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DIVERSITY AND DISTRIBUTION OF EPIPHYTIC ORCHIDS IN KIBALE NATIONAL PARK, UGANDA

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ABSTRACT. The diversity and the distribution of epiphytic orchids in Kibale National Park were investigated. Sampling was by the canopy-based methods that included the Single Rope Technique and a local climber. There were 57 species dominated by genera *Polystachya, Bulbophyllum, Tridactyle, Angraecum,* and *Diaphananthe.* There was a weak positive correlation between the orchid's species and basal area of the host trees, but no significant difference in the number of orchid's species between the logged and un-logged forests. Bark inhabitant orchids were characterized by succulence as one of the structural adaptations for water conservation against drought. Most species occurred in the light humus substrate that consisted mainly of bryophyte mats with adequate water retention capacity. Epiphytic orchids were characterized by host preference and not specificity. The most favored phorophytes in un-logged and logged forests were *Parinari excelsa, Strombosia scheffleri, Symphonia globulifera, Mitragyna rubrostipulata* and *Pseudospondias microscarpa.* The general pattern of the vertical distribution of epiphytes was that of an increase from the tree base to branch zones and thereafter a decline to the top branch zone. The canopy zones had similar epiphyte communities that were different from that of the host trunk zone.

Key words: epiphytic orchids, host trees, substrate

INTRODUCTION

Epiphytes represent 25% of all vascular plant species in tropical and sub tropical regions (Nieder et al. 2001, Trapnel & Hamrick 2006). Epiphytic orchids form part of the vascular epiphytes common in tropical forests. The epiphytic flora in Africa is less diverse and abundant compared to Malaysia and South America, possibly due to repeated bouts of aridity and a lack of a moist refuge during the late Pleistocene (Dressler 1981, Benzing 1983, Johansson 1989). The Orchidaceae contains 60% of all epiphytic species and ten times as many epiphytic species as any other family of vascular plants (Trapnel & Hamrick 2006). Effective conservation of the endangered orchid species requires adequate information on their interactions and habitat requirements. Different continents have different orchid floras, suggesting separate orchid evolution after separation of the continents (Dressler, 1981). Epiphytes are numerous, diverse, and abundant where tree crowns are humid most of the year (Benzing 1983).

The distribution pattern of vascular epiphytes varies horizontally between host species and forest types, and vertically within the host individual (ter Steege & Cornelissen 1989, Bogh 1992). Tree species composition affects the epiphytic vegetation through substratum characteristics provided by each tree species such as bark characteristics, cover and characteristics of litter, bryophyte mats and humus deposits in branch forks (Dressler 1981, Freiberg 1996). Host size influenced the distribution of orchids with a tendency of common hosts being the large sized ones (Migens & Ackerman 1993, Mehltreter, Flores-Palacios & Garcia-Franco 2005). Large hosts provide large surface area for colonization and greater chance for epiphytic seeds to contact the host (Migens & Ackerman 1993).

The vertical distribution of epiphytes is determined by patterns in light intensity, temperature and humidity in subsequent forest strata (ter Steege & Cornelissen 1989, Wolf 1994). Temperature and drought are important factors modulating Crassulacean acid metabolism (CAM) in genus *Angraecum.* Zone preference influenced the distribution of orchids on hosts (Migens & Ackerman 1993).

Epiphytism is one of the best known characteristics of the orchid family, in which 70% of the 25,000 orchid species so far known live in tree canopies (Gravendeel et al. 2004). Sanford (1968) identified 68 species in 20 genera of epiphytic orchids in Southern Nigeria. To date, 119 epiphytic orchid species have been identified in Kenya (Ochora, Stock, Linder, & Norton 2001). Most orchids have fleshy organs in roots, stems and leaves for water and nutrients storage. Other means for acquisition of minerals and water include the bark covered with bryophyte mats, or the formation of "trash baskets" for collection of debris that form humus on which orchids grow (Dressler 1981). The variation in physical conditions of single host trees are, the weaker light and greater moisture in the lower trunk zone, the open shade and moderate moisture in the branch and crotch zones, and the sunlit and low moisture zone in the top branch zone (Perry 1981). Goh and Kluge (1989) associate succulent orchids with the presence of CAM as an adaptation to dry habitats, if succulence is brought about by the existence of homogenous water storing photosynthetic mesophyll.

Fewer studies have been done on patterns of orchid distribution within forests than for orchid distribution patterns globally. There is limited information on the possible impact of logging on the ecology of the epiphytic orchids in Uganda. Logging at different intensities was done in the sixties in Kibale National Park. Logging was expected to influence the composition and the distribution of epiphytic orchids since they are especially sensitive to the unfavorable microclimatic conditions created by opening the forest canopy (Davidson 1985). The study aimed at determining the floristic composition and distribution of epiphytic orchids in the selectively logged and unlogged forest types in Kibale National Park.

MATERIALS AND METHODS

Study Area

Kibale National Park includes a medium altitude (1110–1590 m) transitional, moist forest interposed between dry tropical and wet tropical rain forest in the Albertine zone (latitude 0°13′–41′N and longitude 30°19′–30°32′E) of Western Uganda. The protected area of 766 km^2 was declared a National Park in 1993. Kibale Forest covers numerous hills, valleys, swamps and streams. The rainfall is low, ranging from 1490 mm/year in the south to 1622 mm/year in the north and distributed in two wet seasons during March to May and September to November (Struhsaker 1997). Mean annual temperature is low (20.5°C) and varies little during the year. Kanyawara site was sampled in three compartments: 1) Compartment K-30 consists of about 300 ha of mature tropical mixed forest. It is disturbed only by the removal of 3–4 large stems/100 ha (Kasenene 1987). Skorupa and Kasenene (1984) reported no evidence that this activity had altered the forest structure and composition. 2) The compartment K-14 supports about 390 ha of secondary forest that was selectively cut in 1969 (Kasenene 1987, Skorupa 1988). That harvest was moderate, averaging 14 m^3/ha (saleable volume only); 75.1% of the forest was left in place (26.7 m^2/ha) (Skorupa 1988). The K-15 compartment includes about 360 ha of forest that was more heavily cut between September 1968 and April 1969 (Kasenene 1987). The total harvest averaged 21 m^3/ha, with 53.4% left in place (19.0 m^2/ha). The Ngogo study area is located in the southern block of Kibale Forest Reserve that is relatively undisturbed. The Kanyancu study area is located in the southern block of Kibale Forest Reserve that is relatively undisturbed. The results of a timber stock inventory prior to logging show tree density, basal area, forest canopy cover and species diversity were relatively constant for all subtypes of *Parinari* forest (Kingston 1967, Kasenene 1987).

Species Richness

The forest types described earlier (Kanyawara K-30, K-14, K-15, Ngogo and Kanyancu) were sampled by locating 30 random points within each of the forest types. Around each point, a mature tree heavily loaded with epiphytes was identified for a detailed sampling for epiphytic orchids. A total of 100 major hosts were identified from a total of 150 points. Random selection of host plants was necessary for adequate data comparisons. A single rope technique was used to access the canopy of host trees (Perry 1981, Petzel 1992). Voucher specimens were collected, dried and identified at the Makerere University Herbarium and by referring to a checklist. Measurement of the diameter at breast height (dbh) of the host trees was done by a diameter tape. Cluster analysis (simple matching coefficient) of the species composition in the forest types and the species association analysis (group average) were done by PC–ORD–VERSION 4 (McCune & Mefford 1999). Correlation analyses using a computer-based program MSTAT were done to establish the relationship between epiphytic orchids and the tree basal area.

Vertical Distribution

The vertical zonal distribution of epiphytes was determined subjectively by subdividing the host tree into five zones (Johansson 1974, 1989; Lowman & Nadkarni 1995): lower stem (LS), upper stem (US), based branch (BB), mid branch (MB), and top branch (TB), with the last three zones resulting from subdividing the crown into equal thirds. To determine similarity of the height zones, the Jaccard's coefficients (JI) were calculated for each pair (A and B), where JI = a/(a + b + c), where ***a*** is the number of orchid species that zones A and B have in common, ***b*** is the number of orchid species present in zone A but absent from zone B, and ***c*** is the number of orchid species present in zone B but absent from zone A (Ludwig & Reynolds 1988). Cluster analysis (simple matching coefficient) and ordination (group average) of the similarity between height zones on the basis of orchid species in both logged and unlogged forests were done by PC–ORD–Version 4.

Substrate Requirements

Substrate requirement was differentiated according to whether the species was a bark, light humus or heavy humus user. The substrate categories were adopted from Benzing (1995) and described as bark users for those growing on naked bark. Species growing on bryophyte mats were described as "light humus" users, while those restricted to thick layers of organic matter were described as "heavy humus" users. Cluster analysis (simple matching coefficient) and ordination (group average) of the similarity between substrate types on the basis of orchid species in the logged and unlogged forests were done by PC–ORD–VERSION 4.

RESULTS

Species Richness

Chi square statistics revealed no significant ($P \geq 0.05$) difference between the numbers of orchid species found in previously logged (21.5 ± 6.4) and un-harvested (20 ± 4.6) forests. A total of 44 orchid species were recorded in all the forest types (TABLE 1). Kanyawara had 36 species; Ngogo had 21 orchid species; while Kanyancu (part of the south block of Kibale forest) had 15 species. The most common genera in Kibale National Park were *Polystachya* with 15 (34.1%) species, *Diaphananthe* with 5 (11.4%) species, *Tridactyle* with 4 (9.1%) species and *Bulbophyllum* with 3 (9%) species, and the most common orchid species in Kibale National Park were *Eggelingia ligulifolia* Summerh., *Angraecum distichum* Lindl., and *Polystachya bennettiana* Rchb. f.

Kanyawara site had a significantly higher ($x^2 = 18.375$, df = 2, $P < 0.01$) number of orchid species than Ngogo and Kanyancu areas. Most orchid species were rare in occurrence. *Diaphananthe bilobata* (Summerh.) Rasm. was restricted to Ngogo, while most species in genera *Polystachya* such as *Polystachya golungensis* Rchb.f. and *Bulbophyllum* were sited only in the northern part of the Kibale National Park. *Diaphananthe kamerunensis* Summerh. was sited only once in Ngogo outside the sample plot and not included in the analysis. Correlation analysis revealed a non-significant positive ($r = 0.81$, df = 75, $P > 0.05$) relationship between the orchid species and the basal area of the host trees in Kibale National Park. The diversity of the orchid species in Kibale National Park was similar when logged and un-logged forest types were compared.

Host Preference

The orchid species showed host preference by being selective in their utilization of the tree species. The most preferred tree species were *Parinari excelsa* Sabine, *Bersama abyssinica* Fresen., *Mitragyna rubrostipulata* (K. Schum.) Havil., and *Neobutonia melleri* (Muell. Arg.) Prain for the logged forests (TABLE 2). The common hosts in the unlogged forests were *Parinari excelsa, Strombosia scheffleri* Engl., *Symphonia globulifera* L.f., *M. rubrostipulata* and *Pseudospondias microcarpa* (A. Rich.) Engl. It was also observed that the common host tree species, such as *M. rubrostipulata, N. melleri* were restricted to the valley, or in the case of *P. excelsa, S. schefflera, S. globulifera, P. microcarpa,* and *B. abyssinica,* on the lower slopes. *Parinari excelsa* had the highest number of epiphytic orchids in both logged and un-logged forests. The highest number of orchid species on a single large tree was found on *P. excelsa* with 13 species in the heavily logged forest type (Kanyawara K-15) and also in the unlogged forest at Ngogo. The tree species second to *P. excelsa* was *S. globulifera,* which had 12 orchid species on a single tree in the unlogged forest at Kanyawara (K30).

Vertical Distribution

The general pattern revealed in both the logged and unlogged forest types was that of an increase in number of orchid species from the tree base to mid branch zones, and thereafter a decline to the top branch zone (FIGURE 1). Correlation analysis revealed a non-significant positive ($r = 0.607$; $r = 0.636$, df = 3, $P \geq 0.05$) relationship between the number of orchid species and height (zones) of the host trees for both logged and unlogged forests respectively.

Cluster analysis of the vertical distribution of orchid species revealed two main groups when 0.25 was used as a minimum index for defining the clusters (FIGURE 2). Cluster one consisted of the lower and upper stem zones (trunk) in the logged and unlogged forests. Cluster two included the low, mid and top branch zones in both logged and unlogged forests. Cluster one had the lower and upper stem zones in logged and unlogged forests. Cluster two had the base and mid branch zones with similar species in both logged and unlogged forests, with the most similar being the base branch zones. The top branch zones in both forests had different species from those in the base and mid zones.

TABLE 1. Occurrence and life form (T = terrestrial) of epiphytic orchid species on trees sampled in the logged (Kanyawara K14 and K15) and unlogged (Kanyawara K30, Ngogo and Kanyancu) forests by the Single Rope Technique (SRT) in Kibale National Park.

Species and author	Abbreviation	Life form	K-30	K-14	K-15	NGO	KANY
Acampe pachyglossa Rchb. f.	Aca pac	T	−	−	−	−	+
Aerangis columncygnii Summerh.	Aer col	T	+	−	−	−	−
Aerangis luteoalba var. *rhodosticta* (Kraenzl) J.Stewart	Aer lut	T	+	−	−	−	+
Aerangis ugandensis Summerh.	Aer col	T	+	+	+	−	+
Angraecopsis sp	Ang sp	T	−	−	+	−	−
Angraecum brevicornu Summerh.	Ang bre	T	+	−	−	−	−
Angraecum distichum Lindl.	Ang dis	T	+	+	+	+	−
Angraecum gracilima	Angr gac	T	+	−	−	+	+
Angraecum minus	Angr min	T	−	+	+	−	−
Bolusiella irridifolia sp *irridifolia* (Rolfe) Schltr.	Bol irr	T	−	−	+	−	−
Bolusiella maudae (Bolus) Schltr.	Bol mau	T	+	+	+	+	+
Bulbophyllum bequaertii	Bulb beq	T	+	−	+	−	−
De Wild		T	+	−	+	−	−
Bulbophyllum nr falcatum (Lindl.) Rchb.f.	Bulb nr	T	+	−	−	−	−
Bulbophyllum falcatum (Lindl.) Rchb.f.	Bulb fal	T	+	−	+	−	−
Bulbophyllum mahonii Rolfe	Bulb mah	T	−	−	+	+	−
Calyptrochilum chrystianum (Rchb.f.) Summerh.	Cal chr	T	+	−	−	+	+
Chamaeangis odoratissima (Rchb.f.) Schltr.	Cham odo	T	+	+	+	−	−
Chamaeangis nr vesicata	Cham ves	T	−	−	−	+	−
Diaphananthe bilobata	Diap bil	T	−	−	−	+	+
Diaphananthe fragrantissima (Rchb. f.) Schltr.	Diap frag	T	+	−	+	+	−
Diaphananthe rutila (Rchb.f.) Summerh	Diap rut	T	+	+	+	−	−
Diaphananthe xanthopollinia (Rchb. f.) Summerh.	Diap xan	T	−	+	+	−	−
Eggelingia ligulifolia Summerh.	Egg lig	T	+	+	+	+	+
Microcoelia koehleri (Schltr.) Summerh.	Micr koe	T	−	+	−	−	−
Polystachya adansoniae Rchb.f. var. elongata Summerh.	Poly ada	T	−	−	+	−	−
Polystachya bennettiana Rchb.f.	Poly ben	T	+	+	+	+	−
Polystachya bicarinata Rendle	Poly bic	T	+	−	−	−	−
Polystachya cultriformis (Thon.) Spreng.	Poly cul	T	+	−	+	−	−
Polystachya golungensis Rchb.f.	Poly gol	T	−	−	+	−	−
Polystachya leucocephala Cribb	Poly leu	T	−	−	−	+	−
Polystachya lindblomii Schltr.	Poly lin	T	+	+	+	+	+
Polystachya modesta Rchb.f.	Poly mod	T	−	−	+	−	−
Polystachya nyanzensis Rendle	Poly nya	T	+	−	+	−	−
Polystachya odorata Lindl.	Poly odo	T	−	−	−	+	+
Polystachya paniculata (Sw.) Rolfe	Poly pan	T	+	−	+	−	−
Polystachya sp1	Poly sp 1	T	−	+	+	+	−
Polystachya sp2	Poly sp 2	T	−	+	−	+	−
Polystachya sp3	Poly sp 3	T	−	+	+	−	−
Polystachya tessellate Lindl.	Poly tes	T	+	+	+	+	+
Rangaeris muscicola (Rchb.f.) Summerh.	Ran mis	T	+	+	+	+	+
Tridactyle bicaudata (Lindl.) Schltr.	Trid bic	T	−	−	−	+	−
Tridactyle filifolia (Schltr.) Schltr.	Trid fil	T	+	+	−	+	+
Tridactyle sp 1	Trid sp1	T	+	−	−	+	+
Tridactyle sp 2	Trid sp2	T	−	−	−	+	−

Ordination analysis of both data from the unlogged and the logged forest blocks revealed that most orchid species utilized the canopy zones rather than the trunk zones (FIGURE 3). While most orchid species were in the mid and top branch zones in the unlogged forests, the logged forests had most of their species in the base, mid and top branch zones. Few orchid species such as *Aerangis collumncygni* Summerh., *Aerangis ugandensis* Summerh., and *Diaphananthe rutila* (Rchb. f.) Summerh. were common in the lower and upper stem zones in the

TABLE 2. Host tree species and their mean number of epiphytic orchids sampled by Single Rope Technique in the logged and un-harvested forests in Kibale National Park.

Tree species	Mean no. (χ^2 ± SD) of epiphytic orchid species/tree species: Logged	Un-harvested
Parinari excelsa	7 ± 4.0	7 ± 4.0
Strombosia scheffleri	2 ± 1.0	5 ± 2.0
Pseudospondias microcarpa	0	4 ± 3.0
Celtis durandii	1 ± 1.0	2 ± 2.0
Mimusops bagshawei	1 ± 0	2 ± 2.0
Monodora myristica	0	1 ± 1.0
Ficus dawei	0	3 ± 2.0
Symphonia globulifera	0	5 ± 7.0
Mitragyna stipulosa	4 ± 1.0	4 ± 5.0
Piptadeniastrum africanum	0	3 ± 1.0
Balanites wilsoniana	0	2 ± 2.0
Sapium ellipticum	0	2 ± 2.0
Sterculia africana	0	2 ± 2.0
Aningeria altissima	0	2 ± 2.0
Chrysophyllum albidum	0	1 ± 1.0
Cynometra alexandri	0	1 ± 1.0
Warbugia ugandensis	0	0
Albizia sp.	0	0
Prunus africana	0	1 ± 1.0
Lovoa swynnertornii	0	1 ± 1.0
Bersama abyssinica	6 ± 3.0	0
Milletia dura	3 ± 4.0	0
Olea welwitschii	3 ± 3.0	0
Markhamia lutea	3 ± 1.0	0
Neobutonia melleri	4 ± 1.0	0
Celtis africana	1 ± 1.0	0
Premna angolensis	2 ± 3.0	0
Linociera johnsonii	2 ± 2.0	0
Diospyros abyssinica	1 ± 1.0	0

logged and unlogged forests. Kanyawara site had more moisture loving orchid species of genera *Bulbophyllum, Diaphananthe,* and *Polystachya* than Ngogo and Kanyancu sites. The average number of orchid species in the branch zones was significantly higher ($x^2 = 8.066$, df = 1; $P \leq 0.01$) than that on the trunk in both logged and unlogged forest types. The orchid species common in the top branch zone were *Diaphananthe fragrantissima* (Rchb. f.) Schltr., *Tridactyle filifolia* (Schltr.) Schltr., *Microcoelia koehleri* (Schltr.) Summerh., *Bolusiella maudae* (Bolus) Schltr., *B. iridifolia* (Rolfe) Schltr., *Calyptrochilum christyanum* (Rchb.f.) Summerh., *Bulbophyllum mahonii* Rolfe, and *Bulbophyllum bequaertii* De Wild in the logged and unlogged forests (FIGURE 3).

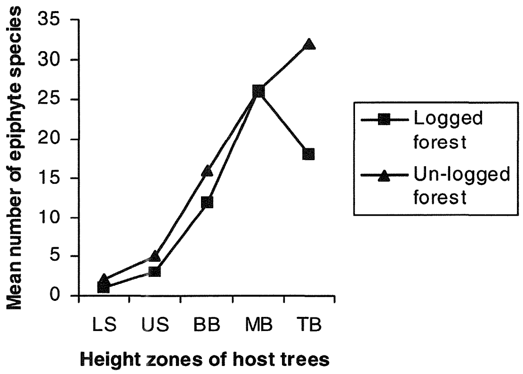

FIGURE 1. The mean number of epiphytic orchid species per height zone (LS. Lower stem; US. Upper stem; BB. Base branch; MB. Mid branch; TB. Top branch) of the host trees in Kibale National Park.

Substrate Utilization

Cluster analysis on the basis of species of both the unlogged and logged forest blocks revealed two main groups of similarity. The first one consisted of the species on bark substrate in the logged forests; species in heavy humus were found in both the unlogged and logged forests (FIGURE 4). The second group had the species of the light humus in both the logged and unlogged forests and those of the bark substrate in the unlogged forest. In the latter group, the species of the light humus in both the logged and unlogged forest blocks were more similar to one another than to those of the bark substrate in the unlogged forests.

Ordination analysis of the data of the substrate utilization in both the unlogged and logged forests showed that the species in the unlogged forest blocks were different from those in the logged ones (FIGURE 5). Within each forest type, species utilizing the heavy humus substrate

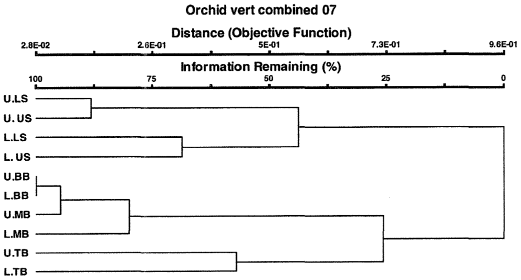

FIGURE 2. Cluster analysis of the similarity between the vertical zones of the host trees on the basis of orchid species in the logged and unlogged forests. **Figure abbreviations:** LLS, Logged Lower stem; LUS, Logged Upper stem; LBB, Logged Base branch; LMB, Logged Mid branch; LTB, Logged Top branch; ULS, Unlogged Lower stem; UUS, Unlogged Upper stem; UBB, Unlogged Base branch; UMB, Unlogged Mid branch; UTB, Unlogged Top branch.

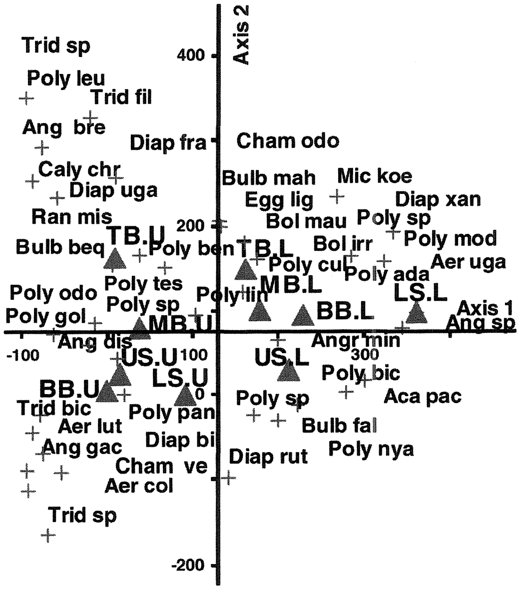

FIGURE 3. Ordination of the distribution of the orchid species in the vertical zones of the host trees in the logged and unlogged forests.

Figure abbreviations: Aer col, *Aerangis columncygnii*; Aer uga, *Aerangis ugandensis*; Aer lut , *Aerangis luteo alba var. rhodosticta*; Aca pac, *Acampe pachyglossa*; Ang dis, *Angraecum distichum*; Ang sp, *Angraecopsis* sp; Angr min, *Angraecum minus*; Ang bre, *Angraecum brevicornu*; Angr gac, *Angraecum gracilima*; Angr dis, *Angraecum distichum*; Bulb beq, *Bulbophyllum bequaertii;* Bulb fal, *Bulbophyllum falcatum*; Bulb mah, *Bulbophyllum mahonii*; Bol irr, *Bolusiela irridifolia*; Bol mau, *Bolusiela maudae*; Diap rut, *Diaphananthe rutila*; Cal chr, *Calyptrochilum chrystianum*; Cham odo, *Chamaeangis odorotissima*; Cham ves, *Chamaeangis nr vesicata*; Diap bil, *Diaphananthe bilobata*; Diap frag, *Diaphananthe fragrantissima*; Diap uga, *Diaphananthe ugandensis*; Diap xan, *Diaphananthe xanthopollinia*; Egg lig, *Eggelingia ligulifolia*; Micr koe, *Microcoelia koehleri*; Poly ada, *Polystachya adansoniae*; Poly ben, *Polystachya bennettiana*; Poly bic, *Polystachya bicarinata*; Poly cul, *Polystachya cultriformis*; Poly gol, *Polystachya golungensis*; Poly leu, *Polystachya leucocephala*; Poly lin, *Polystachya lindblomii*; Poly mod, *Polystachya modesta*; Poly nya, *Polystachya nyanzensis*; Poly mod, *Polystachya modesta*; Poly odo, *Polystachya odorata*; Poly pan, *Polystachya paniculata*; Poly tes, *Polystachya tesselata*; Pol sp 1, *Polystachya* sp1; Pol sp 2, *Polystachya* sp2; Pol sp 3, *Polystachya* sp3; Pol sp 4, *Polystachya* sp4; Ran mis, *Rangaeris miscicola*; Trid fil, *Tridactyle filifolia*.

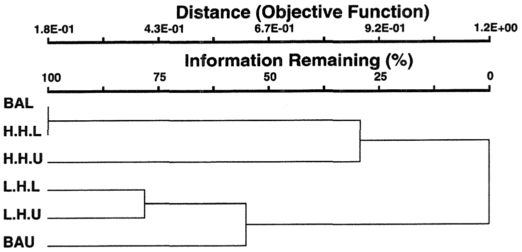

FIGURE 4. Cluster analysis of the similarity between the substrate types on the host trees on the basis of orchid species in both unlogged and the logged forests.

Figure abbreviations: BAL, Bark substrate in logged forests; **H.H.L,** Heavy Humus substrate in logged forest; **H.H.U,** Heavy Humus substrate in unlogged forest; **L.H.L,** Light humus substrate in logged forests; **L.H.U,** Light humus substrate in unlogged forests; **BAU,** Bark substrate in unlogged forests.

were different from those of the light humus and the bark types of substrates. Most orchid species were growing in the light humus substrate composed mainly of bryophyte mats. The mean numbers of 19 orchid species in logged and 17 species in unlogged forests were light humus users. The dominant orchid species using light humus were *Angraecum distichum* Lindl. and *Eggelingia ligulifolia* Summerh. The second preferred substrate was that of bark with mean numbers of 7 and 11 orchid species encountered in logged and unlogged forests respectively. Dominant bark users were *D. fragrantissima T. filifolia, C. christyanum,* and *M. koehleri.* The least favored substrate was that of the heavy humus with a mean number of four species in logged and five species in unharvested forests. The dominant orchid species in the heavy humus was *Polystachya bennettiana* Rchb. f.

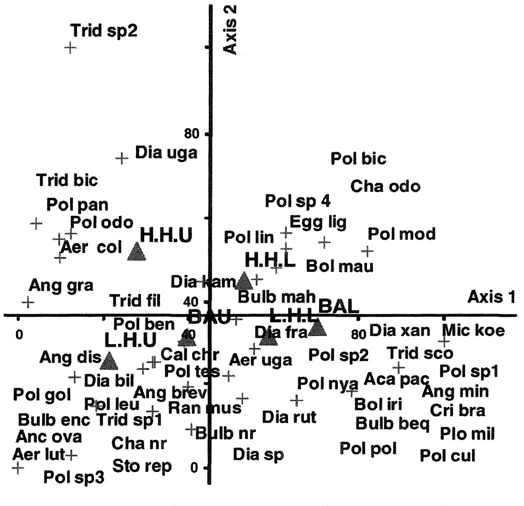

FIGURE 5. Ordination of the distribution of the orchid species in the substrate types on the host trees in both unlogged and logged forests.

Key: As in figure 3.

DISCUSSION

An investigation of the epiphytic orchids in Kibale National Park revealed that they were dominated by genera *Polystachya, Bulbophyllum, Diaphananthe,* and *Tridactyle.* When Kibale forest is compared to West African forests, it has more orchid species belonging to genus *Polystachya* than *Bulbophyllum*, which is the reverse for the West African forests (Sanford 1968, Johansson 1974). The pattern of the diversity of orchids from Kanyawara to Kanyancu sites seems to correspond to that of rainfall pattern. They decrease from the northern (wetter) to southern (drier) parts of the forest along a decreasing moisture gradient. This analysis is complicated by the nature of the forest disturbance by logging. There was no significant difference in the epiphytic orchid diversity detected between logged and unlogged forests. Orchid species, however, did not increase significantly with increasing basal area of the host trees, although an increase in basal area may possibly increase the required surface area for attachment for the epiphytes.

The common host tree species were *P. excelsa, S. schefflera, B. abyssinica,* and *S. globulifera* in both logged and unlogged blocks. The preferred host tree species were not the dominant species in terms of density in Kibale National Park (Mucunguzi 2007). The results indicate host preference by orchid species in Kibale National Park. There was no evidence for host specificity. This agrees with what has been noted that the chance of a tree to be used as a host depends on the age of the tree, changes in humidity, light, substrate characteristics and presence of mycorhizae (Zimmerman & Olmsted 1992, Migens & Ackerman 1993, Wolf 1994, Benzing 1995, and Laube & Zotz 2006).

The most preferred tree species occupied lower slopes and valleys near swamps that supply moisture. *Parinari excelsa* is a canopy tree species which therefore exposes orchids to adequate light. It was observed to be among the large trees in the study area, hence providing a large surface area for colonization over a long period of time. *Parinari excelsa* has an "open" crown with large spreading branches with a rough and stable bark. *S. globulifera,* a smooth barked tree, was favored as a host by its proximity to valleys and presence of the bryophyte mats on the trunk. The orchid's diversity increased from lower trunk to mid branch and thereafter declined to top branch as reported by Migens and Ackerman (1993).

The vertical pattern exhibited by epiphytes on host trees is related to the high moisture and substrate requirements (ter Steege & Cornelissen 1989). A species rich community in the lower canopy zones may reflect an optimum balance between light and moisture requirements. The low orchid diversity in the top branch zone is due to low humidity, while low diversity of orchids in the lower stem zone is due to light limitations (Migens & Ackerman 1993). Madison (1977) associated the increasing pattern of orchid species from tree base to canopy zones with wind velocity patterns in the forest. Wind velocity that increases from the forest floor to the canopy may help in the dispersal of the minute seeds produced by the orchid species. Niche diversification, forks of big branches, and the large surface area available on the large branches have been identified as contributory functions to high diversity of orchids in the canopy zones where nutrient and water availability are greatest (Migens & Ackerman 1993). Another hypothesis that may explain the recovery and maintenance of the orchid diversity in Kibale National Park is a factor of disturbance (Sousa 1984, Everard, Van Wyk, & Midgley 1994). Although not investigated directly, the selective logging activity and the natural causes of disturbance may have contributed to the observed higher diversity in the logged than unlogged forests.

Orchids have adaptations to overcome desiccation, since most species often were observed to be succulent, such as *D. fragrantissima,* or leafless with high root ramification and very short stem, such as *M. koehleri.* Others are small bodied with succulent branches, such as *B. maudae* and *B. iridifolia. Bulbopyllum* species and some *Polystachya* species were observed to have pseudobulbs as either leaf bases or stem modification for water storage. Succulent epiphytic orchids have been associated with the presence of Crassulacean acid metabolism (CAM) physiology described as an adaptation to water stress in the canopy environment (Kluge et al. 1989, Kluge, Vinson & Ziegler 1998). Most orchids were independent of a rooting medium as they occurred either as bark or light humus users. This means that they probably obtain part of their moisture and nutrients from the atmosphere as well as from the bryophyte mats. Nutrient ions available to the epiphytes come from a variety of sources, such as bark or humus, and also from atmospheric depositions (Nadkarni & Matelson 1991, Benzing 1995). However, the species of orchids that grow in a light humus substrate mainly of bryophyte mats have an advantage over bark epiphytes. This type of substrate can be useful in increasing the capture and retention of the minute seeds; it also provides moisture and nutrients for the growing orchid, especially on smooth barked trees. Neither the diversity of the epiphytic orchids, nor their horizontal and vertical distribution differed significantly between logged and unlogged forest types. Although there is lack of data collection during a few years before logging, a 28 year post-logging period suggests potential for the recovery of orchid diversity from presumed effects of selective logging.

CONCLUSION

Kibale National Park is fairly rich in epiphytic orchid species dominated by genera *Polystachya, Bulbophyllum, Diaphananthe,* and *Tridactyle.* The orchids exhibit host preference with no evidence for host specificity. The most preferred tree species for orchid colonization was *P. excelsa.* The vertical zonation pattern exhibited by the orchid is that of increasing from the tree base to the canopy, with the most similar zones being the base and mid branch zones. A period of 28 years after selective logging suggests the possibility of recovery of the epiphytic orchid diversity from effects (if any) of selective logging. Further investigations are required in the areas of micro climate data collection, nutrient dynamics, eco-physiology, and reproductive biology of epiphytic orchids.

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LITERATURE CITED

Benzing, D.H. 1983. Vascular epiphytes: a survey with special reference to their interactions with other organisms. *In* S.L. Sutton, T.C. Whitmore, and A.C. Chadwick, eds. Tropical Rain Forest: Ecology and Management. Blackwell Scientific. Publ., Oxford.

———. 1995. Vascular epiphytes, Pp. 225–254 *in* M.D. Lowman and N.M. Nadkarni, eds. Forest Canopies. Academic Press, San Diego.

Bogh, A. 1992. Composition and distribution of the vascular epiphytic flora of an Ecuadorian Montane Rain Forest. Selbyana 13: 25–34.

Davidson, J. 1985. Economic use of tropical moist forests. Commission on Ecology papers No. 9 Gland, IUCN.

Dressler, R.L. 1981. The Orchids: Natural History and Classification. Harvard Univ. Press, Cambridge, Mass.

Everard, D.A., G.F. Van Wyk, and J.J. Midgley. 1994. Disturbance and the diversity of forests in Natal, South Africa: lessons for their utilization. *In* B. Huntley, ed. 1994. Botanical Diversity in Southern Africa. Creda Press, Cape Town.

Freiberg, M. 1996. Spatial distribution of vascular epiphytes on three emergent canopy trees in French Guiana. Biotropica 28(3): 345–355.

Goh, C.J. and M. Kluge. 1989. Gas exchange and water relations in epiphytic orchids. *In* U. Luttge, ed. Vascular Plants as Epiphytes: Evolution and Ecophysiology. Springer-Verlag, Berlin.

Gravendeel, B., A. Smithson, F.J.W. Silk, and A. Schuiteman. 2004. Epiphytism and pollinator specialisation drivers for orchid diversity? Phil. Trans. R. Soc. Lond. B. 359(1450): 1523–1535.

Johansson, D. 1974. Ecology of Vascular Epiphytes in West African Rain Forest. Acta Phytogeogr. Suec. 59: 1–136.

———. 1989. Vascular epiphytism in Africa. *In* H. Lieth and M.J.A. Werger, eds. Ecosystems of the World: Tropical Rainforest Ecosystems. Elsevier, New York.

Kasenene, J.M. 1987. "The Influence of Mechanical Selective Logging, Felling Intensity and Gap Size in the Regeneration of a Tropical Moist Forest in the Kibale Forest Reserve, Uganda." Ph.D. diss., Michigan State University.

Kingston, B. 1967. Working Plan for the Kibale and Itwara Central Forest Reserves, Uganda. Uganda Forest Department, Entebbe.

Kluge, M., P. N. Adhani, and C. J. Goh, 1989. Gas exchange and water relations in epiphytic tropical orchids. *In* U. Luttge, ed. Vascular Plants as Epiphytes: Evolution and Eco-physiology. Springer-Verlag, Berlin.

———, B. Vinson, and H. Ziegler. 1998. Ecophysiological studies on orchids of Madgascar; incidence and plasticity of Crassulacean acid metabolism in species of genus *Angraecum* Bory. Plant Ecology 135(1): 43–57.

Laube, S. and G. Zotz, 2006. Neither host-specific nor random: vascular epiphytes on three tree species in a Panamanian lowland forest. Ann. Bot. 97(6): 1103–1114.

Lowman, M.D. and N.M. Nardkarni. 1995. Forest Canopies. Academic Press, New York.

Ludwig, J.A. and J.F. Reynolds. 1988. Statistical Ecology: a Primer on Methods and Computing. John Wiley and Sons, N.Y.

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

McCune, B. and M.J. Mefford. 1999. Multivariate analysis of ecological data, Version 4. Mim Software Design, Glenden Beach, Oregon.

Mehltreter, K., A. Flores-Palacios, and J.G. Garcia-Franco. 2005. Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico, J. Trop. Ecol. 21: 651–660.

Migens, L.E. and J.D. Ackerman. 1993. Orchid-Phorophyte relationships in a forest Watershed in Puerto Rico. J. Trop. Ecol. 9(2): 231–240.

Mucunguzi, P., J. Kasenene, J. Midgley, P. Ssegawa, and J. Tabuti. 2007. Distinguishing forest tree communities in Kibale National Park, western Uganda using ordination and classification methods. Afr. J. Ecol. 45(3): 99–108.

Nadkarni, N.M. and T.R. Matelson. 1991. Fine litter dynamics within the tree canopy of a tropical cloud forest. Ecology 72(6): 2071–2082.

Nieder, J., J. Prosperí, and G. Michaloud. 2001. Epiphytes and their contribution to canopy diversity. Pl. Ecol. 153: 51–63.

Ochora, J., W.D. Stock, H.P. Linder, and L.E. Newton. 2001. Symbolic seed germination in twelve Kenyan orchid species, Syst. Geogr. Pl. 71: 585–596.

Perry, D.R. 1981. The tropical rain forest canopy: a method providing total access. Biotropica, 13: 283–285.

Petzl, S.A. 1992. Single Rope Climbing System. Z.I. Crolles, F 38190 Crolles, France.

Sanford, W.W. 1968. Distribution of epiphytic orchids in semi-deciduous tropical forest in Southern Nigeria. J. of Ecol. 56(3): 697–705.

Skorupa, J.P. 1988. "The effects of selective timber harvesting on rain-forest primates in Kibale Forest, Uganda." Ph.D. diss., Univ. of California, Davis.

——— and J.M. Kasenene. 1984. Tropical forest management: can rates of natural tree falls help guide us? Oryx 18:96–101.

Sousa, W. P. 1984. The role of disturbance in natural communities. Ann. Rev. Ecol. Syst. 15: 353–391.

Struhsaker, T.T. 1997. Ecology of an African Rain forest. University Press of Florida, Gainesville.

ter Steege, H. and J.H.C. Cornelissen. 1989. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. Biotropica 21(4): 331–339.

Trapnell, D.R. and J.L.H. Hamrick. 2006. Variety of phorophyte species colonized by the neotropical epiphyte, *Laelia rubescens* (Orchidaceae). Selbyana 27(1): 60–64.

Wolf, J.H.D. 1994. Factors controlling the distributions of vascular and non-vascular epiphytes in the Northern Andes. Vegetation 112–15–28.

Zimmerman, J.K. and I.C. Olamsted.1992. Host tree utilization by vascular epiphytes in a seasonally inundated forest (Tintal) in Mexico. Biotropica 24(3): 402–407.