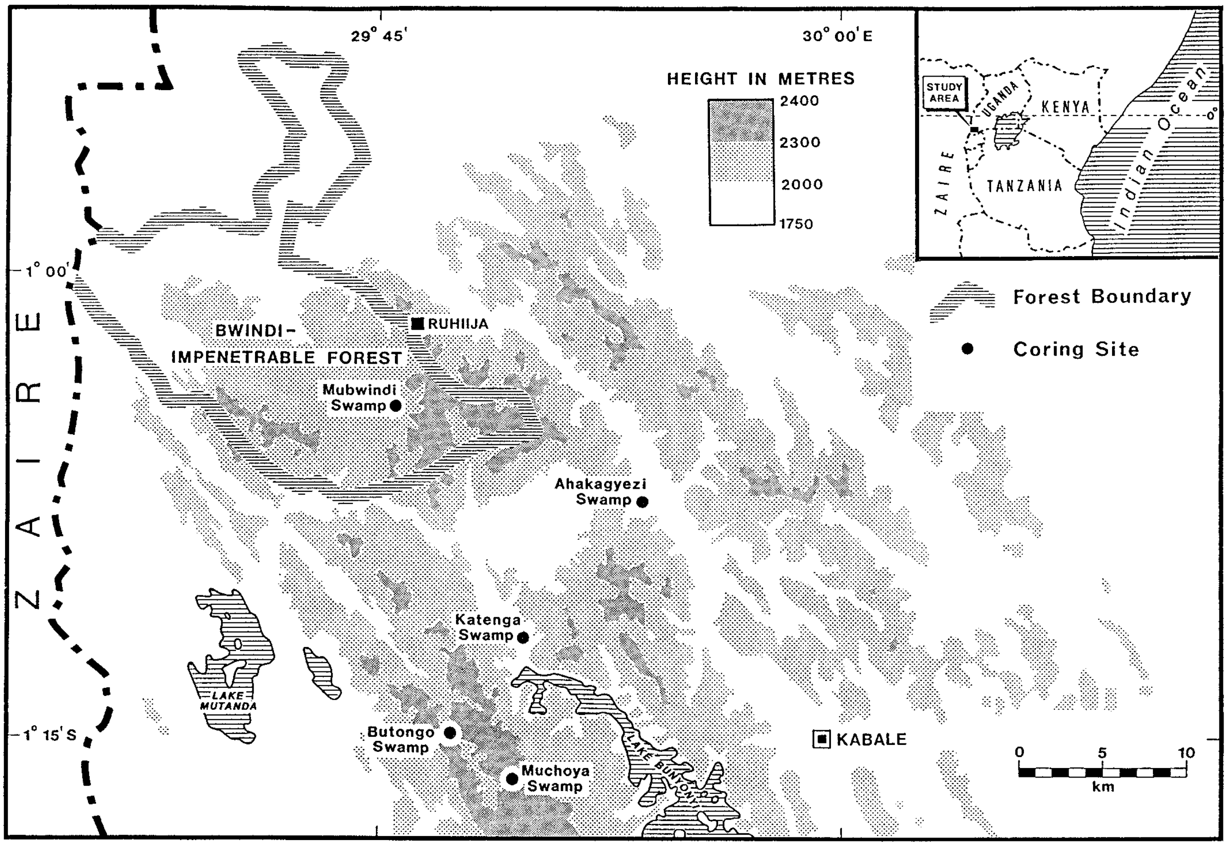


FIG. 1. The Rukiga Highlands, showing regional relief and the location of sites with paleoenvironmental records.

tion as a result of local climatic and edaphic factors. The montane forest belt, containing broad-leaved hardwood trees and less frequently conifers (Hamilton, 1982), would be the most common vegetation type in the Rukiga highlands in the absence of human activity. Several different zones are recognized within this broad vegetation belt by different authors (Chapman and White, 1970; Hedberg, 1951; Langdale-Brown *et al.*, 1964; Lind and Morrison, 1974). The classification proposed by Hamilton (1982) and adopted by Taylor (1990, 1992) is used here. According to this scheme, the montane forest belt is divided into upper and lower altitudinal zones with the adjectives moist and dry being used where appropriate. Bamboo forest is not regarded as an individual forest type, rather it is considered a successional stage toward moist lower montane forest.

Bwindi Forest, with an area around 320 km^2, represents the largest fragment of seminatural vegetation (Hamilton, 1974); most of the remainder of the Rukiga highlands has been heavily affected by people. The northern sector of Bwindi Forest is characterized by lower elevation, lower rainfall, a relatively subdued topography, and taxa associated with the upper altitudinal limits of lowland semievergreen forest (e.g., *Entandrophragma excelsum, Newtonia buchananii, Strombosia scheffleri,* and *Symphonia globulifera*). By comparison, the southern sector is altitudinally higher and wetter and has a much more rugged topography. The southern sector includes a number of deeply incised, poorly drained valleys, one of which contains Mubwindi Swamp. Within the southern sector there is a distinct vertical zonation of species. *Neoboutonia macrocalyx* and *Syzygium cordatum* are common on the lower slopes of valleys, while on land at mid-altitude *Chrysophyllum albidum* and *C. gorungosanum* are abundant in association with *Cassipourea ruwenzoriensis*, *Drypetes gerrardii*, and *S. scheffleri* (Hamilton, 1969). At higher altitudes taxa such as *Faurea saligna, Hagenia abyssinica*, and *Nuxia congesta* become common. *Podocarpus milanjianus* and *Olea capensis* ssp. *hochstetteri*, historically common on ridge and hilltop locations, have now largely been removed by pit-sawing activity (Howard, 1991). Large clear-cuts in both sectors contain *Alchornea hirtella, Macaranga kilimandscharica, N. macrocalyx,* and *Polyscias fulva* in association with *Acalypha* spp., *Mimulopsis solmii*, *Rubus* spp., and *Smilax* spp.

Mubwindi Swamp (Fig. 2) is situated at an altitude of 2100 m at the confluence of four valleys. The river below the valleys' confluence, presently toward the southern part of the swamp, has cut through the swamp sediments to

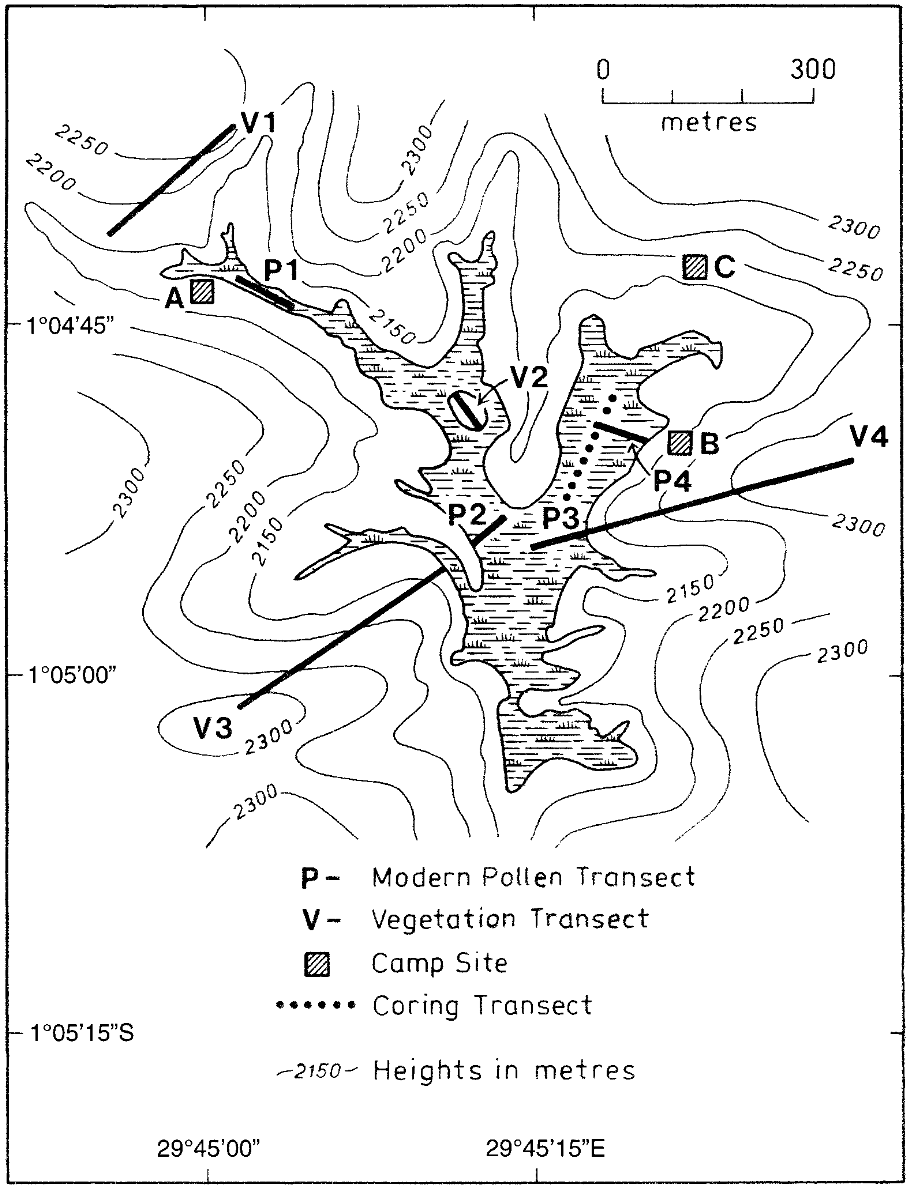


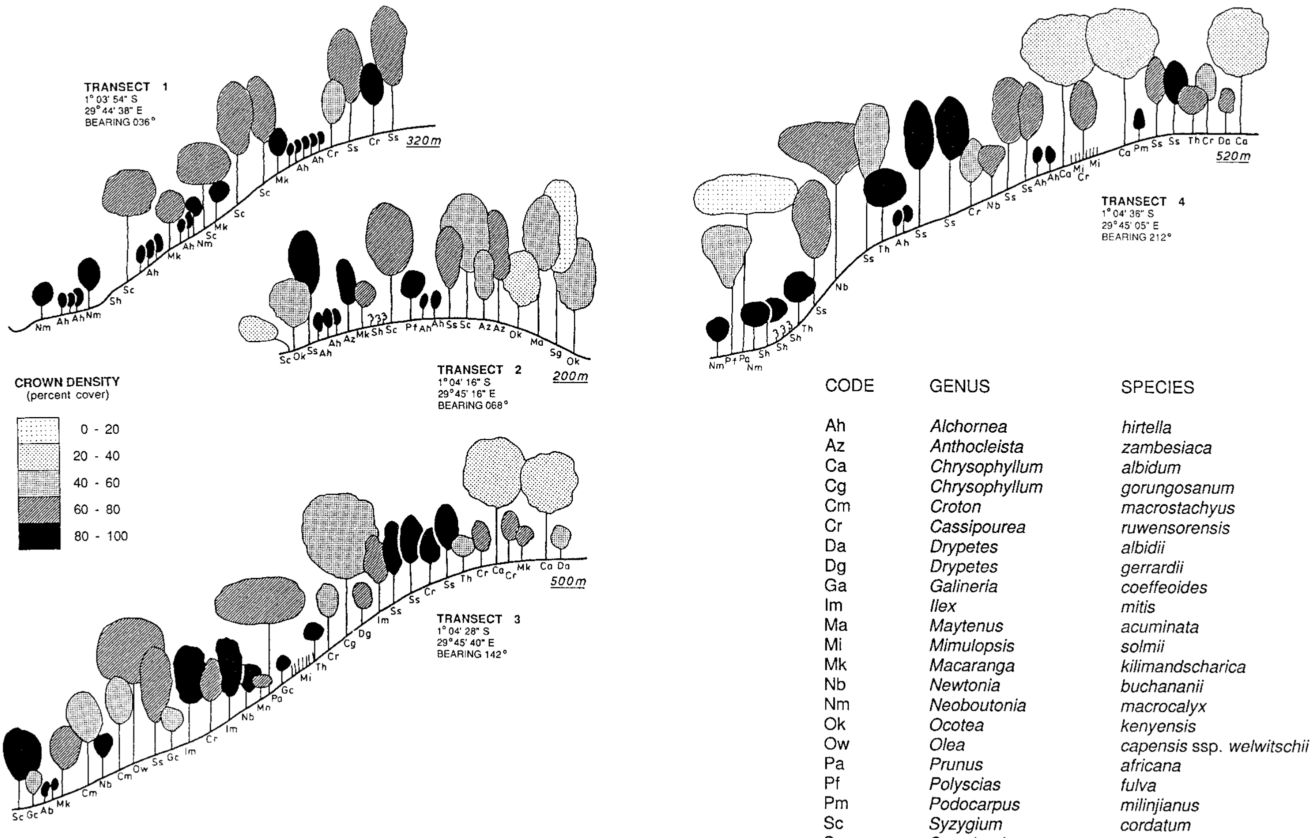
FIG. 2. Mubwindi Swamp, showing the topography and the location of vegetation survey, modern pollen survey, and coring transect.

the underlying rock. The vegetation at the swamp margin is characterized by swamp forest dominated by trees such as *Myrica salicifolia*, *S. cordatum*, and the swamp grass *Miscanthus violaceum* interspersed with open water. Further from the swamp margin, vegetation is characterized by tall sedges dominated by *Cyperus denudatus* in the wettest parts and *C. latifolius* in dryer areas. Common components of the ground cover at Mubwindi Swamp are *Alchemilla* spp. and several species of ferns including *Blechnum* spp. Occasional tree heathers (*Erica* spp.) are also found. A broken, fringing band of *A. hirtella* is found on the dry land immediately adjacent to the swamp.

METHODS

Modern Pollen–Present Day Vegetation Relationship

To relate modern pollen deposition to contemporary vegetation within the Mubwindi Swamp catchment, tree species were recorded along four, 5-m-wide, belt transects, running from the swamp edge to the surrounding hill crests. For each tree species, girth at breast height, crown density, and tree height were noted. The four transects probably incorporate a representative range of forest types found within the catchment. The tree species recorded, together with the codes



CODE	GENUS	SPECIES
Ah	*Alchornea*	*hirtella*
Az	*Anthocleista*	*zambesiaca*
Ca	*Chrysophyllum*	*albidum*
Cg	*Chrysophyllum*	*gorungosanum*
Cm	*Croton*	*macrostachyus*
Cr	*Cassipourea*	*ruwensorensis*
Da	*Drypetes*	*albidii*
Dg	*Drypetes*	*gerrardii*
Ga	*Galineria*	*coeffeoides*
Im	*Ilex*	*mitis*
Ma	*Maytenus*	*acuminata*
Mi	*Mimulopsis*	*solmii*
Mk	*Macaranga*	*kilimandscharica*
Nb	*Newtonia*	*buchananii*
Nm	*Neoboutonia*	*macrocalyx*
Ok	*Ocotea*	*kenyensis*
Ow	*Olea*	*capensis* ssp. *welwitschii*
Pa	*Prunus*	*africana*
Pf	*Polyscias*	*fulva*
Pm	*Podocarpus*	*milinjianus*
Sc	*Syzygium*	*cordatum*
Sg	*Symphonia*	*globulifera*
Ss	*Strombosia*	*scheffleri*
Th	*Tabernaemontana*	*holstii*

FIG. 3. Distribution of vegetation types along the four surveyed transects.

used, forest composition, crown density, and relative height are portrayed in Figure 3.

Modern pollen surface sediment samples were collected from 12 locations. These were taken at 15, 30, and 45 m along four transects on the Mubwindi Swamp surface (Fig. 2). Pollen was extracted from surface sediment samples using the standard preparatory technique (Faegri and Iverson, 1989). Results for individual tree taxa are displayed for each transect as a percentage of the nonhydrophytic pollen sum (i.e., non-swamp-inhabiting taxa). Cyperaceae and Gramineae concentrations are also represented, but as percentages of the total pollen sum (Fig. 4).

Analysis of Sediments

A total of 23 cores of sediment have been extracted from Mubwindi Swamp along six transects, using a combination of Russian (D-section) and Hiller corers. This paper focuses on cores MB6 and MB3, collected from one of these transects in the northern part of the swamp (Fig. 5). Core MB6, 9 m deep, is believed to contain the most complete paleoenvironmental record of the 23 cores collected. Additional analysis on core MB3 provides supportive information. The stratigraphy for sediments within each core (Fig. 5) was described in the field using the Tröels-Smith method (Tröels-Smith, 1955).

Samples from cores MB3 and MB6 for pollen analysis were prepared using the standard preparatory technique (Faegri and Iverson, 1989). Loss on ignition (LOI) and charcoal content of samples from core MB6 were established using the gravimetric method of Winkler (1985); results are portrayed in Figure 6. Dating control (Table 1) is provided by nine radiocarbon ages available from core MB6 and by three radiocarbon ages from core MB3.

Pollen Analysis

At least 500 pollen grains were counted for each sample, in line with the recommendation of Hamilton (1972). Pollen data from cores MB6 and MB3 are portrayed in percentage form (Figs. 6 and 7 respectively), where the sum upon which the percentage calculations are based includes only those pollen types though to come exclusively from non-swamp-inhabiting taxa (i.e., nonlocal species). This nonswamp

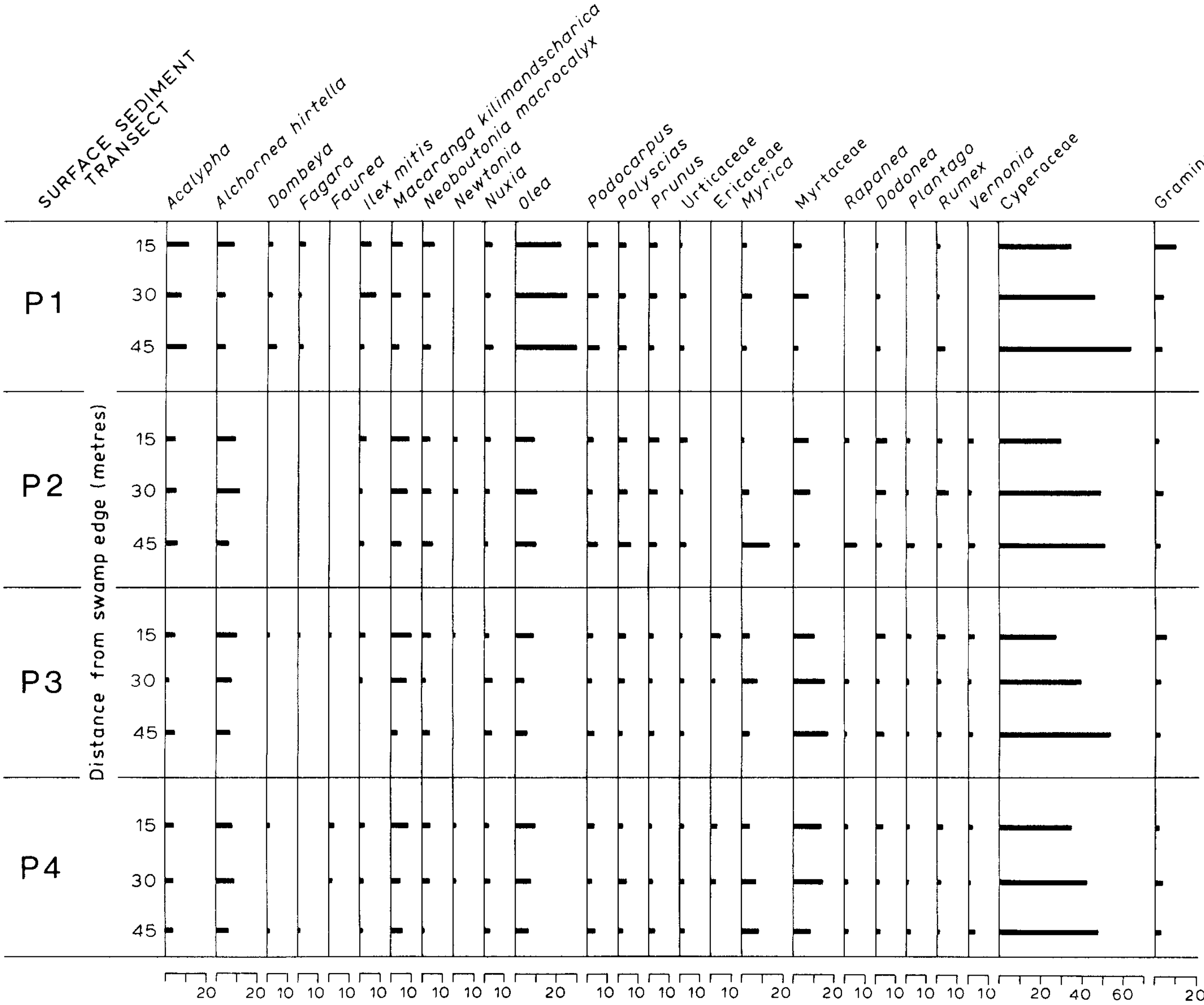


FIG. 4. Percentages of pollen in surface sediment samples.

group comprised between 65 and 238 pollen grains per sample. Based on the ecology of the likely parent taxa, the pollen were divided into four categories: montane forest, high altitude forest, degraded forest, and swamp forest. The first two categories are synonymous with Hedberg's (1951) Montane Forest Belt and Ericaceaous Belt, respectively, the latter two categories are vegetation associations found within Montane Forest as a result of local anthropogenic, climatic, and/or ecological impact. Figures 6 and 7 were plotted using the PC-based software TILIA and TILIAGRAPH (Grimm, 1991). The pollen data from core MB6 were classified into four pollen zones (MB6.1 to MB6.4) according to a stratigraphically constrained, numerical clustering package within TILIA. A comparable zonation scheme is applied to the pollen data from core MB3. The locations of boundaries between zones were determined on the calculations of Euclidean distance between contiguous samples, after removal of pollen types that never exceeded a value greater than 2% of the nonlocal pollen sum.

RESULTS

Modern Vegetation and Pollen Data

Vegetation along transect 1 has been affected by the relatively recent activities of pit-sawyers and is characterized by a high occurrence of trees associated with disturbed forests, such as *A. hirtella, M. kilimandscharica,* and *N. macrocalyx,* and by a dense shrub layer. Mature *S. cordatum* trees are also present and are noted at altitudes higher than on other transects, possibly due to a relatively moist location. By comparison, vegetation along transect 2 has been relatively little affected by pit-sawyers, as it includes species such as *Anthocleista zambesiaca, Ocotea kenyensis, Maesopsis eminii,* and *S. globulifera.* Gaps in the canopy were

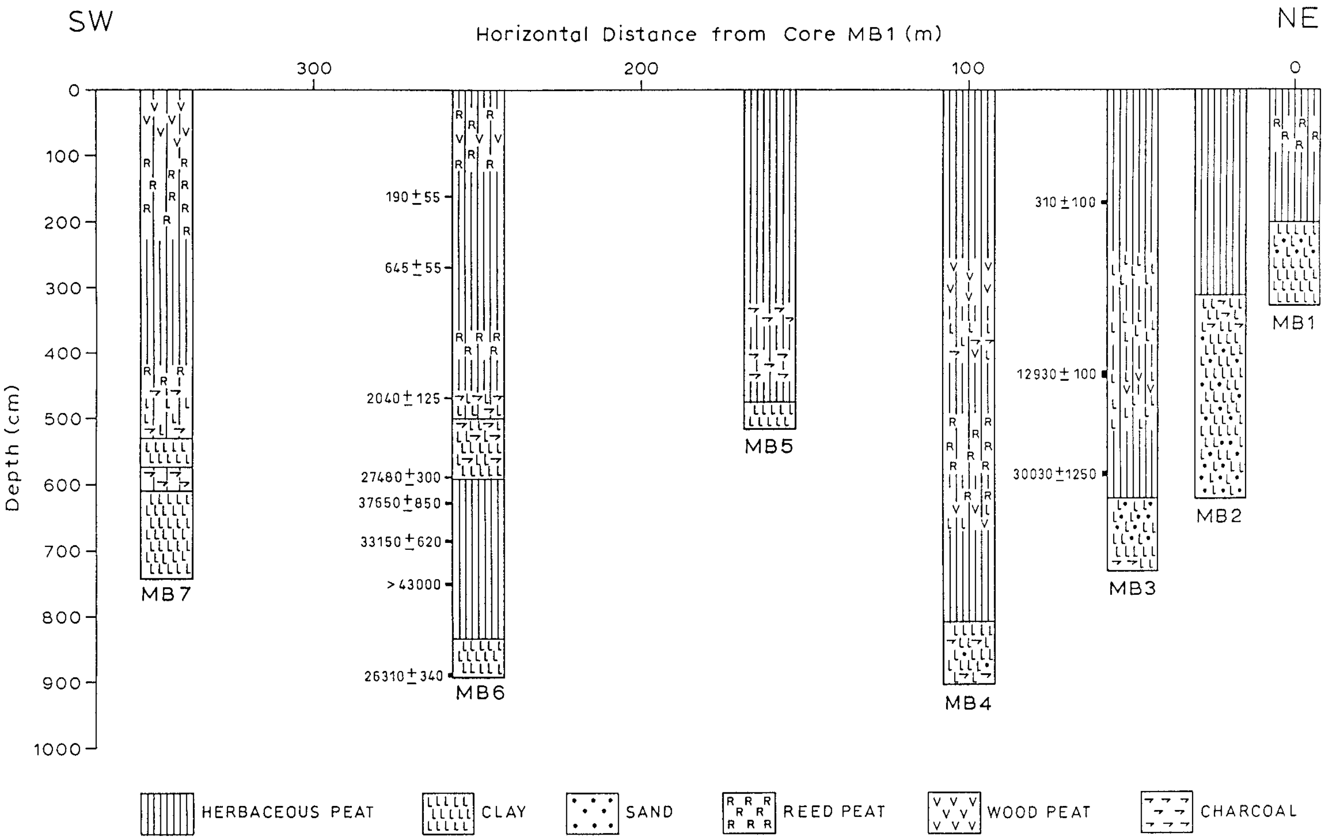


FIG. 5. Stratigraphy along the coring transect.

present, probably as a result of natural tree falls and elephant damage. Away from the gaps the canopy contains distinct strata.

Transects 3 and 4 have similar length, slope, and altitude, but differ in aspect and vegetation, particularly in the lowermost parts of the profiles. Whereas *Ilex mitis* and *Olea capensis* ssp. *hochstetteri* are found on the colder, wetter, west-facing slopes of transect 4, the larger *N. buchananii* and *Prunus africana* specimens are found on the relatively dryer, warmer, east-facing slopes of transect 3. Ridge-top vegetation on both transects is dominated by *C. ruwensorensis, Chrysophyllum albidum,* and *D. gerrardii.* Past pit-sawing on both transects is indicated by very young *Podocarpus milanjianus* and *N. buchananii* on transect 3 and by young *N. buchananii* on transect 4. Further evidence for disturbance is the presence of *A. hirtella* and *N. macrocalyx* on transect 3 and *A. hirtella* and *M. kilimandsharica* on transect 4.

Moderately well dispersed pollen types such as *Alchornea, Macaranga, Neoboutonia,* and *Polyscias* (Hamilton, 1972), the parent taxa of which are characteristic of degraded forest, are present in all 12 surface samples. *Dombeya* and *Vernonia* pollen types are found in small quantities. Hamilton (1972) described *Dombeya* and *Vernonia* pollen as very poorly dispersed pollen types and indicative of degraded forest in central and east Africa. Pollen types belonging to characteristic montane forest taxa such as *Ilex, Newtonia, Olea, Podocarpus, Prunus,* and *Zanthoxylum* are well represented. *Olea* and *Podocarpus,* despite their low concentrations in the surrounding vegetation, are present at high concentrations in the surface samples, supporting the idea that these pollen types are produced in large amounts and have a high relative export ability (Hamilton, 1972; Hamilton and Perrot, 1980). Pollen originating from trees associated with a swamp habitat are dominated by Myrtaceae, with the most likely source being *S. cordatum.* Cyperaceae dominates the total pollen sum, accounting for up to 60% of all pollen identified. Gramineae pollen is present in significant amounts and has probably originated from grasses growing within both forest and swamp habitats. There are, however, some differences in relative importance between taxa recorded on the belt transects and their representation in the pollen spectra. For example *Cassipourea* spp., *Chrysophyllum* spp., and *S. scheffleri* are well represented in the surrounding vegetation but not by their pollen in the surface sediments; these pollen types are poorly dispersed (Hamilton, 1972). Conversely, *Faurea,* Ericaceae, and *Nuxia* pollen are present in the surface sediments but the parent taxa are minor parts of the surrounding vegetation.

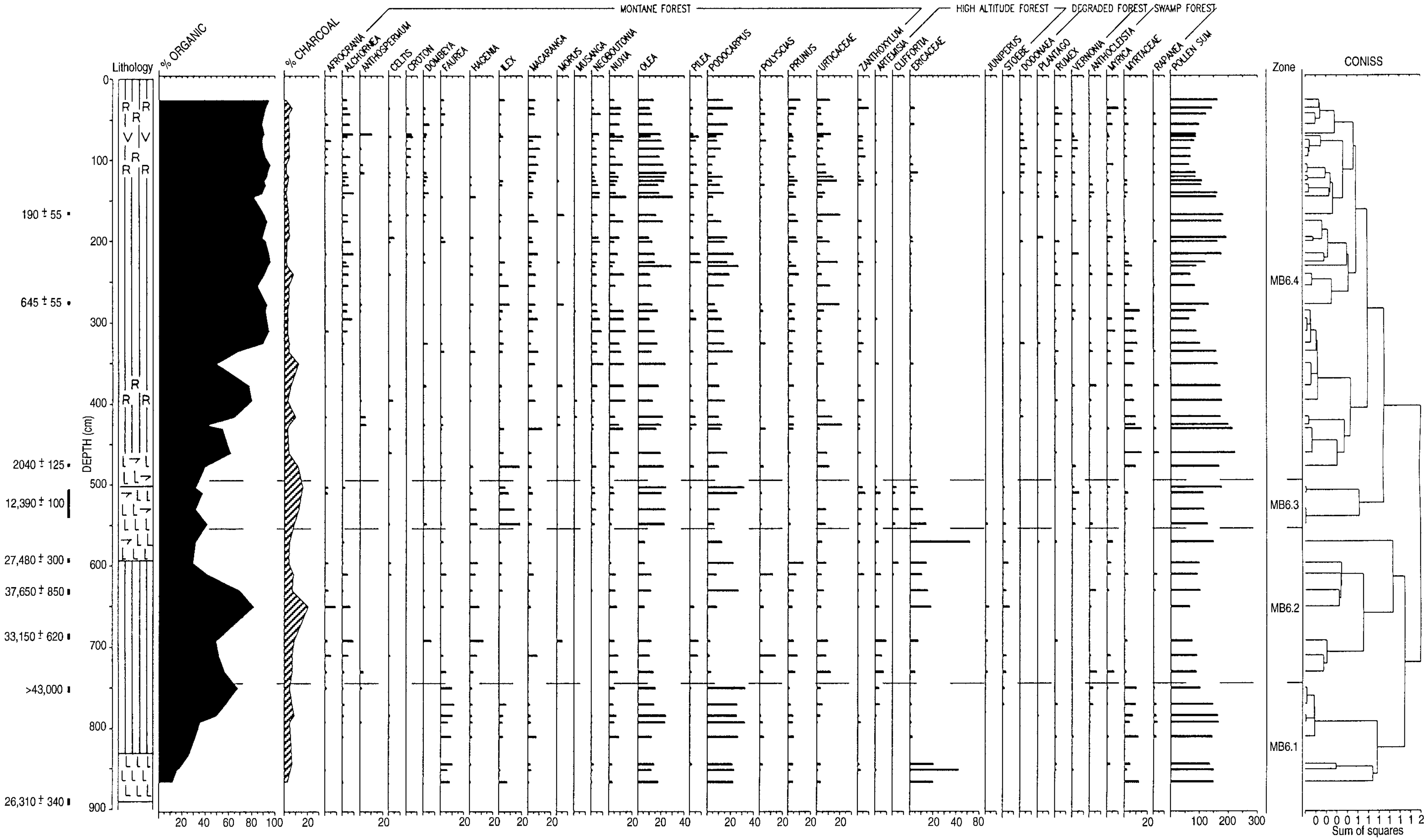


FIG. 6. Pollen diagram from core MB6 including percentage of charcoal and organic sediment. The pollen total on which the percentages are based includes only those pollen types derived from nonhydrophilous sources.

TABLE 1
Radiocarbon Ages

Depth (cm)	Age (^{14}C yr B.P.)	Laboratory code
	Core MB6	
163–167	190 ± 55	AA-12396
273–277	645 ± 55	AA-12397
473–477	2110 ± 55	AA-12398
473–477	1970 ± 55	AA-13909
590–595	27,480 ± 300	AA-17153
628–635	37,650 ± 850	Beta-82554
683–690	33,150 ± 620	AA-17154
748–755	>43,000	Beta-82553
886–894	26,310 ± 340	AA-17155
	Core MB3	
170–177	310 ± 100	Beta-61809
430–443	12,930 ± 100	Beta-60065
580–588	30,030 ± 1250	Beta-60066

Radiocarbon Chronology

Nine standard and three AMS carbon dates were obtained for sediments from Mubwindi Swamp (Table 1); three from core MB3 and nine from core MB6. Ages of 2110 ± 55 and 1970 ± 55 ^{14}C yr B.P. result from repeat counts on the same sample; for this level a mean of the two radiocarbon ages (2040 ± 125 ^{14}C yr B.P.) is used in the chronology. MB3 dates are extrapolated to core MB6 on the basis of similar sediment and pollen characteristics between the two cores. The more extensive dating control from core MB6 has been used to construct an age–depth curve (Fig. 8). We ignore the age of 26,310 ± 340 ^{14}C yr B.P. (AA-17155) from the base of core MB6. This age may reflect contamination by sediments further up the sedimentary sequence, most likely during coring. The radiocarbon ages from the late Holocene indicate that sediments within Mubwindi Swamp have been accumulating continuously since the radiocarbon age of 2110 ± 55 ^{14}C yr B.P. (AA-12398).

The dating shows that sedimentation at Mubwindi Swamp has been sporadic in the late Quaternary. The record contains at least two long hiati: between the radiocarbon ages of 27,480 ± 300 ^{14}C yr B.P. (AA-17153) (core MB6) and 12,930 ± 100 ^{14}C yr B.P. (Beta-60065) (core MB3) and between 12,930 ± 100 ^{14}C yr B.P. (Beta-60065) (core MB3) and 2110 ± 55 ^{14}C yr B.P. (AA-12398) (core MB6).

Sediment Stratigraphy

Although some stratigraphic units extend across much of Mubwindi Swamp, more minor differences in sediment composition exist both within and between cores. These differences are thought to reflect changes in the sedimentary environment of Mubwindi Swamp.

A basal clay horizon is found in all cores extracted along transect 1 (Fig. 5), which in core MB6 is characterized by a constant charcoal content. This horizon is overlain by a band of decomposed, herbaceous peat in the longer cores. The transition between basal clay and overlying herbaceous peat is dated in core MB6 to before 43,000 ^{14}C yr B.P. (Beta-82553). The herbaceous peat varies considerably in depth and composition along the transect and attains its greatest thickness (220 cm) in core MB6. There are large variations in charcoal and organic content within this sediment horizon (Fig. 6). A second band of clay overlies this herbaceous peat; in core MB6 this clay band is distinguished by an increase in the charcoal content (Fig. 6). The transition to the second clay band has been dated in core MB6 to 27,480 ± 300 ^{14}C yr B.P. (AA-17155). The boundary to the overlying herbaceous peat, which forms the highest unit right across transect 1, is dated in core MB3 at just after 12,930 ± 100 ^{14}C yr B.P. (Beta-60065) and in core MB6 just before 2110 ± 55 ^{14}C yr B.P. (AA-12398). In core MB6 this uppermost sequence contains fluctuating amounts of charcoal and inorganic sediment. On the basis of the radiocarbon ages from cores MB3 and MB6, this top horizon of herbaceous peat is thought to contain a complete record for approximately the past 2500 years. The uppermost horizon of herbaceous peat includes wood peat, clay bands, and reed fragments.

Fossil Pollen Record

Pollen zone MB6.1 extends from the base of the core at 884 to 745 cm and includes the radiocarbon ages of 26,310 ± 340 ^{14}C yr B.P. (AA-17155) and >43,000 ^{14}C yr B.P. (Beta-82553). As discussed previously, the younger of the two dates is though to be erroneous and reflect contamination. Within the montane forest category pollen zone MB6.1 is identified by high proportions of *Faurea*, *Olea*, and *Podocarpus* pollen types. *Hagenia*, *Ilex*, *Macaranga*, *Nuxia*, *Prunus*, and Urticaceae pollen are all present in relatively low amounts. *Afrocrania*, *Anthospernum*, *Celtis*, *Neoboutonia*, *Pilea*, *Polyscias*, and *Zanthoxylum* pollen are all present but at low sporadic percentages and never reaching a quantity of greater than 5% of the nonlocal pollen sum. The high altitude forest category is dominated by Ericaceae pollen at the base of pollen zone MB6.1, although this rapidly declines to a low, constant level. Toward the top of the pollen zone there is a slight increase in the amount of *Artemisia* and *Stoebe* pollen. A similar pollen assemblage is present in pollen zone MB3.1 (Fig. 7).

The large quantities of *Faurea* pollen present in pollen zones MB6.1 and MB3.1 suggest that the parent taxon was growing on the hillsides adjacent to Mubwindi Swamp. The pollen spectra also indicate that *Ilex*, *Olea*, and *Podocarpus* were significant components of the surrounding vegetation. Taxa such as Ericaceae, *Myrica*, *Ra-*

FIG. 7. Pollen diagram from core MB3. The pollen total on which the percentages are based includes only those pollen types derived from nonhydrophilous sources.

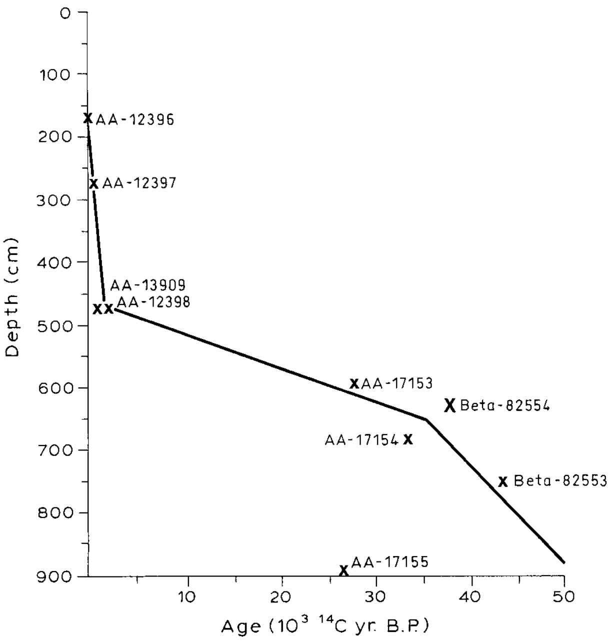


FIG. 8. Age–depth curve for core MB6.

panea, and *Syzygium* were also growing close to the coring site. The latter three taxa are thought to have comprised swamp forest, as they did at Ahakagyezi Swamp until very recently (Taylor, 1993). Toward the top of the pollen zones there is a gradual increase in the amount of taxa from an altitudinally higher vegetation type.

Pollen zone MB6.2, between 745 and 555 cm in core MB6, includes the radiocarbon ages of 33,150 ± 620 ^{14}C yr B.P. (AA-17154), 37,650 ± 850 ^{14}C yr B.P. (Beta-82554) and 27,480 ± 300 ^{14}C yr B.P. (AA-17153). On the basis of similarities in pollen spectra, pollen zone M6.2 would include the radiocarbon age of 30,030 ± 1250 ^{14}C yr B.P. (Beta-60066) from core MB3. Pollen zone MB6.2 is identified by relatively high levels of *Afrocrania, Alchornea, Hagenia, Nuxia, Olea, Prunus,* and Urticaceae pollen from the montane forest category. There is a low, but sustained level of *Faurea* pollen throughout the pollen zone, whereas *Ilex, Macaranga, Podocarpus,* and *Zanthoxylum* pollen increase toward the top of the pollen zone. From the high altitude forest category there is a relatively high amount of *Artemisia* pollen at the base of the pollen zone, with low but consistent amounts of Ericaceae, *Juniperus,* and *Stoebe* pollen. Toward the top of pollen zone MB6.2 there is an increase in the amount of Ericaceae and *Stoebe* pollen. Pollen derived from the degraded and swamp forest categories are present at low percentages, although their amounts increase toward the top of the pollen zone.

Pollen zone MB3.2 appears analogous to pollen zone MB6.2, although with some notable differences, particularly in the uppermost samples. In pollen zone MB3.2 *Artemisia, Cliffortia,* and *Stoebe* pollen make a significant contribution to the pollen spectra, as do *Myrica* and *Rapanea* pollen from the swamp forest category. The pollen present in these zones indicates that a combination of ericaceous belt vegetation and montane forest was present within the Mubwindi Swamp catchment. However, the composition of the reconstructed vegetation fluctuates markedly throughout the pollen zone. In the base of the pollen zone *Artemisia* and members of the Ericaceae are present, with relatively high densities of *Hagenia, Nuxia, Olea,* and *Prunus* and, to a lesser extent, *Alchornea* and *Afrocrania.* Toward the top of the pollen zone the composition of the ericaceaous belt vegetation changes to an *Artemisia, Cliffortia,* and *Stoebe* association, with increased dominance from members of the Ericaceae.

Pollen zone MB6.3 lies between 550 and 495 cm. On the basis of similarities in pollen spectra, this zone is thought to contain sediments of an age similar to those in core MB3 (Fig. 7) which include the radiocarbon age of 12,930 ± 100 ^{14}C yr B.P. (Beta-60065). Pollen zone MB6.3 is characterized by high levels of *Ilex, Olea,* and *Podocarpus* pollen and to a lesser extent *Hagenia, Macaranga, Neoboutonia, Nuxia, Polyscias, Prunus,* Urticaceae, and *Zanthoxylum* pollen from the montane forest category. Within pollen zone MB6.3, relative to pollen zone MB6.2, the pollen derived from the high altitude forest category decreases. However, there is a notable peak in *Cliffortia* pollen relative to pollen zone MB6.2. Within the high altitude forest category, Ericaceae pollen still dominates, although *Artemisia, Juniperus,* and *Stoebe* pollen are also present.

Comparisons with the pollen flora of core MB3 (Fig. 7) indicate that pollen zone MB6.3 is analogous to pollen zone MB3.3. These pollen zones reflect an increased abundance of montane forest taxa within the Mubwindi Swamp catchment. All the high altitudinal taxa decrease, apart from *Juniperus.* This pollen type is likely to originate from *Juniperus procera,* a tree associated with dry montane conditions.

Pollen zone MB6.4 contains the record between 495 cm and the top of the core. The zone includes the radiocarbon ages of 2110 ± 55 ^{14}C yr B.P. (AA-12398), 1970 ± 55 yr B.P. (AA-13909), 645 ± 55 ^{14}C yr B.P. (AA-12397) and 190 ± 55 ^{14}C yr B.P. (AA-12396). On the basis of a similar pollen flora with core MB3 (Fig. 7), this zone would also contain the radiocarbon age of 310 ± 100 ^{14}C yr B.P. (Beta-61809). The zone is characterized by increased levels of *Celtis, Macaranga,* Myrtaceae, *Neoboutonia, Nuxia, Polyscias, Prunus,* Urticaceae, and *Zanthoxylum* pollen compared to that seen in zone MB6.3. Toward the top of pollen zone MB6.4 *Alchornea, Croton, Dodonaea, Dombeya, Myrica, Neoboutonia, Rumex,* and *Vernonia* pollen types increase, concomitant with decreases in the abundance of *Ilex, Nuxia, Olea,* and *Podocarpus* pollen types.

Comparisons with the pollen flora of core MB3 indicate that pollen zone MB6.4 is analogous to pollen zone MB3.4.

These zones represent the presence of moist lower montane forest within the Mubwindi Swamp catchment. The changes in pollen toward the top of the zone probably represent a decrease in some primary forest taxa in the catchment and an increase in taxa associated with degraded and regenerating forest. It is noteworthy that pollen from ruderal plants increased significantly only after the radiocarbon age of 310 ± 100 ^{14}C yr B.P. (Beta-61809) from core MB3 and therefore much later than in other cores from the Rukiga highlands. This may reflect a relatively low level of human activity within Bwindi Forest over the past 2000 yr, with increased activity restricted to the past few hundred years.

DISCUSSION

Pollen zones MB6.1 and MB3.1 resemble to the lowermost pollen zone in core MC4 from Muchoya Swamp which Taylor (1990) suggests predates 42,000 yr B.P. Pollen spectra from these zones indicate the widespread presence of moist lower montane forest in the Rukiga highlands from an unspecified time, but likely to predate 50,000 yr B.P. The composition of this forest appears to have varied with altitude. Within the Muchoya Swamp catchment (140 m above Mubwindi Swamp), the forest contained abundant *Croton, Cyathea, Ilex, Neoboutonia,* and *Podocarpus.* By comparison, forest around Mubwindi Swamp was dominated by Myrtaceae, probably species of *Syzygium.* Species of *Faurea, Nuxia, Olea,* and *Podocarpus* were also present within the vegetation. Pollen spectra similar to those of MB6.1 and about the same age have also been recorded for Kamiranzovu Swamp (1950 m) in Rwanda (Hamilton, 1982). Taken together, the data suggest environmental conditions similar to those of present day. Thus the evidence from Mubwindi and Muchoya swamps suggest a humid, forested period in the Rukiga Highlands during the early part of the last glacial.

Pollen zones MB6.2 and MB3.2 are identified by increasingly high pollen percentages from taxa associated with ericaceous belt vegetation such as *Artemisia, Cliffortia,* Ericaceae, and *Stoebe.* Although some pollen from montane forest taxa is present, it is of a lower level than that recorded from zone MB6.1. These zones are thought to correlate to the lowermost three pollen zones in core MC2 from Muchoya Swamp, which Taylor (1990) dates as being earlier than the radiocarbon age of 21,540 ± 160 ^{14}C yr B.P. (SRR-2962). Pollen from Muchoya Swamp indicates the presence of ericaceous belt vegetation within the catchment, together with relatively low amounts of pollen from montane forest taxa. During the same period trees such as *Olea, Macaranga, Myrica, Podocarpus, Rapanea,* and *Syzygium* also supplied pollen to sediments accumulating in Kashiru and Kamiranzovu swamps in Burundi and Rwanda (Bonnefille and Riolett, 1988; Bonnefille *et al.,* 1992; Hamilton, 1982). These findings point to the presence of moist montane forest in central Africa, prior to the last glacial maximum of northern latitudes. Altitudinal gradients of vegetation appear to have been compressed relative to the present, thus allowing taxa presently associated with ericaceous and lower montane forest vegetation to occur within the Mubwindi Swamp catchment. It is possible that this compression was due to higher adiabatic lapse rates arising from reduced atmospheric moisture levels and lower mean annual temperatures. Vincens (1993), using a pollen record from Lake Tanganyika, inferred lower temperatures and mean annual precipitation during this period, while Bonnefille *et al.* (1990) calculated falls in temperature of about 4°C and precipitation by up to 40% in equatorial Africa toward the late glacial maximum.

Pollen zones MB6.3 and MB3.3 were probably preceded and followed by sedimentary hiati. Potential causes include an increased input of water on the Mubwindi Swamp surface, with consequent erosion of unconsolidated sediments. A sedimentary hiatus is also recorded between approximately 21,000 and 12,000 yr B.P. at Rusaka Swamp (2070 m) in Burundi (Bonnefille *et al.,* 1995), although a forcing mechanism is not suggested for the origin of this break.

In 1994 we observed wet-season erosion of sediments from forested hillsides surrounding the swamp. Such erosion may be enhanced during periods of less dense vegetation cover in the catchment, higher levels of effective precipitation or phases of vegetation change. A clay deposit dated to approximately 11,000 ^{14}C yr B.P., followed by a significant break in sedimentation, described by Taylor (1990, 1992) at Muchoya Swamp, may have had a similar origin. Similarly, the well dated, high resolution study from Ahakagyezi Swamp (Taylor, 1993) records an inwash of clay and a distinct layer of sand dated at the Pleistocene to Holocene transition. Kamiranzovu Swamp also stopped accumulating peat about 11,000 yr B.P. (Hamilton, 1982). The record at Kashiru Swamp (Bonnefille and Riolett, 1988) also contains a sedimentary break from the late Pleistocene–Holocene transition through to the mid- to early Holocene.

As these breaks in sedimentation appear to occur around the Pleistocene–Holocene transition, it is possible that a significant factor in causing these hiati was erosion brought about by increased levels of effective precipitation due to the reinstating of the southwest monsoonal circulation (Kutzbach and Otto-Bliesner, 1982; Kutzbach and Street-Perrot, 1985; Street-Perrot and Perrot, 1990; Rossignol-Stick, 1983). Peat accumulation at Mubwindi Swamp may have recommenced only once levels of effective precipitation had fallen during the late Holocene. Reduced levels of precipitation during the late Holocene have been recorded elsewhere in the Rukiga highlands, beginning around 3400 yr B.P. at Muchoya Swamp (Taylor, 1992) and around 3100 yr B.P. at Ahakagyezi Swamp (Taylor, 1993). A late Holocene arid period has been suggested at sites from Madagascar (Burney, 1993) and across equatorial Africa (Elenga *et al.*, 1994; Hamilton, 1982; Jolly *et al.*, 1994; Stager, 1984; Street and Grove, 1979; Vincens, 1989, 1994; Vincens *et al.*, 1993).

Pollen zones MB6.3 and MB3.3 represent a more widespread occurrence of lower montane forest within the Mubwindi Swamp catchment, concomitant with a decrease in pollen from high altitude forest sources. These pollen zones can be correlated to zone 6 in core MC2 from Muchoya Swamp, which has been dated from approximately 13,800 to 11,100 yr B.P. (Taylor, 1990). The pollen zones are thought to reflect climatic ameriolation following full glacial conditions and a mixing of moist lower and upper montane forest taxa within the Mubwindi Swamp catchment. Montane forest pollen types occur at much higher percentages within the Mubwindi Swamp sediments than nearby sites during the time period represented by these zones. This suggests that moist forests were located in the immediate vicinity of Mubwindi Swamp compared with the sites previously studied in central Africa. It seems highly likely, on the basis of the pollen spectra, that small fragments of moist forest may have persisted within the Mubwindi Swamp catchment itself, possibly as a result of the more favorable topography and edaphic conditions compared to other sites so far investigated along the Western Rift.

Pollen zones MB6.4 and MB3.4 contain pollen spectra indicative of moist lower montane forest with a composition similar to that of the more remote areas of Bwindi Forest at present. Fluctuations in the composition of forests at Mubwindi Swamp, apparent in pollen spectra for zones MB6.4 and MB3.4, are likely to have been caused by some combination of exogenic (e.g., climatic, human) and endogenic (e.g., successional) factors. Selective utilization of the forest by humans is indicated in the pollen spectra of zone MB6.4 by an increase in the pollen from taxa associated with a ruderal habitat and an associated decline in pollen from montane forest taxa, from 300 yr B.P. Additional support for the presence of more recent and stratigraphically distinct disturbance within the catchment comes from the relatively high incidence of inorganic material and charcoal. Other sites within the Rukiga highlands show unreversed forest clearance commencing at least 2000 yr ago (Taylor, 1992, 1993), long before disturbance at Mubwindi Swamp. Regional forest clearance placed pressure on the Bwindi Forest to be used as a timber resource (Taylor and Marchant, 1996) but the pollen record suggests that Bwindi Forest escaped intensive logging. From the Mubwindi Swamp pollen and vegetation survey data it appears that selective logging has played an important role in determining the present-day composition of Bwindi Forest over only the past few hundred years.

CONCLUSIONS

(1) Modern pollen rain at Mubwindi Swamp comes largely from plants growing within the immediate catchment. This further supports the suggestion by Taylor (1993) that the swamps in the Rukiga highlands are suitable for palynological study of changes in vegetation and climate.

(2) Vegetation within the Mubwindi Swamp catchment has changed during the late Pleistocene and Holocene. Between approximately 43,000 and 26,000 yr B.P. there was a spread of taxa from high montane forest and the ericaceous belt, although some taxa from lower altitudinal forest persisted at a reduced extent. A precursor of the present Bwindi Forest possibly survived this cool, dry period, as a result of favorable soils and topography.

(3) Montane forest taxa increased within the Mubwindi Swamp catchment during the Pleistocene–Holocene transition. A ''refugia'' for montane forest existed near or within the Mubwindi Swamp catchment during full glacial time. This refugia was probably dispersed, as specimens of montane forest taxa within altitudinally higher vegetation.

(4) Mubwindi Swamp catchment has been surrounded by moist lower montane forest similar to that found in parts of Bwindi Forest today throughout the past 2500 yr, during a period when forests in other parts of the Rukiga highlands were widely cleared.

(5) The pollen record for approximately the past 300 yr reflects the selective use of the forest surrounding Mubwindi Swamp, most likely by pit-sawyers. Disturbance of the forest is supported by changes in pollen and sediment composition and results from the present day vegetation surveys.

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