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Liana Abundance in Three Tropical Rain Forests of Western Uganda

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Abstract. Liana abundance was documented in three tropical forests of the Albertine Rift in western Uganda between 1997 and 1998. The lianas and their living hosts of diameter ≥1 cm were inventoried in 1-ha transects (20 × 500 m) in mature forest sites. The study recorded the following four major plant families with lianas (total species percentages in parentheses): Celastraceae (24%), Apocynaceae (10%), Rubiaceae (8%), and Icacinaceae (7%). Liana abundance was lower in climax *Cynometra* forest than in less mature mixed forest. The presence of six liana species in Bwindi Impenetrable National Park forest and not in the other two Ugandan forests studied suggests closer links between Bwindi and the Congo forests where these species also are known to occur.

Key words: Lianas, Uganda, tropical rain forest, Albertine Rift, quantitative inventory

Introduction

Despite the relative poverty of African forest flora (Richards 1939, Hamilton 1989), natural high forests of Uganda are biologically rich. The reasons for this diversity are several. For example, Uganda contains seven of Africa's 18 phytochoria (White 1983), more than any other African country. African phytochoria, which are classified primarily on the basis of distribution patterns of species, have boundaries that correspond closely to those of major regional vegetation types (White 1979). White recognizes four types of phytochoria at the regional level in Africa: regional centers of specific endemism, archipelago-like centers of specific endemism, regional transition zones, and regional mosaics. Uganda is located in a zone of overlap between ecological communities characteristic of the dry African savanna to the north and east and those of the African rain forest to the west and south (Howard 1991); the result is a diversity of habitats. In addition, rich topographic diversity ranges from an altitude of less than 600 m at the bottom of the rift valley to more than 5000 m at the top of Rwenzori Mountain (Howard 1991). Forests in western Uganda near the Albertine Rift are of particular interest because they support endemic, rare, and threatened fauna and flora (Hamilton 1982). These forests are mainly south of the equator near the proposed central African forest refuge in the border region between Uganda and Congo. Biotic inventories of their diverse fauna and flora are thus needed.

Lianas, as a key component of tropical rain forests, contribute to closing the forest canopy and filling gaps between neighboring trees. By greatly increasing the shade cast, they compete with trees for space and light (Richards 1966). The largest lianas and the greatest species diversity are found in the tropical lowlands (Hegarty 1989). Climbing plants occur in about half of the angiosperm families (Jacobs 1976) but are prevalent in only about 12 families. Estimates vary, though, because of the many scandent forms that may be included with trees and shrubs. Lianas are estimated to make up about 18% of tropical forest flora. The three major regions of the world with a humid tropical climate are south and central America, Indo-Malaya (from India to southern China and New Guinea), and tropical Africa. Each region seems to have a different liana flora (Appanah et al. 1992, Richards 1996). In Africa, the Apocynaceae dominate (Gentry 1988), and rattans are relatively scarce compared to southeast Asia. This suggests differences in the liana ecology of African and Indo-Malayan rain forests.

Climbing plants are little studied in Uganda, despite being a key component of the forest and despite their use by local communities mainly for medicinal purposes and as ropes. In the past, foresters often regarded lianas as weeds and eradicated them, making them one of the most threatened plant life forms (Jacobs 1976). Although a well-delimited biological group, lianas are poorly investigated floristically, perhaps because of the difficulty in collecting flowers and fruits high in the canopy. Hall and Swaine (1976), sampling relatively dry forests in Ghana, found that climbers constituted up to 30% of plant species. Records of liana species from Africa (e.g., Emmons & Gentry 1983, Gentry 1988) include Mount Cameroon with 49 species and Makokou (Gabon) with 47 species. Synnott (1985) lists about 43 species of woody climbers in mature vegetation of the Budongo Forest Reserve in Uganda. Eggeling (1947) observed in

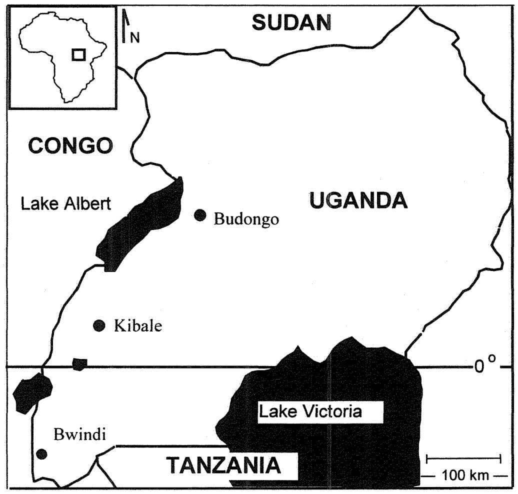

FIGURE 1. Outline map of Uganda locating study forests in the Albertine Rift in western Uganda: Bwindi Impenetrable National Park (BINP), Budongo Forest Reserve (BFR), and Kibale National Park (KNP).

the same forest that the stratification of climbing synusiae was bound inextricably with successional processes. For example, the lianas were absent from the early stages of colonizing forest, very abundant in mixed forest, and scarce in climax forest. The early stages of colonizing forest were rich in herbaceous climbers.

Among the factors affecting the abundance of vines in mature tropical forests is rainfall, whose influence on liana abundance is not well known. In a study of the structure of Neotropical forests, Holdridge et al. (1971) found no significant correlation between liana abundance and rainfall. Gentry (1988), however, found a positive correlation between rainfall and liana species richness.

This article reports basic liana demographic data, including abundance, diversity of plant families that include lianas, and the relationship between lianas and their trellises (living hosts). The data resulted from a study carried out between 1997 and 1998.

METHODS AND MATERIALS

Study Area

Three tropical forests were studied in western Uganda: the Bwindi Impenetrable National Park, the Budongo Forest Reserve, and the Kibale National Park (FIGURE 1). Two plots were sampled from each forest: Bwindi 1 and Bwindi 2 (Kayonza), Kibale 1 (Kanyawara), Kibale 3 (Kanyanchu), Budongo 2 (Nyakafunjo), and Budongo 3 (Pabidi). The study plots are designated Bw 1 and Bw 2 (Bwindi), Ki 1 and K 3 (Kibale), and Bu 2 and Bu 3 (Budongo).

Bwindi is located in the Kigezi highlands overlooking the western rift valley. The forest (0°53′–1°08′S, 29°35′–50′E) totals 331 km^2, less than half the area of either Kibale or Budongo (760 km^2 and 825 km^2 respectively). Bwindi lies south of the equator, while Kibale (0°12′–40′N, 30°20′–35′E) and Budongo (1°35′–55′N, 31°18′–42′E) lie north, with Budongo the northernmost. Bwindi is isolated from other protected areas by densely populated agricultural lands, unlike Budongo, which is contiguous with the Murchison Falls National Park, Bugungu Game Reserve, and Karuma Game Reserve. Kibale, like Budongo, is contiguous with a network of other protected areas via the Queen Elizabeth National Park; but most Kibale boundaries adjoin agricultural smallholdings.

The elevation of Bwindi forest is 1160–2607 m above sea level. The topography is rugged with steep-sided hills and narrow valleys. The elevation of Kibale forest is 1110–1590 m, and the Budongo Forest Reserve lies between 700 m and 1270 m. The terrain in both Kibale and Budongo is gently undulating. Budongo generally is more flattened than Kibale, whose elevation ranges from ridge tops to valley bottoms of 150–200 m (Chapman & Chapman 1997). The soils are broadly classified as ferralitic (Langdale-Brown et al. 1964). Bwindi has two soil types: non-differentiated ferralitic soils of high altitude and non-differentiated ferralitic soils with dark horizons. In Kibale, the soils are red ferralitic sandy loams of low to moderate fertility, except for a small area in the west where fertile eutrophic soils occur on volcanic ash. In Budongo the soils are ferralitic mainly sandy or sandy clay loams of low to moderate fertility.

The climate at the study sites is tropical with two rainfall peaks: March–May and September–November. Mean annual rainfall is 1100–1900 mm, with the rainfall in Bwindi (1400–1900 mm) generally higher than in Kibale and Budongo (1100–1600 mm and 1150–1500 mm respectively). Mean annual rainfall was determined for different years in each forest: Bwindi 1963–1993 (Butynski 1994), Kibale 1977–1984 (Struhsaker 1997), and Budongo 1933–1943 (Eggeling 1947).

Bwindi forest vegetation is described as high-altitude forest in the south and as medium-altitude evergreen forest in the north, the area sampled in this study (Langdale-Brown et al. 1964). The altitude of the northern sector of Bwindi is ca.1500 m, with *Parinari excelsa* Sabine the characteristic species (Howard 1991). Bw 2 is in relatively mixed forest with species such as *Strombosia scheffleri* Engl. and *Drypetes* spp. The Kibale vegetation is described as a medium-elevation transitional forest (Struhsaker 1997). This forest type falls between dry tropical and wet tropical forest. The northern part of the forest is broadly classified as medium-elevation moist evergreen forest, and the lower regions in the south are classified as medium-elevation moist semi-deciduous forest (Langdale-Brown et al. 1964, Osmaston 1959, Wing & Buss 1970). Grassland and swamp communities, some planted with exotic conifers, occupy about 23% of Kibale. Ki 1, in the northwestern part of the forest, is relatively mature and undisturbed with *Parinari excelsa* as the dominant species. A similar vegetation type was sampled in Bwindi. Ki 3, along a riverbank in the southern part of Kibale, is dominated by *Cynometra alexandri* C.H. Wright. The forested portion of Budongo that covers 428 km^2 has been described as medium-elevation moist semi-deciduous forest at less than 1500 m (Langdale-Brown et al. 1964). Bu 2, located in a nature reserve, is considered a mixed forest (Eggeling 1947), with characteristic emergent species such as *Entandrophragma cylindricum* (Sprague) Sprague and *Chrysophyllum albidum* G. Don. The Bu 3 plot is in the northern part of the reserve in an ancient species-poor forest type dominated by *Cynometra alexandri.* This forest type, also sampled in the south Kibale, is described as *Cynometra-Celtis* forest of lower elevation zones along the western rift in western Uganda.

Considerable local variation in forest types within comparatively small areas is a characteristic feature of many Ugandan forests (Howard 1991), with past human activity a major factor. Howard (1991) described the disturbance status of the study sites. In Bwindi, 61% of the forest has been heavily exploited by pitsawyers, 29% has been "creamed" of the best timber trees by selective pitsawing activity, and 10% is classified as essentially intact. In Kibale, the status of 67% of the forested land is unknown, 17% has been selectively felled by sawmillers, and 16% is affected by encroachment. Substantial areas of the forest described as "of unknown status" may be in a relatively undisturbed state, except for the *Parinari* forest type, 82% of which has been felled. In Budongo ca. 22% of the forested portion has not been affected by both timber harvesting operations, and ca. 88% has been affected by timber harvesting operations and poisoning of "undesirable" tree species in some parts.

Vegetation Sampling

For this study, 1-ha plots of 20 × 500 m were established in subjectively selected sites of intact forest. Some of the major variations in vegetation types within each forest were taken into account. The plots were laid out to run within intact forest and to cover topographical variation. Diameters of lianas ≥1 cm rooted within the plot were measured at 1.3 m (from the base) along the stems of the lianas (diameter at breast height, dbh). Lianas rooted in the plot (determined by position of the midpoint of the base) but growing on trees outside the plot were included, but hemi-epiphytes and stranglers were excluded. An individual was considered to be an independently climbing stem (Putz 1984). Branches of lianas that fell to the ground, rooted, and then grew upward were tallied as separate individuals.

Herbarium specimens were collected using tree-climbing methods. Identifications were made in the field and later in Makerere University herbarium (MHU) and the herbarium of the Royal Botanic Gardens, Kew (K). The identifications were based on vegetative field characteristics with reference to appropriate scientific identification keys and published floras (Beentje 1994, Eggeling & Dale 1952, Hamilton 1991, Polhill 1952 onward).

Trellises (≥1 cm diameter) rooted in the plot and supporting lianas were measured for dbh. Inclusion was determined by position of the midpoint of the base. Trellises rooted outside the plot but supporting lianas rooted in the plot were excluded.

RESULTS

Abundance per Plot

A total of 2783 liana individuals were recorded from the 6 ha of forest sampled. Abundance of lianas ≥1 cm dbh ranged between 155 and 743 individuals/ha for the six forest sites (FIGURE 2). The highest abundance of 743 individuals/ha (Ki 1) is more than four times the lowest abundance recorded (155 individuals/ha for Bu 3), but no clear trend is detectable among liana abundance in the study forests. Within each forest, abundance is related to successional status (determined from disturbance status), with abundance decreasing with the maturity of the sampled sites. For example, Bu 2 and Bw 2 (mixed forest) had more than twice as many lianas as did Bu 3 (*Cynometra* dominant forest) and Bw 1 (*Parinari* dominant forest). *Cynometra* dominant forest is considered to be the climax forest type for Budongo (Eggeling 1947), and *Parinari* dominant forest is considered the climax forest type at ca. 1500 m elevation in Bwindi. In Budongo, Plumptre (1996) found trees in the unlogged regions (N15 and K11–13, where Bu 2 and Bu 3 are located respectively) to have low

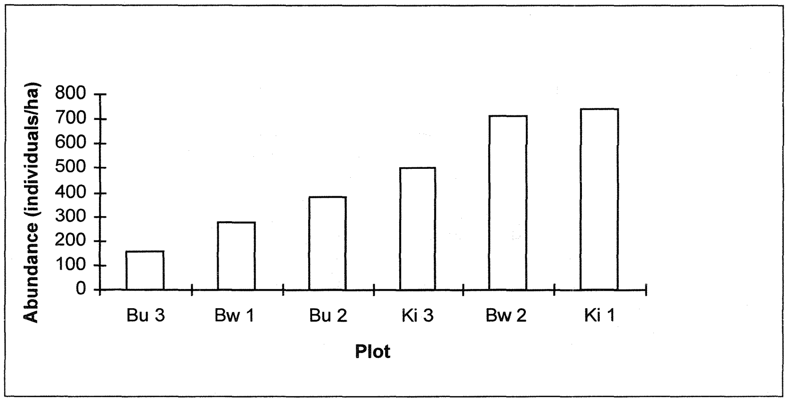

FIGURE 2. Total number of individuals of lianas ≥1 cm dbh per ha plot of tropical forest, western Uganda, 1997–1998.

liana scores compared to the logged sites. In Kibale the relatively mature *Parinari* forest (Ki 1) had about one and a half times as many individuals as did the *Cynometra* dominant site (Ki 3).

Abundance by Diameter Size

The number of lianas in stem-diameter classes decreased with increase in size class (TABLE 1). High proportions of lianas were found in the smaller diameter-size classes. This pattern was similar for all plots (FIGURE 3). Bu 3, which had the lowest abundance of lianas, also had the largest individual liana (15.25 cm diameter) compared to the largest individual in Bu 2 (12.85 cm diameter).

Abundance per Trellis

Most of the trellises in Bu 2 (86.4%) and Bu 3 (95.7%) were each host to one or two lianas. Bu 2 had no trellises hosting more than 10 lianas, and Bu 3 had no trellises hosting more than nine lianas. Abundance per trellis followed a trend similar to liana density in all six study sites.

TABLE 1. Distribution of lianas by diameter-size class per hectare in western Uganda, 1997–1998.

Study plot	No. stems/size class/ha by cm diameter				
	1–4.9	5–9.9	10–14.9	15–19.9	20+
Bw 1	220	47	7	5	0
Bw 2	586	110	17	0	1
Ki 1	707	33	2	1	0
Ki 3	463	35	8	0	0
Bu 2	340	41	4	0	0
Bu 3	139	10	5	1	0

FIGURE 4 shows that trellises 1–10 cm dbh supported the most lianas (more than 40%), followed next by trellises 11–20 cm, then by trellises 21–30 cm, and lastly by trellises >30 cm diameter. Although results are presented only for Budongo, the other study sites showed a similar pattern.

Diversity by Family

A total of 41 liana families were recorded and positively identified in the Ugandan plots (TABLE 2). The 15 most abundant liana families had 2404 individuals, which represented 86.4% of the 2783 individuals recorded from the 6 ha. The top-four families by number of individuals were Celastraceae (24.2%), Apocynaceae (9.9%), Rubiaceae (7.6%), and Icacinaceae (7.5%). The remaining 27 families contributed 379 individuals (13.6%). The contribution of the lowest 23 families was less than 1% each. The most abundant liana families in Bwindi were Celastraceae, Icacinaceae, Apocynaceae, Rubiaceae, and Loganiaceae. In Kibale the Celastraceae, Piperaceae, Verbenaceae, Rubiaceae, and Apocynaceae dominated. In Budongo the dominant families containing lianas were Celastraceae, Apocynaceae, Dichapetalaceae, Menispermaceae, and Dilleniaceae. The Celastraceae dominated overall in the six study plots. The numbers of families recorded per plot varied between 16 (Bu 3) and 28 (Bu 2). In terms of families containing lianas, Bu 2 was the most diverse (28), followed by Bw 2, Ki 1, Ki 3, Bw 1, and Bu 3 (27, 25, 25, 21, and 16 families respectively). Generally higher numbers of families were recorded for the mixed forest types.

Species richness of the study sites ranged from 35 (Bu 3) to 62 (Bu 2). Six of the species

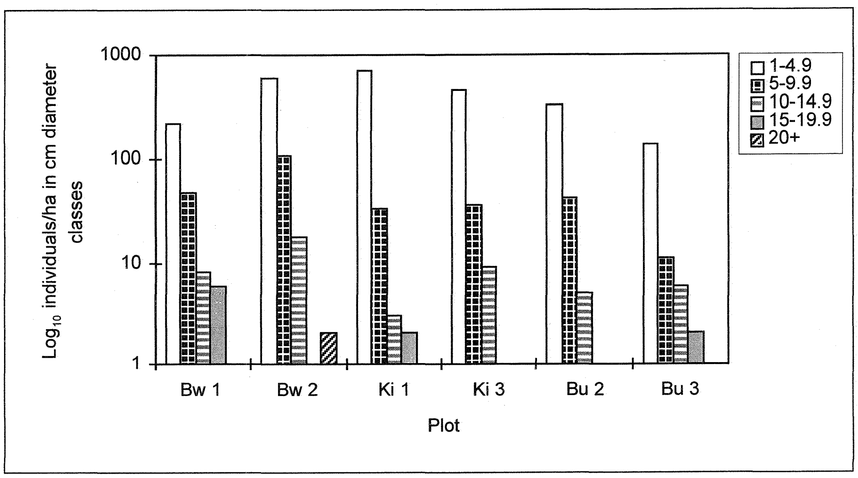

FIGURE 3. Distribution of lianas in stem-diameter classes for each of six 1-ha plots in three study forests. Note: Diameter classes are in cm, with more individuals occurring in small size classes, 1–4.9 cm and 5–9.9 cm.

recorded in Bwindi were not encountered in the other two forests. One of the species, *Efulensia montana* de Wilde (Passifloraceae), contributed ca. 7% of the individuals in Bw 2. The rest of the species were *Landolphia foretiana* (Pierre ex Jumelle) Pichon (Apocynaceae), *Loeseneriella apiculata* (Welw. ex Oliv.) R. Wilczek (Celastraceae), *Momordica jeffreyana* Keraudren (Cucurbitaceae), *Tarenna eketensis* Wernh. var. *auricluna* N. Hallé (Rubiaceae), and *Clerodendrum welwitschii* Guerke (Verbenaceae).

DISCUSSION

Overall the mature forest sites had lower liana abundance than mixed forest types. Liana abundance recorded in Ugandan forests is generally low compared to that recorded in eight west African sites by Gentry (1988), who found an average of 106 lianas >2.5 cm diameter per 0.1 ha.

Abundance decreased with increasing diameter-size class, as is the case for trees in naturally regenerating forest (Putz 1984, Hegarty 1989). According to Hegarty and Caballe (1991), larger vines inhabited tall (mature) forests, suggesting that sites with larger stemmed vines were generally more mature and that the occurrence of large-stemmed individuals may be used as an indicator of forest maturity. Gentry (1988) found an average of 20 lianas >15 cm diameter per ha in seven Amazonian forest sites. In contrast, the

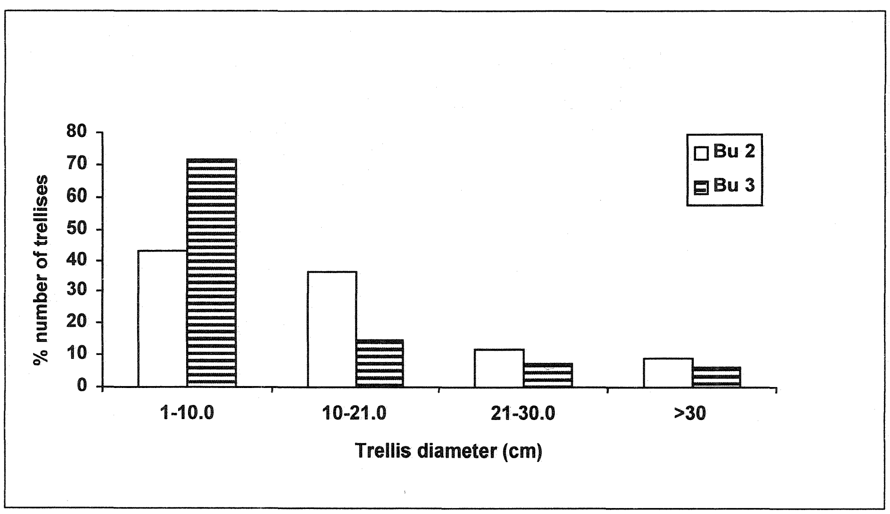

FIGURE 4. Trellis diameters climbed by lianas, with % of trellises per tree-diameter class in cm dbh.

TABLE 2. Abundance of families that include lianas in 6 ha of study rain forests of western Uganda, 1997–1998.

	No. individuals/study plot							
Family	Bw 1	Bw 2	Ki 1	Ki 3	Bu 2	Bu 3	Total	Lianas %
Celastraceae	68	138	220	60	108	80	674	24.22
Apocynaceae	30	57	86	23	57	24	277	9.95
Rubiaceae	20	57	64	54	14	3	212	7.62
Icacinaceae	57	130	—	7	14	—	208	7.47
Piperaceae	1	—	47	110	11	—	169	6.07
Verbenaceae	5	16	91	28	8	2	150	5.39
Menispermaceae	—	12	63	17	21	2	115	4.13
Connaraceae	21	33	20	5	11	—	90	3.23
Loganiaceae	8	62	—	2	3	6	81	2.91
Passifloraceae	13	52	—	9	5	—	79	2.84
Dichapetalaceae	3	1	1	33	34	5	77	2.77
Annonaceae	8	9	30	5	21	—	73	2.62
Asclepiadaceae	—	—	10	56	2	4	72	2.59
Urticaceae	11	43	8	—	6	—	68	2.44
Vitaceae	2	8	1	36	8	4	59	2.12
Leguminosae	18	17	4	4	4	3	50	1.80
Sapindaceae	—	11	27	10	—	—	48	1.72
Rhamnaceae	1	25	4	12	1	—	43	1.55
Amaranthaceae	—	—	29	—	—	—	29	1.04
Combretaceae	7	9	3	—	2	2	23	0.83
Dilleniaceae	—	—	—	1	20	2	23	0.83
Acanthaceae	—	2	11	—	5	1	19	0.68
Convolvulaceae	—	—	—	—	2	13	15	0.54
Malpighiaceae	—	7	5	2	—	—	14	0.50
Hernandiaceae	—	5	—	—	8	—	13	0.47
Thymelaeaceae	—	—	—	8	4	—	12	0.43
Euphorbiaceae	1	—	—	—	9	1	11	0.40
Polygalaceae	1	3	7	—	—	—	11	0.40
Cucurbitaceae	1	9	—	—	—	—	10	0.36
Myrsinaceae	2	—	4	3	1	—	10	0.36
Linaceae	—	4	—	—	—	3	7	0.25
Tiliaceae	—	1	—	1	3	—	5	0.18
Aristolochiaceae	—	—	4	—	—	—	4	0.14
Araceae	1	2	—	—	—	—	3	0.11
Capparaceae	—	1	—	—	1	—	2	0.07
Meliaceae	—	—	—	2	—	—	2	0.07
Moraceae	—	—	2	—	—	—	2	0.07
Nyctaginaceae	—	—	—	—	2	—	2	0.07
Rutaceae	—	—	1	1	—	—	2	0.07
Asteraceae	—	—	1	—	—	—	1	0.04
Dioscoreaceae	—	1	—	—	—	—	1	0.04
Grand total	279	715	743	506	385	155	2783	100.00

numbers of large lianas for the Ugandan plots were comparatively low.

Most lianas grasped trellises of medium-size diameter. This is to be expected, for smaller diameter trellises should be more abundant, if they conform to J-inverse diameter distributions (Richards 1966). Putz (1984) observed that the dimensions of the supports on which the lianas could climb also depended partly on the climber mechanism used.

The impact of lianas on trees depends on their abundance per host tree, which is influenced by, among other factors, abundance within the plot, which in turn depends partly on the successional status of the forest. The low liana loads shown mainly by trees in mature forest sites suggest that, as the forest matures, more trees become liana-free. This theory, if applied in managing timber production forests, could discourage climber-cutting operations and thus avoid further loss of biodiversity.

The most abundant liana families in the six Ugandan plots agreed with findings for other parts of continental Africa (Gentry 1988). The diversity of liana families was generally lower for the relatively mature sites. Budongo's *Cy-*

nometra forest is recognized as an example of a low-diversity tropical forest (at least in terms of tree species diversity). According to Eggeling (1947), the understory in *Cynometra* forest can be quite open and free of lianas, which contrasts with the tangles and dense undergrowth found in younger forest. The presence of six liana species in Bwindi that were not recorded in the other forests suggests closer links between Bwindi Forest and the Congo/Rwanda forests, where these species also are known.

Conclusion

Differences in composition of plant families that include lianas occurred within the study forests. These differences may be attributed partly to historical factors (e.g., human disturbance) that have influenced the successional stages within the forests. Presence of large-diameter vines may be a good indicator that a forest has not been subjected to serious disturbance for many years.

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