EPIPHYTIC VEGETATION AND ECOLOGY IN CENTRAL AFRICAN FORESTS (RWANDA, ZAÏRE)[1]

Nadja Biedinger & Eberhard Fischer

Botanisches Institut der Universität Bonn, Meckenheimer Allee 170, D-53115 Bonn, Germany

Abstract. Floristic composition and important aspects of the ecology of phanerogamic and cryptogamic epiphytes were studied in montane rainforests, montane forests and dry forests of Rwanda and Zaïre (850-3500 m a.s.l.). A total of 167 species of vascular epiphytes was recorded on 80 phorophyte individuals. 45 species of mosses, 82 liverworts, 78 corticolous lichens and 57 epiphyllous lichens were identified. Orchidaceae, with 52%, made up the greatest part of the vascular plants. Ferns followed with 33%. Other important families were Balsaminaceae, Begoniaceae and Piperaceae. The epiphyte index (percentage of the flora) of the entire phanerogamic flora of the region investigated was approximately 2.5%. Distribution of phanerogamic epiphytes on the phorophyte was concentrated in zones 2 and 3 (modified zones after Johansson 1974) of the canopy. The highest number of vascular epiphytes documented on a single tree was 40. Studies on pollination biology of holoepiphytes (mainly orchids) showed a surprisingly high percentage of myophilous and melittophilous flowers (78%). The epiphytic angiosperm inventory differed completely between a montane forest in Rwanda (2000 m a.s.l.) and a montane rainforest in Zaïre (900 m a.s.l.) only 100km away. Floristic differences evidently correlate with affiliations to different phytochoria resulting from climatic and historical differences: epiphytic vegetation of the Zaïrian montane rainforest is mainly composed of Guineo-Congolian elements, whereas many epiphytes growing in Rwandan montane forests are restricted to the Afromontane center of endemism. Following the analysis of epiphyte species numbers it is assumed that vascular epiphyte diversity is determined by the limited number of niches on one tree and in one forest. Low landscape diversity explains low epiphyte species richness in Africa. *Accepted 2 December 1996.*

Key words: Diversity, ecology, endemics, epiphytes, Rwanda, vegetation, Zaïre.

INTRODUCTION

Tropical rainforests represent the most species-rich plant communities on earth. Covering only 7% of the continents, rainforests contain more than 60% of all species. Erwin & Scott (1980) estimate the number of species on earth at around 30 million, which greatly surpasses the 1.7 million species described up to now. Studies made in tropical forests are often insufficient to allow a profound understanding of their biology. Detailed investigations concerning vegetation, ecology and diversity of tree canopies are especially rare.

Epiphytes are extreme specialists adapted to climatically and ecologically harsh conditions in the canopy: they represent an important and interesting plant group that has hardly been studied within a wider conceptional framework until now.

The term "epiphyte" was introduced to the literature by Martius (1842). Following the terminology of Schimper (1888), Richards (1952), Ma-

dison (1977), Wallace (1981) and Kress (1986), holoepiphytes are distinguished from hemiepiphytes. Plants that live exclusively on a tree are called holoepiphytes, whereas hemiepiphytes are plants that for a certain period during their life-cycle are connected to the ground.

Physiology, ecology and vegetation of epiphytes have only been analyzed for particular plant groups and certain regions or countries (e.g., Ackerman 1986a, 1986b, 1989 [orchids]; Benzing 1981, 1986, 1990 [bromeliads, general aspects]; Benzing & Ott 1981 [bromeliads]; Gentry 1982, 1986 [Neotropics, Colombia]; Gentry & Dodson 1987a, 1987b [Neotropics, Ecuador]; Lüttge 1989 [physiology of vascular epiphytes]; a survey of literature concerning vascular epiphytes is given in Watson *et al.* 1987).

For Africa, the only comprehensive work that deals in detail with the ecology and vegetation of vascular epiphytes is that of Johansson (1974), who studied epiphytes in West African forests in the Nimba Mountains in Liberia.

Vegetation of epiphytic ferns has been investigated intensively in Africa by Pichi Sermolli (1983,

1985) and Lawalrée (1969–1990), and has recently been studied in the Kahuzi-Biega National Park and Irangi Field Station in Eastern Zaïre by Becker (1994). Cryptogamic moss and liverwort vegetation was studied during the BRYOTROP-field work in Africa (Frahm 1985, 1993, 1994a,b, Kürschner 1995).

A comprehensive study of epiphytic cormo- and thallophytes of Central African forests, as well as, detailed research on cormophytic vegetation, has yet to be made.

In this study, complete cryptogamic and phanerogamic epiphyte inventories were made in dry and moist forests in Rwanda and Zaïre. Forests were chosen along an altitudinal gradient. A survey of epiphytic vegetation with emphasis on phanerogams is given. Ecological and phytogeographical aspects are documented and discussed.

METHODS

Epiphytic ecology, diversity and vegetation of moist forests was studied comparatively in two montane forests in Rwanda, a montane rainforest in Zaïre along an altitudinal gradient, and in two dry forests in Rwanda (see Fig. 1). Epiphytes were studied by climbing in the Akagera National Park, the Bugesera region, the Nyungwe Forest Reserve and the Virunga Volcanoes. In Zaïre and in the Nyungwe Forest Reserve, studies were made using trees which had been cut down a short time before or had fallen naturally. Field studies took place in October/November 1992 and October to December 1993.

Complete inventories of the cryptogamic and phanerogamic epiphytic vegetation of the principle phorophyte species of all study sites (see Fig. 1) were assessed. Of several hundred trees investigated, inventories of 80 phorophytes were made.

Growing sites of all epiphytes were documented (according to the modified zones from Johansson 1974, see Fig. 2). Furthermore, ecological and structural parameters of epiphytes and phorophytes were studied, such as abundance, growth form, shoot length, age, bark structure and bark contents (absence or presence of latex and resin was documented), tree architecture (diameter and angle of inclination of branches), possible adaptations to water uptake or
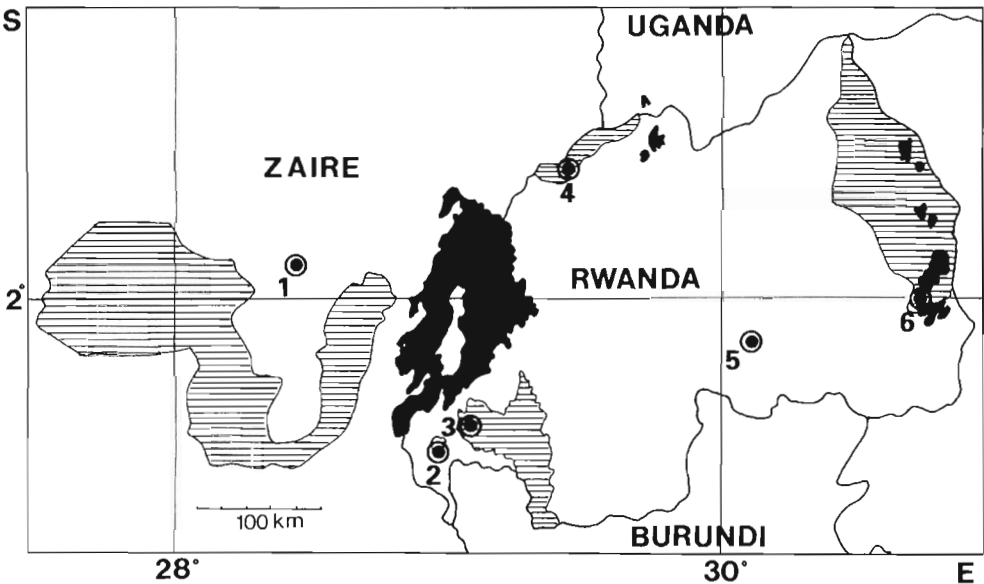

FIG. 1. Geographical position of the study sites investigated. 1. Montane rainforest (850-950 m a.s.l.), Irangi Station, Zaïre; 2. Cyamudongo Forest (1600 m a.s.l.), Rwanda; 3. Montane forest (2000 m a.s.l.), Nyungwe Forest Reserve, Rwanda; 4. Afroalpine forest (3000 m a.s.l.), Virunga-National Park, Rwanda; 5. Dry forest (1300 m a.s.l.), Bugesera, Rwanda; 6. Dry forest (1300 m a.s.l.), Akagera National Park, Rwanda; hatched regions show the largest National Parks in Rwanda and Eastern Zaïre.

water storage of epiphytes, and reproductive biology. Pollination biology was studied by analyzing the floral syndrome. In the two forests in Rwanda and Zaïre, certain synecological aspects like constancy of phanerogamic epiphytes were studied.

Alpha-diversity and beta-diversity for the epiphytes in a forest or single phorophytes were analyzed comparatively. Alpha-diversity was understood as species richness and abundance. Beta-diversity was measured by the commonly used Jaccard Similarity Index ($C = j / (a+b-j)$, with j = species in common, a = species number of one site/tree, b = species number of another site/tree), which gives a rough estimation of beta-diversity (Magurran 1988).

Nomenclature follows several floristic works of the region: Flore du Congo Belge et du Ruanda-Urundi (1948–58), Flore du Congo Belge et du Ruanda-Burundi (1960–63), Flore du Congo du Ruanda et du Burundi, Flore d'Afrique Centrale (Zaïre, Rwanda, Burundi, 1972–84), Flore du Rwanda (Troupin 1978-87).

STUDY SITES

1. Climate
Climate is of typical equatorial character, modified by the wide altitudinal range (1000–3500 m a.s.l.) of the Rwandan landscape. The rainy season lasts from the middle of February until the end of May/beginning of June. The dry season follows from June until August and is ended by a short rainy season from the middle of September to the middle of December. Then a short dry season follows until the middle of February. Average annual rainfall in the montane forests (1800–2200 m a.s.l.) is 1600–2000mm in Rwanda. In the dry forests investigated (both study sites at c. 1300 m a.s.l.) annual average rainfall does not exceed 900 mm. The average temperature lies between 15° and 21°C (Sirven et al. 1974).

In the montane rainforests (800–900 m a.s.l.) studied in Zaïre, annual rainfall is about 1800–2500 mm, which mainly falls in the rainy seasons from the end of Febuary until the beginning of June, and the middle of September until the middle of December. Temperature in this region close to the equator is on average 23–28°C (Dieterlen 1978).

2. Vegetation
Phytogeographically the forests studied are situated within the "Lake Victoria Regional Mosaic" (White
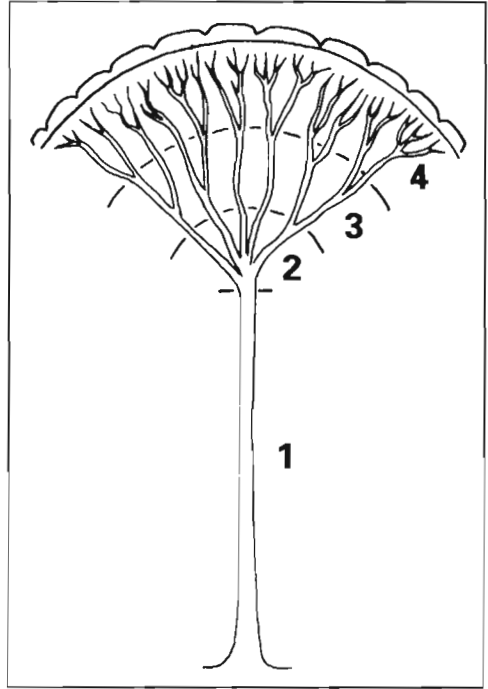

FIG. 2. Subdivision of a phorophyte into different zones (modified after Johansson 1974).

1983). Guineo-Congolian, Sudano-Zambezian, Somali-Masaian and Afromontane elements make up the flora. The region is characterized by a high degree of habitat differentiation within small areas, which enables comparative studies in different height and climatic zones to be carried out. Within this region, site I (see Fig. 1) is situated within the Guineo-Congolian regional center of endemism; sites 2, 3 and 4 lie within the Afromontane Center.

Epiphytic vegetation of dry forests was studied comparatively in two localities in Rwanda: the Akagera National Park (see Fig. 4c) and in the Bugesera region south of Kigali.

Dominant tree species in the Akagera National Park are *Acacia gerrardii*, *Acacia hockii*, *Acacia senegal* (see Fig. 4d), *Combretum collinum*, *Dombeya rotundifolia*, *Euphorbia candelabrum*, *Ficus dekdekana*, *Grewia trichocarpa*, *Lannea schimperi*, *Lannea stuhlmannii*, *Markhamia obtusifolia*, and *Parinari curatellifolia* (Troupin 1966).

Dry forests in the Bugesera region are dominated by trees such as *Acacia hockii*, *Acacia sieberiana*,

Albizia adianthifolia, Combretum gueinzii, Dichrostachys cinerea, Grewia trichocarpa, and *Lannea stuhlmannii.*

The Rwandan evergreen montane forests were studied in the eastern part of the country in the Nyungwe Forest Reserve (see Fig. 4b). The primary forests of the Nyungwe Forest Reserve are subdivided (according to Fischer & Hinkel 1990) into three zones: lower (1800–2300 m a.s.l.), middle (2300–2600 m a.s.l.) and upper (more than 2600 m a.s.l.) montane forest zone. The trees investigated were mainly situated in the lower montane zone. Characteristic species of these forests include *Albizia gummifera, Casearia runssorica, Carapa grandiflora, Entandrophragma excelsum, Neoboutonia macrocalyx, Parinari excelsa, Pentadesma reyndersii, Syzygium parviflorum,* and trees that occur in secondary forests such as *Anthocleista grandiflora, Musanga leo-errerae, Newtonia buchananii* and *Polyscias fulva.*

The Virunga volcanoes on the Uganda-Zaïre border in the northwestern part of Rwanda were studied in the *Hagenia-Hypericum* zone of the Bisoke volcano at 3500 m a.s.l.. This zone is characterized by *Hagenia abyssinica, Hypericum revolutum,* and *Senecio johnstoni,* which bear vascular epiphytes in the montane belts. *Arundinaria alpina* forms a belt at lower altidudes (Hedberg 1951). The montane forest belts on the lower slopes are almost completely destroyed in this area.

Epiphytic vegetation of montane rainforests (800–900 m a.s.l.), which are non-existent in Rwanda, were studied in Zaïre (see Fig. 4a). The species-rich evergreen forests are mainly characterized by the Guineo-Congolian species *Gilbertiodendron dewevrei.* Furthermore, *Julbernardia seretii, Albizia gummifera, Anthonotha acuminata, Cynometra alexandri, Garcinia punctata, Diospyros hoyleana, Turraeanthus africana,* and *Pseudospondias microcarpa* are also common species. Rarer species include *Canarium schweinfurthii, Chrysophyllum pruniforme, Khaya anthotheca,* and *Polyscias kivuensis.* For a detailed description of vegetation and altitudinal zonation see Fischer (1996).

RESULTS AND DISCUSSION

1. Epiphytic vegetation of Central African dry forests

Epiphytic vegetation in the Akagera National Park is poor in phanerogamic epiphytes; only a few orchids occur. However, cryptogams such as lichens (see Fig. 4f) and mosses are both abundant and diverse. Comparative studies in a second dry forest within the Bugesera region showed that epiphytic vegetation is rich in orchids, which are abundant but not diverse, and that trees are densely covered by a great number of lichens (see Table 1).

Only three orchid species, *Ansellia africana, Aerangis kotschyana,* and *Polystachya modesta* could be found on phorophytes in the Akagera National Park. Only one liana species, *Sarcostemma viminale* (Asclepiadaceae), was found. Twig orchids like *Microcoelia globulosa* were not seen in this region, whereas in the dry forests in the Bugesera region this species dominated even the outer branches of the canopy (see Table 3).

Two main differences become obvious on comparing the epiphytic vegetation of those forests: species richness and abundance of epiphytic angiosperms are significantly higher in the Bugesera dry forest. Lichen diversity is also markedly higher than in the dry forests of the Akagera National Park.

In Malawi, four epiphytic orchid species were found in savanna regions (Morris 1970). The number of epiphytic orchids in African dry forests may be similar all over the continent because few orchid species can survive those xeric conditions, and African dry forests share many similarities in structure and tree architecture. In Brazilian *cerrado* formations, Gottsberger & Morawetz (1993) found three epiphytic angiosperms as well as three fern species. The occurrence of ferns is certainly the result of more rainfall and a different seasonality in this region compared with the study areas in Africa (c. 2360 mm per year; rainy season from September to May alternating with a short three-month dry period, after Gottsberger & Morawetz 1993).

Lichen diversity, i.e., species richness and abundance, is about twice as high in the Bugesera region as in the Akagera National Park (see Table 1, Appendix). Both forests have similar climatic conditions. The differences in the cryptogamic and phanerogamic epiphytic inventories could be due to more frequent fires and possibly to damage by mammals in the Akagera National Park. Lichens are known to be extremely sensitive to the effects of fire (personal communication U. Becker 1996).

Another difference between the forests is the degree of epiphytic cover on the phorophyte: trees in the Akagera National Park are up to 60% covered by lichens and mosses; orchids occur rarely. However, trees in the Bugesera region have an average epiphyte cover of 80%, including 15–20% orchids. Orchids were found as epiphytes on every tree analyzed.

TABLE 1. Comparison of epiphytic species numbers documented in different study sites, by taxonomic group and habits.

Holoepiphytes	Montane Rainforest (Zaïre)	Montane Forest (Rwanda)	Virunga Volcanoes (Rwanda)	Dry Forest Bugesera (Rwanda)	Dry Forest Akagera (Rwanda)
Angiosperms Total	65	37	1	6	3
Orchidaceae	58	30	1	6	3
Ferns	41	25	15	0	0
Mosses	22	18	17	0	0
Liverworts	51	29	25	5	1
Lichens	46	37	35	48	23
Epiphyll. Lichens	57	0	0	0	0
Facult. Epiphytes	5	4	1	0	0
Lianas	3	2	3	0	1
Parasites	2	1	0	0	0

Average numbers and minima and maxima of the different epiphytes found on individual trees are given in Table 2. In terms of the numbers of epiphytes on a single phorophyte, the Bugesera region is richer in epiphytes.

Dominant plant groups in each of the four zones (modified after Johansson 1974) of the canopy are listed in Table 3. Lichens are the dominant epiphytic plant group in both dry forests. Mosses cover the bark of the phorophytes only sparsely. Gottsberger & Morawetz (1993) report a succession of epiphytes on Brazilian *cerrado* phorophytes: first, lichens colonize the bark and are followed by mosses and liverworts. This phenomenon was not observed in Central African dry forests.

2. Vegetation and phytogeographical affinities of epiphytes in Central African moist forests

Analysis of the epiphytic inventory of phorophytes examined in Zaïrean and Rwandan moist forests shows that among vascular plants Orchidaceae make up more than 50% of the species. Other

TABLE 2. Comparison of epiphytic species documented on single phorophytes in different study sites.

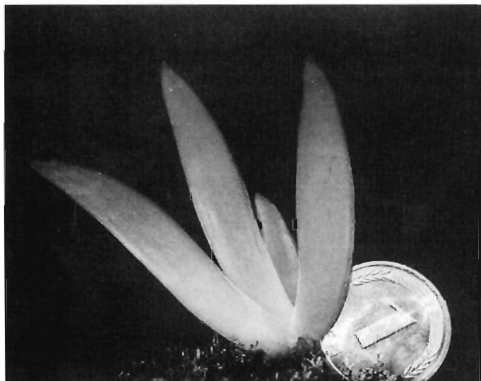| Epiphytes average number/min., max.	Montane Rainforest (Zaïre)	Montane Forest (Rwanda)	Virunga Volcanoes (Rwanda)	Dry Forest Bugesera (Rwanda)	Dry Forest Akagera (Rwanda)
Angiosperms	20	18	2	2	1
Angiosperms max.	33	26	3	3	1
Angiosperms min.	10	7	0	0	0
Orchidaceae	13	11	0	2	1
Orchidaceae max.	23	18	1	3	1
Orchidaceae min.	4	5	0	0	0
Ferns	6	8	3	0	0
Ferns max.	12	11	7	0	0
Ferns min.	2	3	1	0	0
Mosses	7	6	6	0	0
Liverworts	15	12	9	3	1
Lichens	8	11	13	12	4
Lichens max.	13	41	22	24	9
Lichens min.	5	4	8	5	2
Epiphyll. Lichens	13	0	0	0	0

FIG. 3. *Bolusiella maudae* (Bolus) Schlechter (Orchidaceae), typical twig orchid, growing on outer branches of the phorophyte, montane rainforest, Zaïre (diameter of the coin is 1.7cm, photograph N. Biedinger).

dominant families include Aspleniaceae, Balsaminaceae, Begoniaceae, and Piperaceae. In the Zaïrean montane rainforest, most orchids belong to the genus *Bulbophyllum* (see Fig. 5e,f); *Angraecum* and related taxa (see Fig. 5b) also occurred. In the Nyungwe montane forest, *Polystachya* was the most species-rich epiphytic genus (16 species). In montane forests of the Virunga volcanoes, only one epiphytic orchid, *Polystachya kermesina*, was found (see Table 1). Lists of all phanerogamic holo- and hemiepiphytes, as well as lianas and parasites, at all study sites are given in the appendix. Altogether, the epiphyte index (percentage of the flora) of the phanerogamic flora of the region investigated is approximately 2.5%.

Species numbers of angiosperms, ferns, mosses, liverworts and lichens determined in different montane forests are listed (Table 1). Average and maximum and minimum species numbers found on a single phorophyte are given in Table 2.

In all plant groups, total species numbers decrease with increase of altitude. In general, the average number of species, as well as maxima and minima, found on one phorophyte also decrease. Alpha diversity of epiphytes in the Zaïrian forest is higher than in the Nyungwe forest in terms of single phorophytes and the whole study site (see Table 1 and Table 2).

A direct relationship between precipitation and epiphyte species diversity, as postulated by Gentry (1982), cannot provide a full explanation, because especially between the two major study sites (Nyungwe, Zaïre) precipitation differs only slightly (c. 200 mm).

For the low montane rain forest in Zaïre (850–950 m a.s.l.) the Congo basin possibly represents a great "source" of species which surpasses species diversity in the Nyungwe montane forest (2000 m a.s.l.). In the Nyungwe forest, the flora is composed mainly of Afromontane elements. Finally, in the Virunga volcanoes (3000 m a.s.l.), frost limits vascular plant diversity in general and epiphyte diversity in particular because of their anatomical adaptations like succulence, which explains low species numbers in these forests.

Furthermore, decreasing tree height (average 32 m in Zaïre, 22 m in Nyungwe forest, 15 m in the Virungas) with increasing altitude, and, therefore, decreasing surface to settle on, might explain this tendency.

TABLE 3. Phorophyte zonation with dominant epiphytic plant groups in different study sites.

Study Site	Zone 1	Zone 2	Zone 3	Zone 4
Dry Forest Akagera	Lichens Mosses	Lichens Orchidaceae	Lichens Orchidaceae	Lichens Mosses
Dry Forest Bugesera	Lichens Mosses	Lichens Mosses	Lichens Orchidaceae	Lichens Microcoelia
Montane Rainforest Zaïre	Mosses/Liverw. Araceae	Ferns Orchidaceae	Orchidaceae Begoniaceae	Lichens Twig Orchids
Montane Forest Rwanda	Lianas Mosses/Liverw.	Orchidaceae Balsaminaceae	Polystachya Lichens	Lichens Mosses
Virunga-Volcanoes	Mosses/Liverw. Lianas	Ferns Mosses/Liverw.	Mosses/Liverw. Lichens	Lichens Mosses/Liverw.

TABLE 4. Comparison of the distribution ranges of the holoepiphytes recorded in both montane forests (Rwanda, Zaïre).

Distribution of species recorded	Montane Rainforest Zaïre (850-950 m a.s.l.)	Montane Forest Rwanda (2000 m a.s.l.)
West and Central Africa	50%	14%
West, Central and East Africa	16%	4%
Central Africa	15%	32%
Central and East Africa	4%	32%
Tropical Africa	11%	7%
Palaeotropical / Pantropical	4%	11%

Distribution of dominant plants, groups of species, or communities in the different zones of the tree (modified after Johansson 1974, see Fig. 2) is shown in Table 3. The occurrence of twig orchids, such as *Taeniophyllum coxii, Bolusiella maudae* (Fig. 3), and small *Bulbophyllum* species, is characteristic of the outer part of the canopy (zone 4) of phorophytes studied in the Zaïrean forest. However, twig orchids are rare in the montane forest in the Nyungwe Forest Reserve.

In all montane forests, zone 3 is mostly colonized by holoepiphytes (ferns, angiosperms) growing on thick moss layers, and rarely by hemiepiphytes or lianas. Johansson (1974) made similar observations in montane forests in Liberia, which leads to the assumption that the angle of branch inclination in this part of the canopy provides better growing sites, and also that it is not easily reached by hemiepiphytes or lianas. The latter plants are mainly found in zone 2, lianas in particular covering the main stem as well.

Average numbers of vascular epiphytes on a single phorophyte decrease with increasing altitude. The highest number of vascular epiphytes was found on *Anthonotha pynaertii* (Caesalpiniaceae) in the Zaïrean forest: 33 angiosperm and 7 fern species. Average numbers of 18 to 20 vascular epiphytes grew on phorophytes in the two montane forests in Rwanda and Zaïre.

Comparisons with other studies of epiphyte diversity are difficult because they do not obtain complete inventories. Johansson (1974) found on average 7 vascular epiphyte species per tree, but he did not collect the entire epiphytic vegetation of single trees. Dunsterville (1961) documented 49 orchids on a single phorophyte in Venezuela.

Beta-diversity of epiphytic inventories (angiosperms) between phorophytes within one forest was relatively low: many species (54%) were found on several trees, in many cases with several individuals. Species that were only documented by one individual plant on the phorophytes examined were noted on other trees nearby. These results contradict studies made in the Neotropics by Ackerman (1986a), Benzing (1981), Benzing & Ott (1981), and Gentry & Dodson (1987b), in which a scattered distribution of epiphytes is postulated: this means that single individuals of the same epiphytic species only occur at large distances apart within a forest, which clearly cannot be confirmed for the forests studied in Zaïre and Rwanda.

Nevertheless, the similarity between the epiphyte inventories of phorophytes growing close together is low (in average the Jaccard Index was 0.1). This shows low constancy and unpredictability of epiphyte communities for a single tree. Obviously, settlement rapidity or other parameters determine the composition of epiphytes on one tree, whereas epiphyte vegetation within a forest is relatively homogenous.

Phytogeographical affinities of epiphytic angiosperms documented in montane forests in Rwanda and Zaïre were analysed and are listed in Table 4, and here differences between both forests become obvious. Most holoepiphytes described for the montane rain forest (850–950 m a.s.l.) in Zaïre occur only within the Guineo-Congolian phytochorion, whereas the distribution range is much smaller for the epiphyte species in Nyungwe Forest (2000 m a.s.l.) in Rwanda.

Percentage endemism of epiphytic orchids in West and East Africa is about 35%, whereas only

24% of all epiphytic orchids in Central Africa are endemic to the region (compiled from Geerinck 1984, 1992).

Studies in Peru show comparable results concerning endemism indices (Ibisch *et al.* 1996): 26% of holoepiphytic orchids are endemic to Peru. Terrestrial orchids, by comparison, have lower percentages of endemism in tropical Africa and Peru.

The forests studied are only 100km apart. The similarity-coefficient (Jaccard, after Magurran 1988) of the forests is low (C = 0.1) which implies high beta-diversity.

The differences in floristic composition can be explained by the fact that the boundary of two adjacent phytochoria, the Guineo-Congolian and the Afromontane Center, runs between the forests studied. Reasons for these differences can be given by palaeoclimatic influences during the Pleistocene, where a change of climate, here meaning periods of arid conditions, caused a great contraction of lowland rainforest (Hamilton 1982, Sosef 1994). Sosef proposes that tropical Africa carried a savanna vegetation intermixed with patches of montane rainforest. It is generally accepted that those refuge areas lie in Sierra Leone/Liberia, Cameroon, Guinea, Gabon as well as eastern Zaïre and the coastal regions of Tanzania. These patches might well explain the frequent disjunctions on western and eastern mountains in Africa, and also the differences between the Guineo-Congolian and Afromantane flora. However, these differences are surprising for epiphytes, since they are provided with diaspores which are well adapted for long-distance dispersal. Only ten species were found in common in both forests, and among them only seven species are holoepiphytes (e.g., *Begonia poculifera*, see Fig. 5a). Two of them, *Peperomia rotundifolia* and *Rhipsalis baccifera*, even occur on other continents, showing a very wide distribution range for angiosperm epiphytes.

However, comparisons of epiphytic vegetation of the Guineo-Congolian montane rainforest in Zaïre with forests studied by Johansson (1974) in Liberia show many affinities; 29% of the total of holoepiphytic ferns and angiosperms were listed from both regions.

Ninety one out of 238 epiphytic orchids described for Central Africa (compiled from Geerinck 1984, 1992) were documented in the forests studied. Johansson's (1974) results were similar: 101 of 227 West African epiphytic orchids were recorded, 21% of phanerogamic epiphytes were common to both

regions, and 50% of the Orchidaceae documented for Central Africa are distributed in the Guineo-Congolian phytochorion.

A comparison with other regions in Africa and the Neotropics (Ibisch 1996, Johansson 1974, Rauer 1995) shows a similar floristic composition within the phanerogamic epiphyte vegetation in comparable forests: orchids always made up 50% of all vascular epiphytes. This is surprising because in the Neotropics there are numerous dominant families within the epiphytic vegetation such as Bromeliaceae, Cactaceae, Ericaceae and Gesneriaceae, which could influence the dominance of orchids.

3. Ecology of vascular epiphytes in Central Africa

Adaptations of epiphytes to certain stress factors in their habitat, such as lack of nutrients and water or limited space, are well known and many of them have already been described in detail (Martius 1842; Schimper 1888; Goebel 1889; Benzing 1981, 1986; Benzing & Ott 1981; Benzing *et al.* 1983; Winkler 1989).

Generally, many plant families that contain epiphytes, like Begoniaceae, Cactaceae, Ericaceae, Gesneriaceae, Orchidaceae, and Piperaceae, show succulence. Others save water in tanks, such as bromeliads, certain huge ferns, or Commelinaceae (*Cochliostema*). Water uptake is often implemented by specialized absorbing structures like the dead hairs of Bromeliaceae or the velamen of Orchidaceae.

Adaptation to water stress by succulence of either leaves or stem, or both, was found in 90% of all holoepiphytes documented. The majority (75%), which covers the orchid species, have a water-absorbing velamen.

Growth-height of holoepiphytes was another vegetative character which was analyzed. Summarizing all epiphytes, their growth-height was usually between 20 and 50cm. Growth-height in this case means the growing direction of the plant vertically from the substrate. Looking at the holoepiphytes in the most epiphyte-rich forests (Irangi, Nyungwe), a maximum height of 40cm was recorded. Corresponding results have also been observed for epiphytic Cactaceae and Bromeliaceae in the New World (personal communication H. Wilhelmi and J. Nieder).

Studies concerning a possible correlation between bark structure of phorophytes and epiphytic colonization were made in dry and moist forests. The influence of structural characteristics of trees (such

as bark structure, presence or absence of substances like latex or resins, or inclination of branches) on epiphyte settlement has already been observed (Johansson 1974). The degree of epiphytic cover of all phorophytes investigated was examined and a possible correlation with bark structure and tree architecture was attempted.

A rough summary would be that sculptured bark structures and only slightly inclined branches favour epiphytic colonization. However, despite a rough bark structure some phorophyte species do not bear any vascular epiphytes (e.g., *Cynometra alexandri*, *Trichilia* cf. *rubescens*). Apart from phenomena such as the alteration of bark structure with the age of
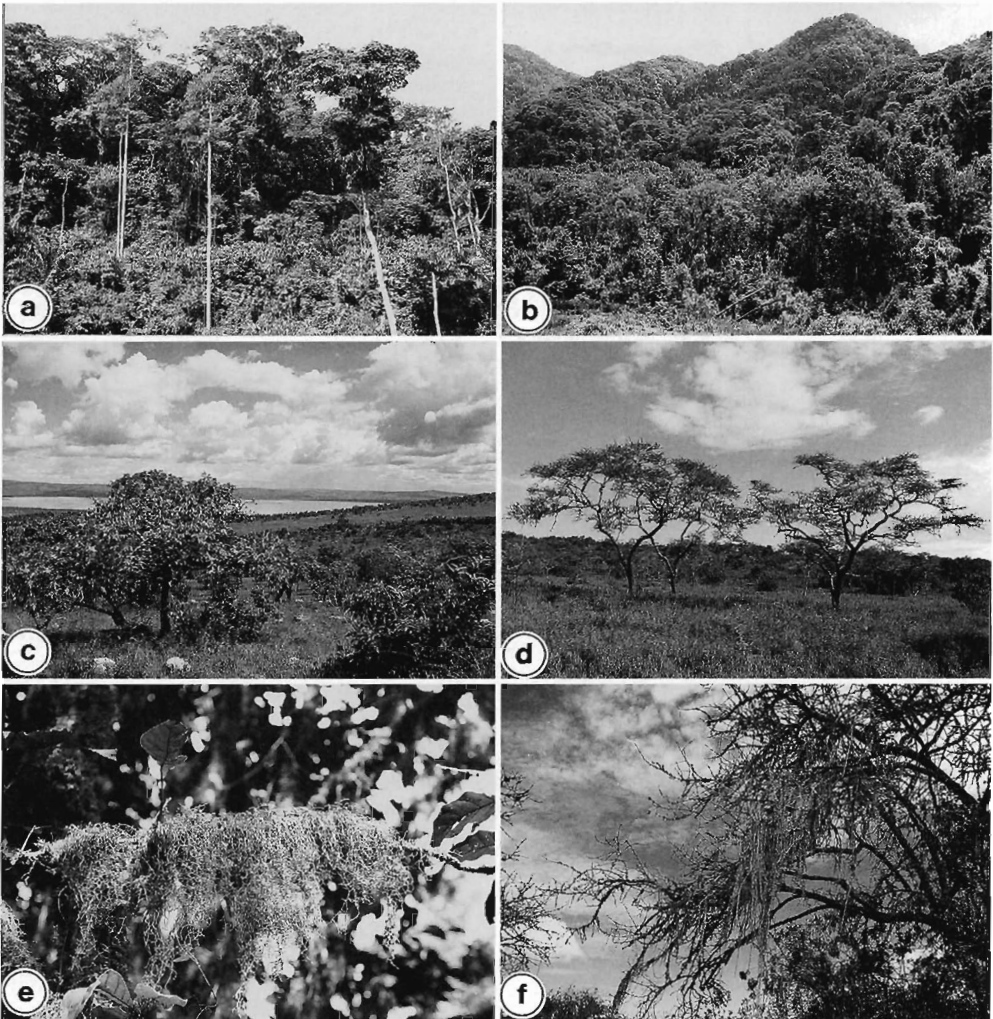

FIG. 4. Aspects of different study sites and typical epiphytic cryptogams in Rwanda and Zaïre (Fig. 4a-f). a) Montane rainforest (950 m a.s.l.), Irangi Station, Zaïre. b) Montane forest (2000 m a.s.l.), Nyungwe Forest Reserve, Rwanda. c) Dry forest near Lac Ihema (1300 m a.s.l.). d) *Acacia senegal* (L.) Willd.(Mimosaceae), typical tree in Akagera National Park, Rwanda. e) *Pilotrichella ampullacea* (C. Müll.) Jäg. (Meteoriaceae), characteristic epiphytic moss, found on all phorophytes in montane forests in Rwanda and Zaïre. f) *Ramalina* sp., typical lichen on trees in the Akagera National Park, Rwanda (photographs by N. Biedinger).

the tree (*Hagenia abyssinica*, *Turraeanthus africanus*, *Uapaca heudelotii*), a general correlation could not be stated.

Many epiphytes (ferns, orchids) adapt to colonization of the space-limited canopy habitat by developing rhizomes, which of course primarily have a storing function; nearly all orchids and ferns documented belong to this group.

Flower biology was studied in detail. A large percentage (78%) of the documented holoepiphytes were melittophilous or myophilous. Trap-lining pollination can almost be excluded. Floral adaptations of holoepiphytes to the extreme canopy habitat have been described by Ackerman (1986a,b, 1989), Gentry & Dodson (1987b) and van der Pijl & Dodson (1966): trap-lining pollination as an adaptation to widely scattered populations of epiphytes in families like Bromeliaceae, Cactaceae, Ericaceae, Gesneriaceae, Melastomataceae or Rubiaceae is mentioned as one strategy. Deceptive flowers that do not offer any reward are found mainly among Orchidaceae and represent another characteristic type of floral adaptation. In contrast to statements in the literature, two main observations of the epiphytes investigated are striking: scattered distribution of holoepiphytes could not be documented, and the frequency of myophilous flowers is obviously much greater than previously estimated. These differences may be due to the focus in other studies on the Neotropics and on often showy or big flowers. In addition, general differences between the Neotropics and Palaeotropics, where other strategies might have evolved as a result of other competitive systems between species, may also contribute to the divergence.

As expected, most seeds of holoepiphytes are dispersed by wind or birds (c. 90%). Only the dispersal of what are commonly regarded as autochorous *Impatiens* seeds remains unexplained. Micromorphological studies of the diaspores of *Impatiens* revealed that species related to the African *Impatiens niamniamensis* are characterized by helical wall-thickenings. They are produced by testa cells, which when wetted glue together and become adhesive (Fischer & Neinhuis 1993). This could be a preadaptation to the epiphytic habit, because those structures only occur in holoepiphytic or facultative epiphytic species. So possibly the diaspores are shot into the feathers of birds, triggered by slight vibration, or even accidentally.

4. Conclusions

In Central African dry forests, lichens dominate the epiphyte covers of phorophytes; only a few orchid genera (*Bulbophyllum*, *Cyrtorchis*, *Microcoelia*), which seem to be well adapted to exposed and dry places, were found. The influence of fire seems to be the main reason for significant differences between epiphyte diversity in two dry forests with similar climatic conditions.

Predictability of phanerogamic and cryptogamic epiphyte vegetation differs within a study site. Distribution ranges of cryptogamic epiphytes are far wider than those of phanerogamic species. Those differences in distribution can be explained by a high incidence of radiation within the angiosperms after the splitting of the continents (personal communication J.-P. Frahm) and by the efficient wind dispersal of the propagules of mosses.

The present study shows that in Central Africa phanerogamic epiphytic vegetation within one forest is more or less homogenous and more or less predictable for one area. The study of the epiphytic inventories of many individual phorophytes in the forest leads us to conclude that – contrary to the complete epiphytic inventory of a forest – similarity between the epiphytic inventories and composition of neighboring single trees is low and not predictable. Obviously, stochastic processes, e.g., more rapid settlement, are responsible for the distribution of epiphyte species on different phorophytes.

Using these results, it can be assumed that epiphytic species richness of a homogenous study site, meaning the number of different species in a forest, is controlled deterministically, inferring a distinct availability of niches. Beta-diversity, understood as the diversity of forest-types along a certain gradient, determines the species richness of the region. Possibly a high beta-diversity causes higher species richness in the Neotropics.

By contrast, the entire Guineo-Congolian phytochorion is characterized by low landscape diversity; the sudden change in floristic composition between the Congolian basin and the adjacent montane forests of the Central African Rift Valley possibly represents one of only a few regions in tropical Africa where landscape diversity is high. High affinities between Zaïrian and Liberian epiphytes also point in this direction.

It is assumed by the authors that centers of phanerogamous epiphyte diversity in Africa can be found

FIG. 5. Characteristic holoepiphytes in Rwandan and Zaïrian montane forests (Fig. 5a-f, from top left to right). a) *Begonia poculifera* Hook f. var. *poculifera* (Begoniaceae), Nyungwe montane forest. b) *Ancistrorhynchus capitatus* (Lindley) Summerh. (Orchidaceae), Zaïre montane rainforest. c) *Impatiens paucidentata* De Wild. (Balsaminaceae), typical ornithophilous flower with traces of pollinating bird, Zaïre montane rainforest. d) *Costus le-testui* Pellegr. (Costaceae), typical psychophilous flower, Zaïre montane rainforest. e) *Bulbophyllum unifoliatum* De Wild. (Orchidaceae), small orchid, Zaïre montane rainforest. f) *Bulbophyllum sandersonii* (Hook f.) Rchb. var. *sandersonii* (Orchidaceae), typical myophilous flower, Zaïre montane rainforest (photographs by N. Biedinger).

in montane forests of Malawi, Liberia, Cameroon, Gabon and the Congolian basin. Total numbers of epiphytes in montane forests studied in Rwanda and Zaïre are lower than in the Neotropics, which can be explained by lower epiphyte diversity in Africa in general. Dramatic climatic changes, and as a consequence a severe reduction in lowland rainforests during the Pleistocene (Hamilton 1982, Sosef 1994), is certainly one explanation for this poverty.

Epiphytic ecology, relating to the vegetative part of the plants was illustrated by well-known features characteristic of epiphytes like succulence, velamen radicum or small body size.

Studies of pollination ecology showed a high percentage of melittophilous and myophilous flowers. Trap-lining pollination and scattered distribution of epiphytic species, which are postulated as typical for epiphytic angiosperms, were not observed. One reason for these surprising results could be the differences between Palaeotropical and Neotropical pollination strategies of epiphytes. Possible focusing on showy flowers, especially of orchids, in the Neotropics overemphasized spectacular pollination strategies and underestimated the high percentage of small-flowered, inconspicuously flowering epiphytic orchids.

CONSERVATION

As has been emphasized many times in scientific and popular literature, tropical forests contain more than 60% of all known angiosperm species. Nevertheless, the extinction of species may be occurring more quickly than their sampling. Beyond that, the complex ecological relationships and specific quality of tropical biodiversity have not yet been understood (Linsenmair 1990).

In Rwanda and Zaïre, overpopulation puts great pressure on the environment. National Parks and reserves require strict protection. Considering that the number of orchid species which were documented on only a few trees constitute more than one third of all epiphytic orchids so far described for Rwanda, Burundi and Zaïre, the urgent need for the protection of these areas is endorsed and emphasized.

ACKNOWLEDGEMENTS

REFERENCES

Ackerman, J.D. 1986a. Coping with the epiphytic existence: pollination strategies. Selbyana 9: 52–60.

Ackerman, J.D. 1986b. Mechanisms and evolution of food-deceptive pollination systems in orchids. Lindleyana 1: 108–113.

Ackerman, J.D. 1989. Geographic and seasonal variation in fragrance choices and preferences of male Euglossine bees. Biotropica 21: 340–347.

Becker, M. 1994. Die Pteridophytenvegetation entlang eines Höhentransektes an der westlichen Randschwelle des zentralafrikanischen Grabens. M.Sc.-Thesis, Rheinische-Friedrich-Wilhelms-Universität, Bonn.

Benzing, D.H. 1981. Why is Orchidaceae so large, its seeds so small, and its seedlings mycotrophic? Selbyana 5: 241–242.

Benzing, D.H. 1986. The vegetative basis of vascular epiphytism. Selbyana 9: 23–43.

Benzing, D.H. (ed.) 1990. Vascular epiphytes. Cambridge.

Benzing, D.H., & D.W. Ott 1981. Vegetative reduction in epiphytic Bromeliaceae and Orchidaceae: its origin and significance. Biotropica 13: 131–140.

Benzing, D.H., Friedman, W.E., Peterson, G., & A. Renfrow 1983. Shootlessness, velamentous roots and the pre-eminence of Orchidaceae in the epiphytic biotope. Amer. J. Bot. 70: 121–133.

Dieterlen, F. 1978. Zur Phänologie des Äquatorialen Regenwaldes in Ost-Zaire (Kivu). Nebst Pflanzenliste und Klimadaten. Dissertationes Botanicae 47: 1–111, Vaduz.

Dunsterville, G.C.K. 1961. How many orchids on a tree? Am. Orchid Soc. Bull. 30: 362–363.

Erwin, T.L., & J.C. Scott 1980. Seasonal and size patterns, trophic structure, and richness of Coleoptera in the tropical arboreal ecosystem: The fauna of the tree *Luehea seemannii* Triana and Planch in the Canal Zone of Panama. Coleopt. Bull. 34: 305–322.

Fischer, E., & H. Hinkel 1990. Untersuchungen zur Einnischung der Herpetofauna in Nebelwäldern Ruandas (Zentralafrika). Festschrift für Wendelin Klaer zum 65. Geburtstag. Mainzer Geowissenschaftliche Studien 34: 485–502.

Fischer, E., & C. Neinhuis 1993. Samenmikromorphologie der Gattung Impatiens (Balsaminaceae) und ihre taxonomische Bedeutung. Pp. 10 *in* Fürnkranz, D., & H. Schantl (eds.). 11. Symp. Morph. Anat. Syst., Salzburg.

Fischer, E. 1996. Die Vegetation des Parc National de Kahuzi-Biéga, Süd-Kivu, Zaire. Erdwissenschaftliche Forschung 35: 1–239, Stuttgart.

Frahm, J.-P. 1985. Afrikanische *Campylopus*-Arten (Dicranaceae, Musci). Bryoph. Bibl. 31: 1–216.

Frahm, J.-P. 1993. Taxonomic results of the BRYOTROP expedition to Zaire and Rwanda. 17. Andreaceae, Bruchiaceae, Dicranaceae, Rhizogoniaceae, Bartramiaceae, Rhacocarpaceae, Hedwigiaceae, Cryphaeaceae, Leucodontaceae. Tropical Bryol. 8: 153–169.

Frahm, J.-P. 1994a. Scientific Results of the BRYOTROP expedition to Zaire and Rwanda. 1. The ecology of epiphytic bryophytes on Mt. Kahuzi (Zaire). Tropical Bryol. 9: 137–152.

Frahm, J.-P. 1994b. Scientific Results of the BRYOTROP expedition to Zaire and Rwanda. 2. The altitudinal zonation of the bryophytes on Mt. Kahuzi, Zaire. Tropical Bryology 9: 153–167.

Geerinck, D. 1984. Flore d'Afrique Centrale. Zaire-Rwanda-Burundi. Orchidaceae I. Jard. Bot. Natl. Belg., Meise.

Geerinck, D. 1992. Flore d'Afrique Centrale. Zaire-Rwanda-Burundi. Orchidaceae II. Jard. Bot. Natl. Belg., Meise.

Gentry, A.H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, pleistocene climatic fluctuations, or an accident of the andean orogeny. Ann. Miss. Bot. Gard. 69: 557–593.

Gentry, A.H. 1986. Species richness and floristic composition of Choco region plant communities. Caldasia 15: 71–91.

Gentry, A.H., & C.H. Dodson 1987a. Contribution of nontrees to species richness of a tropical rain forest. Biotropica 19: 149–156.

Gentry, A.H., & C.H. Dodson 1987b. Diversity and biogeography of Neotropical vascular epiphytes. Ann. Miss. Bot. Gard. 74: 205–233.

Goebel, K. 1889. Pflanzenbiologische Schilderungen 1. Marburg.

Gottsberger, G., & W. Morawetz 1993. Development and distribution of the epiphytic flora in an Amazonian savanna in Brazil. Flora 188: 145–151.

Hamilton, A.C. 1982. Environmental history of east Africa. A study of the Quartenary. London.

Hedberg, O. 1951. Vegetation belts of the East African mountains. Svensk Botanisk Tidskrift 45: 140–202.

Ibisch, P.L. 1996. Neotropische Epiphytendiversität – das Beispiel Bolivien. Wiehl.

Ibisch, P.L., Boegner, A., Nieder, J., & W. Barthlott. 1996. How diverse are Neotropical epiphytes? An analysis based on the "Catalogue of flowering plants and gymnosperms of Peru". Ecotropica 2: 13–28.

Johansson, D.H. 1974. Ecology of vascular epiphytes in West African rain forest. Acta Phytogeo. Suec. 59: 1–136.

Kress, W.J. 1986. The systematic distribution of vascular epiphytes: an update. Selbyana 9: 2–22.

Kürschner, H. 1995. Epiphytische Moosgesellschaften im östlichen Kongobecken und den angrenzenden Gebirgsstöcken (Parc National de Kahuzi-Biega / Zaire, Forêt de Nyungwe / Rwanda). – Wissenschaftliche Ergebnisse der BRYOTROP-Expedition nach Zaire und Rwanda Nr. 4. Nova Hedwigia 61: 1–64.

Lawalrée, A. 1969a. Flore d'Afrique Centrale (Zaire-Rwanda-Burundi). Pteridophytes, Actiniopteridaceae. Meise, Jard. Bot. Natl. Belg.

Lawalrée, A. 1969b. Flore d'Afrique Centrale (Zaire-Rwanda-Burundi). Pteridophytes, Equisetaceae. Meise, Jard. Bot. Natl. Belg.

Lawalrée, A. 1969c. Flore d'Afrique Centrale (Zaire-Rwanda-Burundi). Pteridophytes, Parkeriacae. Meise, Jard. Bot. Natl. Belg.

Lawalrée, A. 1969d. Flore d'Afrique Centrale (Zaire-Rwanda-Burundi). Pteridophytes, Psilotaceae. Meise, Jard. Bot. Natl. Belg.

Lawalrée, A. 1971. Flore d'Afrique Centrale (Zaire-Rwanda-Burundi). Pteridophytes, Blechnaceae. Meise, Jard. Bot. Natl. Belg.

Lawalrée, A. 1975. Flore d'Afrique Centrale (Zaire-Rwanda-Burundi). Pteridophytes, Marsileaceae. Meise, Jard. Bot. Natl. Belg.

Lawalrée, A. 1976. Flore d'Afrique Centrale (Zaire-Rwanda-Burundi). Pteridophytes, Azollaceae. Meise, Jard. Bot. Natl. Belg.

Lawalrée, A. 1989. Flore d'Afrique Centrale (Zaire-Rwanda-Burundi). Pteridophytes, Lycopodiaceae. Meise, Jard. Bot. Natl. Belg.

Lawalrée, A. 1990. Flore d'Afrique Centrale (Zaire-Rwanda-Burundi). Pteridophytes, Davalliaceae. Meise, Jard. Bot. Natl. Belg.

Linsenmair, K.E. 1990. Tropische Biodiversität: Befunde und offene Probleme. Verh. Dtsch. Zool. Ges. 83: 245–261.

Lüttge, U. (Ed.). 1989. Vascular plants as epiphytes. Berlin.

Madison, M. 1977. Vascular epiphytes: their systematic occurrence and salient features. Selbyana 2: 1–13.

Magurran, A.E. 1988. Ecological diversity and its measurement. London.

Martius, C.F.P.v. 1842. Ueber die Vegetation der unächten und ächten Parasiten, zunächst in Brasilien. Gelehrte Anzeigen 14: 353–400.

Morris, B. 1970. The epiphytic orchids of Malawi. The Society of Malawi, Blantyre.

Pichi Sermolli, R.E.G. 1983. A contribution to the knowledge of the pteridophyta of Rwanda, Burundi and Kivu (Zaire). I. Bull. Jard. Bot. Natl. Belg. 53: 177–284.

Pichi Sermolli, R.E.G. 1985. A contribution to the knowledge of the pteridophyta of Rwanda, Burundi and Kivu (Zaire). II. Bull. Jard. Bot. Natl. Belg. 55: 123–206.

Pijl, van der L., & C.H. Dodson 1966. Orchid flowers. Their pollination and evolution. Coral Gables, Florida.

Rauer, G. 1995. Epiphytische Orchidaceae eines westandinen Bergregenwaldes in Ecuador. Msc.-Thesis, Rheinische-Friedrich-Wilhelms-Universität, Bonn.

Richards, P.W. 1952. The tropical rain forest: an ecological study. Cambridge.

Schimper, A.F.W. 1888. Die epiphytische Vegetation Amerikas. Jena.

Sirven, P., Gotanegre, J.F., & C. Prioul 1974. Géographie du Rwanda. Brüssel.

Sosef, M. 1994. Refuge Begonias. Taxonomy, phylogeny and historical biogeography of *Begonia* sect. *Loasobegonia* and sect. *Scutobegonia* in relation to glacial rain forest refuges in Africa. Ph.D. thesis, University of Wageningen.

Troupin, G. 1966. Étude phytoécologique du Parc National de l'Akagera et du Rwanda Oriental. Recherche d'une méthode d'analyse appropriée à la végétation d'Afrique Intertropicale. Institut National de Recherche Scientifique, Butare, Ruanda.

Troupin, G. 1978. Flore du Rwanda. Spermatophytes. Vol. 1. Annales du Musée de Tervuren no. 9.

Troupin, G. 1983. Flore du Rwanda. Spermatophytes. Vol. 2. Annales du Musée de Tervuren no. 13.

Troupin, G. 1985. Flore du Rwanda. Spermatophytes. Vol. 3. Annales du Musée de Tervuren.

Troupin, G. 1987. Flore du Rwanda. Spermatophytes. Vol. 4. Annales du Musée de Tervuren.

Wallace, B.J. 1981. The Australian vascular epiphytes: flora and ecology. Ph.D. thesis, University of New England, New South Wales, Australia.

Watson, J.B., Kress, W.J., & C.S. Roesel 1987: A bibliography of biological literature on vascular epiphytes. Selbyana 10: 1–23.

Winkler, S. 1989. Anpassungsstrategien neotropischer Epiphyten. Pp. 245–256 *in* Hartmann, G. (ed.). Amazonien im Umbruch. Berlin.

White, F. 1983. The vegetation of Africa. A descriptive memoir to accompany the UNECO/AETFAT/UNSO vegetation map of Africa. Natural Ressources Research 20, UNESCO, Paris.

APPENDIX. List of all epiphytes recorded in all study sites (for angiosperms: holoepiphytes (h), facultative epiphytes (f), lianas (l), parasites (p)). A = Akagera National Park; B = Bugesera region; I = Montane rain-forest, Irangi Station, Zaïre; N = Nyungwe Forest Reserve, Rwanda; V = Virunga volcanoes.

Species Recorded	Growth Form	A	B	I	N	V
Acanthaceae						
Barleria sp.	f			X		
Annonaceae						
Monanthotaxis orophila	f				X	
Araceae						
Culcasia falcifolia	f				X	
Culcasia scandens	f				X	
Rhaphidophora africana	f			X		
Araliaceae						
Schefflera goetzenii	l			X	X	
Schefflera kivuensis	l			X		
Schefflera sp.	l			X		
Asclepiadaceae						
Sarcostemma viminale	l	X				
Asteraceae						
Gynura scandens	l					X
Senecio kanzibiensis	h			X	X	
Balsaminaceae						
Impatiens irangiensis	h			X		
Impatiens keilii	h				X	
Impatiens niamniamensis	f				X	
Impatiens paucidentata	h			X		
Impatiens sp.	h			X		
Begoniaceae						
Begonia cf. *ampla*	h			X		
Begonia longipetiolata	h			X		
Begonia meyeri-johannis	h			X	X	
Begonia poculifera var. *poculifera*	h			X	X	
Begonia zaïrensis	f			X		
Begonia sp.				X		
Cactaceae						
Rhipsalis baccifera	h			X	X	
Campanulaceae						
Canarina eminii	h				X	
Costaceae						
Costus le-testui	h			X		
Dioscoreaceae						
Dioscorea sp.				X		

Species Recorded	Growth Form	A	B	I	N	V
Bulbophyllum sandersonii						
ssp. *sandersonii*	h			X		
Bulbophyllum sandersonii						
ssp. *stenopetalum*	h			X		
Bulbophyllum scaberulum	h			X		
Bulbophyllum schimperianum	h			X		
Bulbophyllum unifoliatum	h			X		
Bulbophyllum vulcanicum	h				X	
Bulbophyllum spp.	h		X	X	X	
Cynorkis debilis	f			X		
Cyrtorchis arcuata	h		X		X	
Cyrtorchis chailluana	h			X		
Cyrtorchis praetermissa	h		X			
Cyrtorchis ringens	h			X		
Cyrtorchis sp.	h			X		
Diaphananthe burttii	h				X	
Diaphananthe globulosocalcarata	h			X		
Liparis deistelii	h				X	
Liparis epiphytica	h			X		
Microcoelia bulbocalcarata	h			X		
Microcoelia globulosa	h		X			
Microcoelia sp.	h			X		
Polystachya adansoniae	h			X		
Polystachya adansoniae						
var. *elongata*	h			X		
Polystachya bifida	h				X	
Polystachya brugeana	h			X		
Polystachya cf. *cribbiana*	h				X	
Polystachya cultriformis	h				X	
Polystachya dewanckeliana	h				X	
Polystachya fallax	h				X	
Polystachya fractiflexa	h			X		
Polystachya galeata						
var. *babyloni*	h			X		
Polystachya galeata						
var. *galeata*	h			X	X	
Polystachya kermesina	h					X
Polystachya lindbloomii	h				X	
Polystachya modesta	h		X			
Polystachya odorata	h			X		
Polystachya pachychila	h				X	
Polystachya seticaulis	h			X		
Polystachya spatella	h				X	
Polystachya stauroglossa	h			X		
Polystachya tenuissima	h			X		
Polystachya tesselata	h			X		
Polystachya virginea	h				X	
Polystachya vulcanica	h				X	
Polystachya spp.	h			X	X	
Rangaeris muscicola	h			X		
Solenangis sp.	h			X		
Taeniophyllum coxii	h			X		
Tridactyle cf. *nalaensis*	h			X		
Tridactyle sp.	h				X	

Species Recorded	Growth Form	A	B	I	N	V
Piperaceae						
Peperomia blanda	f			X		
Peperomia fernandopoiana	h			X		
Peperomia rotundifolia	h			X	X	
Peperomia tetraphylla	h				X	
Peperomia sp.				X	X	
Rubiaceae						
Chassalia cristata	l			X		
Galium chlorionanthum	f					X
Rubiaceae indet				X		
Urticaceae						
Procris crenata	f			X		
Ferns						
Anapeltis owariensis				X		
Anthrophyum manianum				X		
Arthropteris cf. anniana					X	
Arthropteris charletiana				X		
Arthropteris orientalis				X		
Arthropteris sp.					X	
Asplenium aff. *aethiopicum*						X
Asplenium africanum				X		
Asplenium barteri				X		
Asplenium dregeanum					X	
Asplenium aff. *elliottii*				X		
Asplenium friesiorum					X	
Asplenium hemitomum				X		
Asplenium holstii				X		
Asplenium laurentii				X		
Asplenium mannii					X	
Asplenium megalura				X	X	
Asplenium sandersonii				X	X	
Asplenium cf. *staudtii*				X		
Asplenium subintegrum				X		
Asplenium spp.				X	X	X
Ctenopteris rigescens				X	X	X
Diplazium humbertii				X		
Drynaria laurentii				X		
Drynaria volkensii				X	X	
Elaphoglossum cf. *aubertii*					X	X
Elaphoglossum aff. *deckenii*					X	X
Elaphoglossum sp.				X		
Huperzia dacrydiodes					X	
Huperzia sooiana				X		
Hymenophyllum cf. *polyanthos*						X
Hymenophyllum spp.				X	X	X
Loxogramme lanceolata				X		
Loxogramme latifolia				X		
Loxogramme sp.				X		
Loxoscaphe thecifera				X	X	
Lycopodium cf. *phlegmaria*				X		
Lycopodium sp.				X	X	X

Species Recorded	Growth Form	A	B	I	N	V
Mecodium kuhnii				X	X	X
Meringium triangulare					X	
Microgramma lycopodioides				X		
Microsorum punctatum				X		
Nephrolepis biserrata				X		
Oleandra distenta				X		
Phymatosorus scolopendria				X		
Pleopeltis cf. *macrocarpa*					X	X
Pleopeltis sp.				X	X	X
Vittaria guineensis				X	X	
Vittaria reekmansii					X	
Vittaria spp.				X		X
Xiphopteris flabelliforme				X	X	X
fern indet				X		
Mosses						
Antitrichia kilimandscharica						X
cf. *Brachythecium*						X
Campylopus sp.				X		X
Cyclodictyon sp.				X		
Dicranaceae sp. *indet*						X
Dicranoloma billardieri					X	
Dicranum johnstonii						X
Hylocomiopsis cylindricarpa				X		
Hypnum cupressiforme						X
Hypnum sp.						X
Leptodontium viticulosoides				X	X	
Leucobryum madagassum					X	
Leucobryum sp.				X		
Macromitriella sp.				X	X	
Macromitrium sp.				X		
Neckera remota						X
Neckeriopsis madecassa				X		
Octoblepharum albidum				X		
Orthotrichum arborescens						X
Orthotrichum firmum				X		X
Pilotrichella ampullacea				X	X	X
Plagiothecium sp.				X		X
Porothamnium sp.				X		X
Porotrichum molliculum				X		
Pyrrobryum spiniforme					X	
Tayloria kilimandscharica					X	X
Tortula cavallii						X
Tortula cf. *fragilis*						X
Liverworts						
cf *Acanthocoleus* sp.				X		
Acrolejeunea emergens			X			
Adelanthus decipiens						X
Andrewsianthus bilobus						X
Aneura pinguis				X		
Bazzania decrescens					X	X
Bazzania roccatii						X
Caudalejeunea africana				X		

Species Recorded	Growth Form	A	B	I	N	V
Caudalejeunea hanningtonii				X		
Caudalejeunea cf. *lewallii*				X		
Ceratolejeunea calabariensis				X		
Ceratolejeunea sp.				X		
Chandonanthus hirtellus					X	X
Cheilolejeunea krakakammae					X	
Cheilolejeunea montagnei					X	
Cheilolejeunea serpentina				X		
Cheilolejeunea sp.				X		X
Chiloscyphus cuspidatus				X	X	X
Chiloscyphus difformis				X		
Chiloscyphus muricatus				X		
Cololejeunea hillebrandii					X	
Cololejeunea minutissima			X		X	
Cololejeunea spp.				X	X	
Drepanolejeunea clavicornis					X	
Drepanolejeunea cultrella				X		
Drepanolejeunea physaefolia				X	X	
Evansiolejeunea roccatii						X
Frullania angulata				X	X	X
Frullania apicalis				X	X	X
Frullania arecae				X		X
Frullania ericoides		X	X	X	X	X
Frullania serrata					X	X
Frullania schimperi				X		
Frullania sp.				X		
Herbertus subdentatus					X	
Jungermannia sp.				X		X
Lejeunea aloba					X	
Lejeunea caespitosa				X	X	
Lejeunea flava				X		
Lejeunea kamerunensis				X		
Lejeunea tabularis				X		
Lejeunea sp.			X	X	X	
Lepidozia stuhlmannii					X	X
Lepidozia succida				X		
Lepidozia sp.				X		
Leptoscyphus infuscatus						X
Leucolejeunea cf. *xanthocarpa*					X	
Lopholejeunea cf. *abortiva*				X		
Lopholejeunea subfusca			X			
Lopholejeunea sp.				X		
Marchesinia excavata				X		
Marchesinia madagassa					X	
Mastigophora diclados				X	X	X
Metzgeria nudifrons						X
Metzgeria sp.				X		X
Microlejeunea africana				X	X	
Plagiochila barteri				X	X	X
Plagiochila colorans						X
Plagiochila ericicola						X
Plagiocila fusifera				X		
Plagiochila heterostipa				X	X	X
Plagiochila integerrima				X		

Species Recorded	Growth Form	A	B	I	N	V
Plagiochila lastii				X		
Plagiochila sinuosa				X		
Plagiochila squamulosa					X	
Plagiochila terebrans				X	X	
Plagiochila sp.				X		
Porella subdentata				X		
Ptychanthus striatus				X		
Radula allamanoi				X	X	X
Radula boryana				X		
Radula holstiana				X		
Radula stipatiflora				X		
Radula voluta				X		
Radula sp.				X		
Riccardia sp.				X		
Schiffneriolejeunea altimontana					X	
Syzygiella sp.						X
Thysanathus spathulistipus				X		
Tylimanthus ruwenzoriensis						X
Lichens						
cf. *Acarospora* sp.			X			
Bulbotrix sp.				X		
Candelaria concolor			X			
Candelaria sp.		X				
cf. *Candelariella* sp.			X			
cf. *Candelaria* sp.		X				
cf. *Cecidea* sp.				X		
Cladonia spp.					X	X
Coccocarpia sp.				X	X	
cf. *Coccocarpia* sp.				X		
Collema sp.			X	X	X	
Diploschistes sp.				X		
Dirinaria cf. *coccinea*		X				
cf. *Dirinaria* sp.		X				
Erioderma sp.					X	
cf. *Erioderma* sp.				X		
cf. *Graphia* sp.				X		
Heterodermia cf. *casarettiana*		X				
Heterodermia comosa			X			
Heterodermia cf. *dactyliza*			X			
Heterodermia diademata			X			X
Heterodermia isidophora			X			
Heterodermia leucomelos		X	X		X	X
Heterodermia loriformis			X			
Heterodermia cf. *obscurata*		X		X	X	X
Heterodermia cf. *speciosa*			X			
Heterodermia sp.		X	X		X	X
Hypotrachyna sp.		X				
cf. *Hypotrachyna* sp.		X	X	X	X	X
cf. *Icmadophila* sp.				X		
crustose lichens spp. indet		X	X	X		
Lecanora sp.				X		
cf. *Lecanora* sp.		X	X			
cf. *Lecidea* sp.				X		

Species Recorded	Growth Form	A	B	I	N	V
cf. *Lepraria* sp.						X
Leptogium sp.				X		
cf. *Leptogium* spp.			X	X		
Lobaria discolor					X	
Lobaria spp.					X	
Nephroma spp.					X	
Normandina pulchella			X			
cf. *Ochrolechia* sp.			X			
cf. *Opegrapha* sp.			X			
Parmelia spp.		X		X	X	X
cf. *Parmelia* sp.		X	X			
cf. *Parmeliopsis* sp.		X				
Parmotrema cf. *andinum*		X				
Parmotrema spp.		X	X	X		X
cf. *Parmotrema* sp.					X	
Peltigera cf. *dolichorhiza*						X
Peltigera spp.						X
Pertusaria sp.				X	X	
Phaeophyscia hispidula			X			
Phaeophyscia sp.		X				
cf. *Phyllopsora* sp.				X		
Physcia verrucosa					X	
Pseudocyphellaria aurata			X	X		
cf. *Pyrenula* sp.					X	
cf. *Pyxine* sp.			X			
Ramalina cf. *africana*			X			
Ramalina cf. *pusiola*					X	X
Ramalina spp.		X	X	X	X	X
cf. *Scoliciosporum* sp.				X		
Sphaerophorus cf. *melanocarpus*					X	
Sticta spp.				X	X	X
cf. *Sticta* sp.						X
Teloschistes flavicans			X		X	
cf. *Trapelia* sp.				X		
Usnea cf. *articulata*					X	
Usnea spp.		X	X	X	X	
Xanthoparmelia spp.			X		X	X
cf. *Xanthoparmelia* spp.			X	X	X	

Epiphyllous lichens (only Irangi Station)
Arthonia accolescens, Aspidothelium fugiens, Aspidothelium sp., Aulaxina cf. epiphylla, Aulaxina cf. minuta, Aulaxina quadrangula, Bacidia vezdana, Bullatina aspidota, Byssoloma subdiscordans, Byssoloma subpolychronum, Calenia thelotremella, Calenia sp. nov., Caleniopsis laevigata, Calopadia puiggarii, Calopadia sp., Dimerella epiphylla, Echinoplaca leucotrichoides, Echinoplaca pellicula, Echinoplaca sp., Fellhanera bouteillei, Fellhanera lambionii, Fellhanera subternella, Gyalectidium filicinum, Gyalidea epiphylla, Gyalideopsis sp. nov., Lasioloma arachnoideum, Loflammia flammea, Mazosia cf. dispersa, Mazosia melanophthalma, Mazosia rotula, Mazosia sp., Opegrapha santessonii, Phyllophiale alba, Phyllophiale fusca, Phylloporis cf. phyllogena, Porina atrocoerulea, Porina doebbeleriana, Porina fusca, Porina mirabilis, Porina rufula, Porina tetramera, Porina trichothelioides, Porina sp., Sporopodium leprieurii, Sporopodium sp., Strigula nemathora, Strigula nitidula, Strigula schizospora, Strigula smaragdula, Strigula sp., Tapellaria phyllophila, Tapellaria sp., Tricharia albostrigosa, Tricharia dilatata, Tricharia vainioi, Trichothelium bipindense, Trichothelium porinoides.