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Sprouting of woody species following cutting and tree-fall in a lowland semi-deciduous tropical rainforest, North-Western Uganda

Edward N. Mwavu *, Ed T.F. Witkowski

Restoration and Conservation Biology Research Group, School of Animal, Plant and Environmental Sciences,
University of the Witwatersrand, PO WITS, 2050 Johannesburg, South Africa

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Abstract

Effective management, conservation and restoration of tropical forests require an understanding of plant responses (e.g. sprouting) to natural and anthropogenic disturbance events. Sprouting among woody plants within Budongo Forest Reserve (BFR) in response to harvesting for poles and saplings, and tree and branch fall disturbances was examined. A total of 835 woody stumps representing 122 species were recorded. Human harvesting accounted for 83% of 835 damaged stumps. Both canopy and sub-canopy trees sprouted prolifically. Of the 122 affected species, 119 (97.5%) from 31 families sprouted from stem stumps, with only *Caloncoba crepiniana* exhibiting stem and root sprouting. Only *Maesopsis eminii*, *Cordia milleni* and *Raphia farinifera* did not resprout. Sprouts/stump ranged from 16.3 ± 1.8 (S.E.) for *Rawsonia lucida*, to 1 for 10 species. Number of sprouts/stump differed significantly among families (Kruskal–Wallis $H = 182.63$, $P < 0.0001$), species ($H = 256.26$, $P < 0.0001$) and stump size-classes ($H = 73.18$, $P < 0.0001$). Mean sprouts/stump was significantly higher for intermediate sized stems of basal diameter (BD) 5.1–20.0 cm. Dead sprouts occurred on 26 species. There were species-specific significant differences in height ($H = 39.92$, $P = 0.0297$) and BD ($H = 52.34$, $P = 0.0011$) of the leading sprout. Stump BD ($\chi_1^2 = 6.62$, $P = 0.0101$), height ($\chi_1^2 = 38.52$, $P < 0.0001$), bark-thickness ($\chi_1^2 = 14.56$, $P < 0.0001$) and height of stump above ground at which the first sprout emerged ($\chi_1^2 = 74.42$, $P < 0.0001$) were significant predictors of sprouting ability among individuals. Hence, this semi-deciduous tropical rainforest has a high proportion of sprouting species and incidence of sprouting stems. Sprouting of small and relatively large stumps, and the survival and growth of sprouts, suggests that sprouting plays an important role in forest resilience to selective timber, pole and sapling harvesting.

Keywords: Bark-thickness; Coppicing; Harvesting; Root suckering; Resilience; Resprouting; Stumps

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1. Introduction

In tropical forests and woodlands, woody plants are subjected to various types of physical disturbance (e.g. timber harvesting, fires, storms, hurricanes, and tree and branch fall), resulting in loss of foliage or stems. In response to these disturbances, plants either resprout/coppice (henceforth referred to as sprouting) along the remaining stem, from the rootstock or die (Kammesheidt, 1998; Paciorek et al., 2000; Bond and Midgley, 2001). Sprouting in woody plants, which results in the production of secondary trunks usually from suppressed buds on the stem or roots of a plant is an induced response to injury or to a dramatic change in surrounding environmental conditions (Del Tredici, 2001). The ability of a plant to resprout after its above ground parts are killed (top-kill) is a typical feature of many plant species from disturbance-prone, terrestrial ecosystems (Cruz et al., 2003). However the potential of a species to establish and persist following disturbance differs among species. It is governed primarily by life history and physiological traits and by the characteristics of the disturbance event (Gómez Sal et al., 1999).

Sprouting is an important life history characteristic of woody species in moist tropical forests, and those subjected to large-scale disturbance events such as hurricanes, logging (e.g., Bellingham and Sparrow, 2000; Del Tredici, 2001) and slash-and-burn agriculture (e.g., de Rouw, 1993). In these places plants of all sizes survive and resprout after being damaged

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* Corresponding author. Present address: Department of Forest Biology and Ecosystems Management, Makerere University, P.O. Box 7062, Kampala, Uganda. Tel.: +27 11 717 6441/+256 41 543647;
fax: +27 11 403 1429/+256 41 533574.
E-mail addresses: edwardm@gecko.biol.wits.ac.za,
emwavu@forest.mak.ac.ug (E.N. Mwavu).

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(e.g., Bellingham et al., 1995; McLaren and McDonald, 2003). Even in forests where large-scale disturbances are infrequent, woody plants still experience significant stem damage from smaller scale disturbances such as pole and sapling harvesting by humans as well as branch and tree fall (e.g., Clark and Clark, 1991; Paciorek et al., 2000). Although the frequency of branch and tree fall is probably similar among rainforests sites, additional causes of stem damage are site specific (Ickes et al., 2003). Consequently the ability of woody plants to resprout should also be a common plant characteristic in areas that only experience relatively minor disturbances. However, little is known of woody plant sprouting in African tropical forests, including Budongo Forest Reserve (BFR) in Uganda. Understanding the natural regeneration processes and plant responses to disturbances has practical applications in the restoration and management of forest vegetation (Vesk et al., 2004), particularly for economic, conservation and environmental benefits. BFR is an important natural forest for biodiversity conservation in Uganda as it contains threatened mammals (e.g., Chimpanzees) and plant species (Plumptre, 1996). It is a prime example of a natural forest where no major natural disturbances such as hurricanes, droughts or fires have been recorded in its history. However, BFR is bordered on the southern side by villages inhabited by subsistence farmers with livelihoods that are entirely dependent on the exploitation of land resources (Mwavu, 2007). This study aimed to identify the major causes and types of disturbances leading to stem damage and consequently sprouting, and to describe sprouting ability among woody plant species and families. To achieve this aim, the following questions were posed; (1) what are the major causes and types of stem damage, and the level of harvesting of the woody species? (2) Are stump characteristics (i.e. basal diameter, height and bark-thickness) predictors of sprouting ability among individuals and species? (3) Does sprouting ability differ between basal diameter size-classes, species, canopy and sub-canopy species and families? (4) What is the relationship between the leading sprout's height and basal diameter, and number of sprouts/stump?

2. Materials and methods

2.1. Study area

Budongo Forest Reserve (BFR) is located at the top of the escarpment, east of Lake Albert, on the edge of the western rift valley in North-Western Uganda, between Masindi town and Lake Albert. It has an area of 793 km^2 and lies between 1°37′ and 2°03′N and 31°22′ and 31°45′E. The altitudinal range is 700–1270 m above sea level, with a mean of 1050 m. This forest has been broadly classified as medium altitude semi-deciduous moist tropical rainforest, because several of the dominant species (e.g. *Celtis* spp., *Maesopsis eminii* Engl., *Ficus* spp., etc,) are at least briefly deciduous (Eggeling, 1947), with the notable exception of the shade-tolerant *Cynometra alexandri* C.H. Wright (Sheil, 1997). Generally, it is a mosaic of forest types, a result of forest dynamics and management history (Plumptre, 1996; Mwavu, 2007). The general ecology, environment, management and history of BFR have been described by Eggeling (1947) and Synnott (1985).

The forest reserve is contiguous with the Murchison Falls National Park to the North, Bugungu Game Reserve to the Northwest and Karuma Game Reserve to the Northeast. However, apart from the common primates (e.g. baboons, chimpanzees, white and red-colobus monkeys), there are currently no large herbivores, such as elephants and buffalos, residing in the forest reserve. The elephant populations inside BFR were eliminated in the 1970s (Laws et al., 1975; Sheil and Salim, 2004). On the eastern, southern, and south-western sides, it borders villages whose inhabitants are subsistence farmers of mixed language, culture and nationality. They are entirely dependent on the land resources for their livelihoods, and use woody plant resources for fuel energy and as raw materials for house construction. The climate is tropical, with two rainfall peaks, March–May and September–November, and a dry season December–February. The mean annual rainfall is 1500 mm. Maximum temperature rarely exceeds 32 °C and only occasionally drops below 24 °C, with low daily variation. This climate supports a regular rain-fed shifting agriculture, with the main crops being sugarcane, maize, sorghum, beans and tobacco.

2.2. Sampling design and sample size

Thirty two 100 × 50 m (0.5 ha) plots were established in forest compartments, including those that have historically been managed as: (a) "nature reserves" (with little or no anthropogenic disturbance), (b) previously selectively logged about 15 years ago (~1990), and those that were (c) mechanically logged and arboricide treated in the 1950s. Some of these areas are close and accessible to surrounding local communities. BFR has a history of intrinsic disturbances such as elephant damage, tree fall, patchy selective logging (both legal and illegal) and pole cutting of specific tree species. In each 0.5 ha plot, all stumps, and the number of sprouts (live and dead) from each stump were enumerated, but only live ones were measured for height and basal diameter. Stump height above ground and diameter above the basal swelling were measured. Species were identified from the stumps using the leaves of sprouts, wood and bark characteristics such as colour, smell and texture (Luoga et al., 2004), with reference to plant identification guides (e.g., Hamilton, 1991), and the Flora of Tropical East Africa (Polhill, 1952 *et seq.*). Basal diameter (BD) was measured since most of the stumps were not tall enough to measure at breast height (1.3 m). Diameter and height of the largest sprout of each stump was measured, and the number of live and dead sprouts per stump enumerated. Height above the ground at which the first sprout appeared on the stump (height at first sprout) and bark-thickness of the stump, using a bark-gauge (HAGLOF Barktax), were also measured. An attempt was also made to identify root sprouting among the plants. The type of disturbance associated with the formation of the stump was established, and if it was anthropogenic, then the purpose for removal assessed with the aid of a local elder and a persistent resource user well acquainted with local ethnobotany and regional forest utilization.

2.3. Data analysis

The total number of stumps for each species was counted, and the number and percentage that sprouted was determined, and compared between species and families. This was not, however, done for the three historical management practice types as it was apparent that tree and pole harvesting patterns were not dependent on management practice, but on accessibility to and convenience of the harvesters. The level of harvesting for each species was also determined as a fraction (percentage) of stumps of the present standing stock. Sprouting ability was calculated as the mean number of sprouts per stump for each harvested species, and comparisons among species and families were undertaken using a Kruskal–Wallis test (*H*-test) (Sokal and Rohlf, 1995). This test was found suitable for these data although the stumps might have been of different ages and probably cut in different seasons. Because of the wide range of sites, localities and stump sizes, variance due to time since cutting or breakage would be small in comparison to all the other sources (Shackleton, 2000). The stump inventory data were also pooled and tallied into BD size-classes of 0–5, 5.1–10, 10.1–15, . . ., 35.1–40, and >40 cm and related to mean sprouts/stump and number of stumps. A statistical difference in sprouts/stump among these size-classes was tested by Kruskal–Wallis test with a Bonferroni multiple comparisons procedure. Each species was classified as canopy or sub-canopy based on Synnott (1985) and Hamilton (1991) classifications, and its overall mean sprouts/stump calculated. To test for differences in sprouting ability between canopy and sub-canopy species, a Mann–Whitney *U*-test was used. Each species was counted as a single data point in the analyses so that abundant species did not dominate the results.

The number of sprouts/stump was related to stump BD, height and bark-thickness using log linear regression models (PROC GENMOD, based on a negative binomial (NB) distribution and a log link function) utilizing SAS version 8.0 (SAS Institute Inc., 2004). The NB distribution provides one way of modelling heterogeneity in a population in that it naturally accounts for over-dispersion better than the Poisson distribution. Only species with ≥ 4 stumps were included in the analyses. The model fit was adequate for the data since values of Pearson Chi-square (= 201.6) and deviance (= 213.9) divided by the number of degrees of freedom (= 210) were close to 1. Species-specific linear regression analyses were also performed to relate sprouting ability (number of sprouts/stump) to stump characteristics (i.e. height, BD, bark-thickness), and height of stump above ground at which the first sprout emerged. In addition, using pooled stump data; linear regression analyses were performed to relate number of sprouts/stump to the basal diameter and height of the leading sprout. Species-specific differences in the height and BD of the leading sprout were also tested using a Kruskal–Wallis test.

3. Results

3.1. Causes and levels of stem damage, and types and levels of sprouting

A total of 835 woody stumps representing 122 species, both cut and broken, were investigated for sprouting, of which 814 (97.5%) from 119 species (within 31 plant families) sprouted (Appendix 1). Only three species, *M. eminii*, *Cordia milleni* Bak. (both canopy species) and *Raphia farinifera* (Gaertn.) Hylander (a palm) did not resprout from the stumps. The first two species are highly sought after for timber, while the latter is of high conservation importance as it is classified as vulnerable. The most harvested and frequently sprouting species were *Celtis mildbraedii* Engl. (104 stumps), *Funtumia elastica* (Preuss) Stapf. (93), *Lasiodiscus mildbraedii* Engl. (81) and *C. alexandri* (46), making up 39.8% of the total stumps sampled. These are the preferred woody species for house construction due to their superior woody quality, pole straightness and high abundance in the forest. Overall harvesting was low since none of the species had more than 5% of the stem standing stock harvested. Of the 119 sprouting species, only *Caloncoba crepiniana* (De Wild. & Th. Dur.) Gilg sprouted from both the stem stump and roots (root suckering). Although there are many types of disturbances leading to stem damage in a forest, the most frequently recorded in BFR was human harvesting (83% of the stumps), targeting mainly saplings and poles, and tree and branch fall breakage (17%). Saplings and poles were mostly harvested for building purposes, while large trees were harvested for timber or as bed-supports for pitsawing. No stem damage from animals was observed despite the fact that this forest is rich in primates and wild pigs.

3.2. Sprouting ability of species

The number of sprouts/stump differed significantly between the plant families sampled (Kruskal–Wallis $H = 182.63$, $P < 0.0001$). Among the families represented by ≥ 3 species, the families with highest mean (±S.E.) sprouts/stump were Ulmaceae (8.99 ± 0.55), Flacourtiaceae (7.54 ± 1.61), and Violaceae (7.37 ± 0.62); while those with the lowest were Annonaceae (3.25 ± 0.88), Sapindaceae (3.20 ± 0.43) and Meliaceae (3.08 ± 0.29). There were also significant species-specific differences observed for number of sprouts/stump (Kruskal–Wallis $H = 256.26$, $P < 0.0001$), and for height ($H = 39.92$, $P = 0.0297$) and BD of the leading sprout ($H = 52.34$, $P = 0.0011$). At the species level, the number of sprouts/stump ranged between 35 for *C. mildbraedii* and one for ten (10) species, with the latter being quite common (8 of 17 stumps) in *Tabernaemontana holstii* K. Schum. About 38.4% of the *C. mildbraedii* stumps had ≥ 10 sprouts and only 10.9% had ≤ 2 sprouts/stump, while those of *T. holstii* mainly had one and rarely exceeded 2 sprouts/stump. The highest mean sprouts/stump was 16.3 ± 1.8 ($n = 3$) for *R. lucida* Harv. & Sond., while the lowest was 1.9 ± 0.3 ($n = 17$) for *T. holstii* (Appendix 1). The 13 species with the highest mean number (≥ 8.0) of sprouts/stump were from 12 families, which included 7 sub-canopies (i.e. *R. lucida*, *Maerua duchesnei* (De Wild.) F. White., *Alchornea laxiflora* (Benth.) Pax & K. Hoffm., *Tapura fischeri* (Engl.) Engl., *Thecacoris lucida* (Pax.) Hutch., *Rinorea ardiisiflora* (Welw. ex Oliv.) Kuntze, and *L. mildbraedii*) and 6 canopy species (i.e. *Strychnos mitis* Moore, *C. mildbraedii*, *Celtis zenkeri* Engl., *Diospyros abyssinica* (Hiern) F. White, *Pouteria altissima* (A. Chiev.) Aubrev. & Pellegr., and *C. alexandri*). Of these species, only 5 (i.e. *C. mildbraedii*, *C. zenkeri*, *D. abyssinica*, *P. altissima*, *and S. mitis*) are regarded as timber species (MNR, 1997), while the rest are harvested for subsistence uses. There was no overall statistically significant difference ($U = 1630.5$, $P = 0.61$, $n = 119$) in sprouting ability (i.e. mean sprouts/stump) between the sub-canopy and canopy species.

There were relatively few dead sprouts on sprouting stumps, with only 26 species (21.8% of 119 species) having any dead sprouts. Dead sprouts/stump ranged from 7.7% (1 of 13 sprouts) in *R. lucida* to 83% (5 of 6 sprouts) in *Senna spectabilis* (DC.) Irwin & Barneby. *S. spectabilis* had the highest mean (±S.E.) dead sprouts/stump (4.0 ± 0.6, $n = 15$), followed by *F. elastica* (2.3 ± 0.3, $n = 12$) and *C. mildbraedii* (2.5 ± 0.6, $n = 6$).

3.3. Relationships between stump characteristics and sprouting ability

Sprouting stumps were of varying BD sizes, ranging from 0.32 cm for *Trichilia drageana* Sond., to 130 cm for *Mildbraediodendron excelsum* Harms. However, about 93% of the sampled stumps were ≤16 cm in BD, with only 1.2% being ≥29.0 cm (Fig. 1a). The relationship between stumps size-class and mean sprouts/stump exhibited a hump-shaped curve, with sprouts/stump rising with increasing size-class and declining beyond the ≥30 cm BD size-class (Fig. 1b). Among the stumps of harvestable size for timber (BD > 60.0 cm) *Chrysophyllum albidum* G. Don. (66.5 cm), and *M. excelsum* (130 cm) sprouted, while *Entandrophragma utile* (Dawe & Sprague) Sprague (70.8 cm) and *M. eminii* (75.0 cm) did not. The mean sprouts/stump differed significantly ($H = 73.18$, $P < 0.0001$) among the stump size-classes. However, pair-wise comparisons with Bonferroni correction only revealed statistically significant differences between the 0–5 cm size-class and the 5.1–10 ($P < 0.0001$), 10.1–15.0 ($P < 0.0001$) and 15.1–20 cm ($P = 0.002$) size-classes. Stumps of BD 5.1–20.0 cm on average had higher sprouts/stump than any other size-class (Fig. 1b).

Stump characteristics (bark-thickness, BD, height and height at first sprout) significantly influenced the number of sprouts/stump. The negative binomial distribution regression model showed that stump bark-thickness ($\chi_1^2 = 14.56$, $P < 0.0001$), BD ($\chi_1^2 = 6.62$, $P = 0.0101$), height ($\chi_1^2 = 38.52$, $P < 0.0001$) and height on stump above the ground at which the first sprout emerged ($\chi_1^2 = 74.42$, $P < 0.0001$) were significant predictors of sprouting ability of the plants when the species data are pooled. On the other hand, species-specific linear regressions detected significant relationships between stump height and number of sprouts for 4 species (3 positive and 1 negative; Fig. 2), and BD and number of sprouts/stump for 5 species (Fig. 3). Furthermore, it detected significant negative relationships for height on stump above the ground at which the first sprout emerged with number of sprouts/stump for 5 species (Fig. 4). There were however, no significant relationships between bark-thickness and number of sprouts/stump.

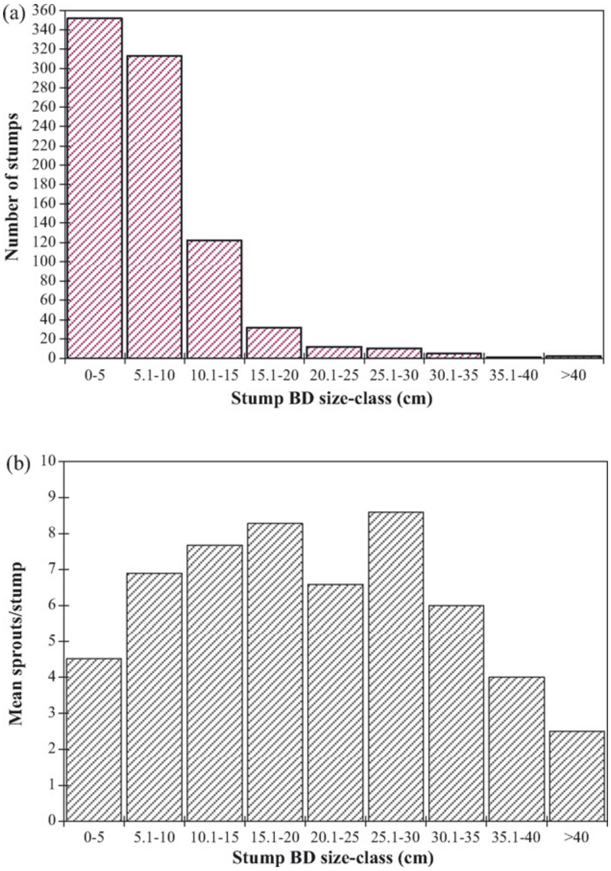

Fig. 1. Relationship between stump basal diameter (BD) size-classes: (a) number of stumps, and (b) mean sprouts/stump for damaged woody species in Budongo Forest Reserve, NW, Uganda.

3.4. Relationship between leading sprout BD and height, and number of sprouts/stump

The number of sprouts/stump was a significant negative predictor for both BD ($\chi_1^2 = 26.17$, $P < 0.0001$) and height ($\chi_1^2 = 20.34$, $P < 0.0001$) of the leading sprout for pooled data (Fig. 5). Thus stumps found with fewer sprouts were expected to have their leading sprouts attaining larger BD and taller sizes, than those densely covered with sprouts. For species having stumps with multiple sprouts, *F. elastica* had both the tallest (15.3 m) and thickest (BD = 8.0 cm) leading sprout, suggesting that it probably has the greatest potential for coppice regrowth and biomass replacement. However, a sawn stump of *M. excelsum* (BD = 130.0 cm) had a single sprout of height 10.0 m and BD of 33.4 cm. This further strengthens the argument that densely sprouting stumps are probably slower at producing tall and thick leading sprouts (Fig. 5).

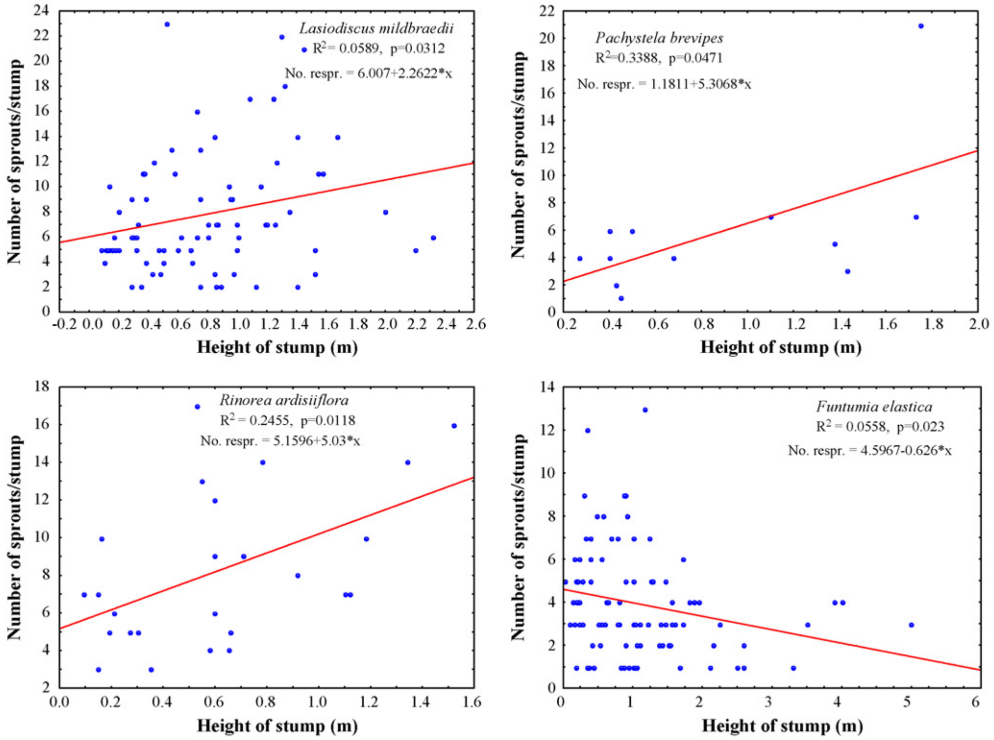

Fig. 2. Regression analyses of height of stump on the number of sprouts/stump produced for four species (which showed significant relationships) following cutting, and tree and branch fall disturbances in Budongo Forest Reserve, NW Uganda.

4. Discussion

Human harvesting of saplings and poles is presently the major cause of stem damage and seems to be also more common in areas, which are more accessible and nearer to human settlements. This is probably because BFR is the main source of wood-based products (e.g. poles, saplings, and fuel-wood) to the local human population as most woodland outside BFR has been cleared for agriculture expansion (Mwavu, 2007), and possibly the absence of elephants. Only one species exhibited root suckering, suggesting that it is not a common type of sprouting in BFR under the present environment conditions, characterised by lack of fires, a closed canopy in almost all parts, and an absence of both heavy logging and large herbivores in the interior (e.g., elephants; Sheil and Salim, 2004). Shady conditions under a closed canopy as encountered in most parts of BFR, reportedly suppress root sucker production among temperate forest trees (Del Tredici, 2001). In tropical rainforests, root suckering is a common mode of regeneration among species in deforested and fire-degraded sites (e.g., Stocker, 1981; Kauffman, 1991) and forests prone to slash-and-burn agriculture and logging (e.g., Kammesheidt, 1999; Marrinan et al., 2005).

The number of sprouting species (119 = 97.5% of 122) recorded in BFR is higher than reported from other tropical forests. For example, in the semi-evergreen rainforest in Queensland, of the 82 species that reappeared after the felling and burning of a forest, 74 (90.2%) coppiced from stumps (Stocker, 1981). Similarly, 48 (94%) of 51 species sampled in a tropical dry limestone forest in Jamaica (McLaren and McDonald, 2003) and only 35 (60.3%) of 58 species for a moist tropical forest in Eastern Paraguay (Kammesheidt, 1998) coppiced from stumps. Furthermore, in Jamaica, Puerto Rico and Nicaragua, 54–87% of trees of various size classes sprouted after hurricane damage (e.g., Zimmerman et al., 1994; Bellingham et al., 1995). Plant species respond differently to disturbances and gradients in environmental variables, resulting in different sprouting abilities among them. For example, humid forests and tropical sites have been identified with higher community-wide sprouting ability than the temperate forests (Everham and Brokaw, 1996).

Results from this study showed that the ability to sprout following stem damage is to some degree common among the woody species of BFR, with both sub-canopy and canopy species showing prolific sprouting. The ability of both sub-canopy and canopy woody species to sprout has also been reported in Jamaican montane forest trees (Bellingham et al., 1994), the Pasoh Forest Reserve in Malaysia (Ickes et al., 2003) and Barro Colorado Island of Panama (Paciorek et al., 2000). The lack of statistically significant differences in sprouting ability (sprouts/stump) between sub-canopy and canopy species in BFR has similarly been reported for moist tropical forest species in Panama (Paciorek et al., 2000). Although sprouting is common among the woody plants of BFR, some species (i.e. *M. eminii*, *C. milleni* and *R. farinifera*) did not sprout. The canopy species, *M. eminii* and *C. milleni*, did not have any smaller-sized stumps (<30 cm BD), which generally show high sprouting ability. Although there was sprouting among all the size-classes analysed, mean sprouts/stump was significantly higher in stems of 5.1–20.0 cm BD. This closely compares with results from other studies (e.g., Putz et al., 1983; McDonald and

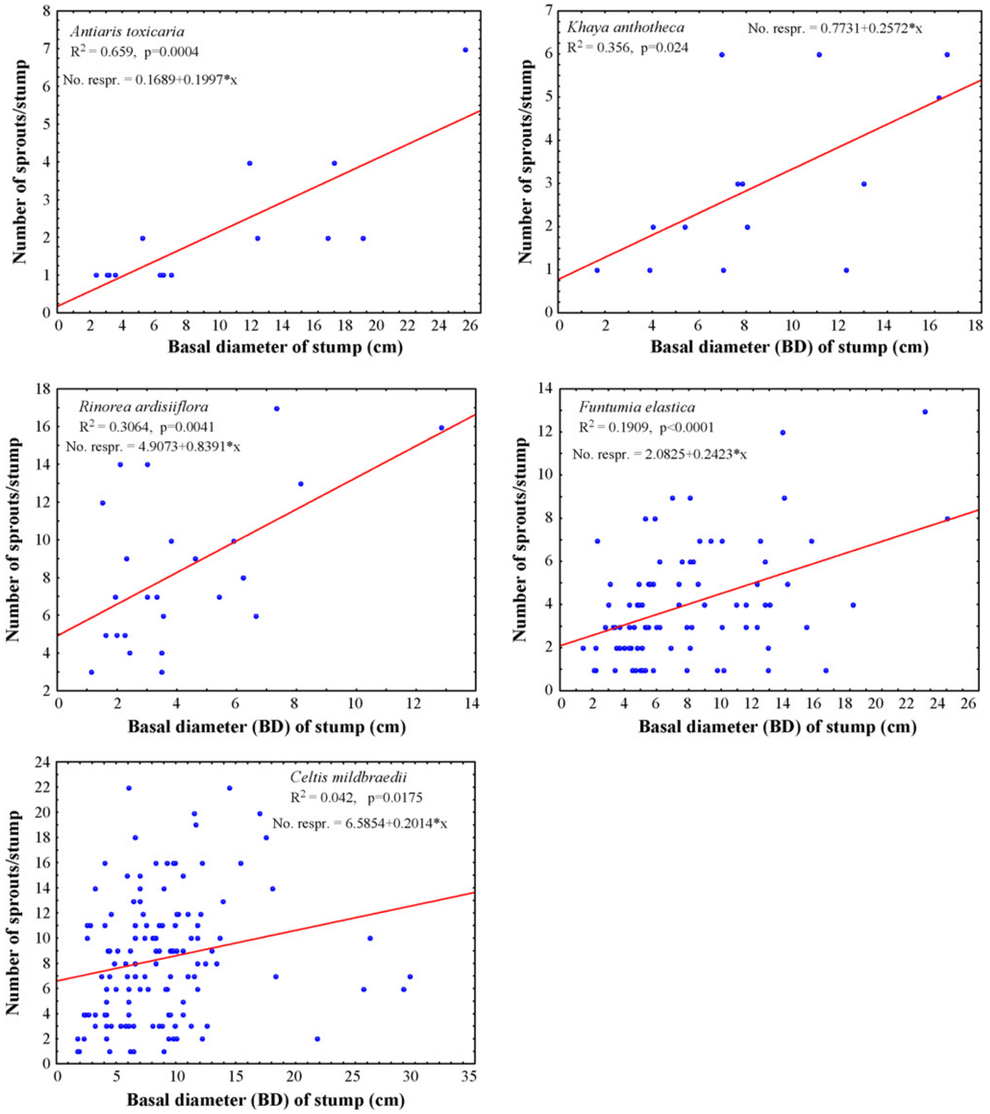

Fig. 3. Regression analyses of basal diameter of stump on the number of sprouts/stump produced for five species (which showed significant relationships) following cutting, and tree and branch fall disturbances in Budongo Forest Reserve, NW Uganda.

Powell, 1983; Tworkoski et al., 1990), which reported higher sprouting ability among woody stumps of $\leq$16 cm and lower for $\geq$30.0 cm BD. Furthermore, if stumps of 5.1–20.0 cm BD are regarded as juveniles (which is reasonable to assume for canopy species), these findings also compare with other studies (e.g., Everham and Brokaw, 1996; Bellingham and Sparrow, 2000; Paciorek et al., 2000) in that many forest tree species sprout as juveniles and then lose the ability to sprout as adults.

Species differences in sprouting ability revealed in BFR is well known in other ecosystems where both strongly and weakly sprouting species occur (e.g., Everham and Brokaw, 1996; McLaren and McDonald, 2003). However the relatively high number of woody species sprouting in BFR may be attributable to most of the tree species being hardwoods (G. Eilu, pers. commun.). Indeed, in Madagascar, some hardwood trees of the family Leguminoseae (Fabaceae) are able to sprout after being cut (Cunningham et al., 2005). The stump characteristics, which were found to be significant predictors for number of sprouts/stump in BFR have also been reported for woody species from other ecosystems (e.g., Weigel and Peng, 2002). The significant positive relationship between stump BD and sprouts/stump for 5 species in BFR, was also reported for 7 woody species in a disturbed tropical dry forest in Jamaica (McLaren and McDonald, 2003), where some species also had significant negative relationships between stem diameter and average height of the leading sprout.

The significant differences in the number of sprouts/stump among families and species in BFR, has also been reported among savanna woody species, and further attributed to plant size/age at the time of cutting and stump height (Shackleton, 2000; Luoga et al., 2004). In the present study, all (98.8% of total) smaller sized stumps (BD < 30 cm) sprouted, while for larger ones (size suitable for timber harvest >30 cm), only 8 of 12 sprouted. This agrees with Lamson (1988), who stated that for most species with small stems, usually <30 cm dbh, had a better sprouting potential than larger stems. However, it is probable that small dead stumps were under-sampled as they would presumably be more easily missed than larger ones,

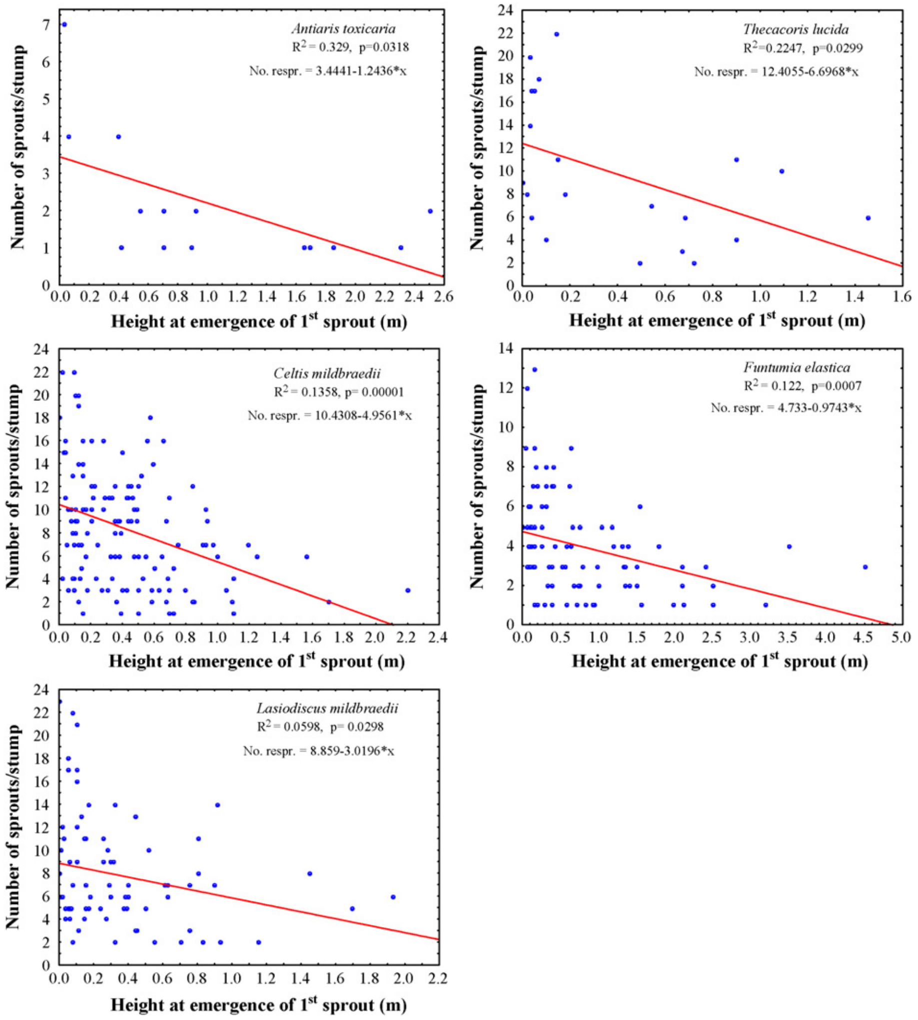

Fig. 4. Regression analyses of height of stump above the ground at which the first sprout emerged on the number of sprouts produced for five species (which showed significant relationships) following cutting, and tree and branch fall disturbances in Budongo Forest Reserve, NW Uganda.

since they decompose quicker than larger stumps. Sprouting ability differences among the >30 cm BD stumps in BFR, suggested that apart from individual stump physical characteristics, other species-specific characteristics (e.g. stem water status, root allocation and stored starch) may play a role. Plant species may also differ in their ability to resprout as a consequence of differences in other factors such as meristematic capacity (numbers of available buds), root–shoot partitioning, stored carbohydrate and nutrient reserves (e.g., Zimmerman et al., 1994). Although sprout survival in BFR is not clearly known, as this is a one time observational study, the attainment of tall and large leading sprouts, even for those with a high number of sprouts/stump, suggests that at least one of the sprouts will survive and grow to replace the lost stem. It further shows that sprouts can survive to play an important role in the persistence of the damaged plants and in this respect sprouting is important in the regeneration process and the future state of BFR in the face of increased human utilization. On the other hand, the death of some sprouts on stumps suggests death due to injury or self-thinning among sprouts. For instance, in temperate forests self-thinning occurs among sprouts as they increase in size (e.g., Rentena et al., 1992).

The tendency of most woody species in BFR to produce sprouts close to the cut end or point of breakage has also been encountered in woody species of Panamian forests, where most sprouts emerged near the top of broken snags (Putz et al., 1983). Hence, these results reaffirm the Cannell (1983) principle that distal buds, near the cut ends, are stimulated to grow more than basal buds (‘acrotony’). Trees respond to damage with the sprouting of suppressed buds immediately below the point of damage and, regardless of the height of the damaged stump, some species have a strong tendency to sprout from the top of the stump or near the edge of the cut (Burns and Honkala, 1990; Smith et al., 1997). In BFR, it was also noticed that the largest and tallest sprout on the stumps of most species was among those emerging closest to the top of the stump. Similarly, Burns and Honkala (1990) pointed out that, generally, buds closest to the point of damage, whether on branches or the trunk, show the most vigorous growth. On the other hand, despite producing a lower than average number of sprouts/stump, the growth of the tallest and largest sprout by *F. elastica*, is in keeping with the observation that stumps with low sprout densities achieve relatively larger sprouts.

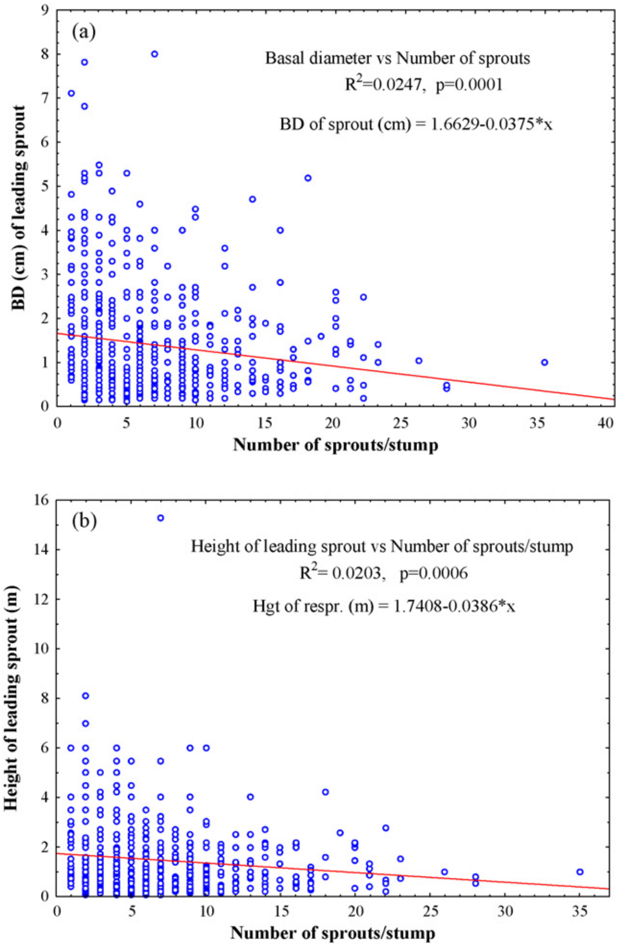

Fig. 5. Regression analyses of the number of sprouts/stump on the (a) basal diameter and (b) height of leading sprout for pooled species stump data in Budongo Forest Reserve, NW Uganda.

4.1. Conclusions and implications for forest management

Human harvesting for poles and saplings for building purposes and tree and branch fall are the major causes of woody stem damage in BFR. This study showed that semi-deciduous tropical rain forests have both a high proportion of sprouting species and incidence of sprouting stems (both small and relatively large diameter sized). The 119 (97.5%) stem sprouting species in BFR is higher than reported from other tropical forests outside the African continent. However, there are no published data for comparison from other African tropical rainforests. There appears to be a high chance of sprout survival and growth to replace the lost stem, making sprouting a key trait in the persistence of woody plant individuals, populations and communities in BFR. Even the sprouting of large stumps of ≥29.0 cm BD (e.g., *C. albidum*, *C. mildbraedii*, etc.), and the survival and growth of sprouts suggests that sprouting may play an important role in the resilience of the forest following selective timber, pole and sapling harvesting. However, the lack of sprouting of stumps ≥60 cm BD for some important timber species threatens their survival, unless they have sufficient seedling banks to replace the lost mature seed trees. Silvicultural interventions for management of sprouts in BFR should involve cutting as low to the ground as possible in order to stimulate the growth of buds from the collar instead of the trunk, and to prevent sprouts from suffering heart rot (Del Tredici, 2001). It is predicted that densely sprouted stumps will be slower at producing tall and thick leading sprouts than sparsely sprouting ones, regardless of the species. Therefore, manual thinning could be important to reduce the number of sprouts on the stump and encourage the faster development of taller and larger sized sprouts in forest areas where timber and pole harvesting is allowed. Although BD, height and bark-thickness of stump, and height at first sprout were found to be good predictors of sprouting ability, additional experimental studies will be required to determine these relationships more precisely. In addition, long-term studies and those relating sprouting to edaphic factors and the frequency and seasonal timing of harvesting will be necessary for a more complete understanding of species sprouting responses, particularly for those frequently harvested and of silvicultural importance.

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Appendix A

Sprouting woody species, listed alphabetically by family, indicating the number of sprouting stumps (= number of damaged plants), mean number of sprouts/stump and the overall number of undamaged plants encountered in 32, 0.5 ha plots within the semi-deciduous Budongo Forest Reserve, NW Uganda

Family	Species	No. of stumps (= no. of damaged plants)	No. of sprouts/ stump mean (±S.E.)	No. of undamaged plants	Growth form
Anacardiaceae	*Pseudospondias microcarpa* (A. Rich.) Engl.	5	4.40 ± 1.40	187	C
	Lannea welwitschii (Hiern) Engl.	1	3	45	C

Appendix A (*Continued*)

Family	Species	No. of stumps (= no. of damaged plants)	No. of sprouts/ stump mean (±S.E.)	No. of undamaged plants	Growth form
Annonaceae	*Cleistopholis patens* (Benth.) Engl. & Diels.	3	2.00 ± 0.58	146	C
	Greenwayodendron suaveolens (Engl. & Diels) Verdc.	2	3.50 ± 0.50	73	C
	Monodora angolense Welw.	1	2	36	SC
	Monodora myristica (Gaertn.) Dunal	1	2	6	C
	Xylopia staudtii Engl.	1	9	4	
Apocynaceae	*Funtumia elastica* (Preuss) Stapf	93	3.90 ± 0.25	1860	C
	Tabernaemontana holstii K. Schum.	17	1.88 ± 0.25	413	SC
	Alstonia boonei De Wild.	1	3	86	C
	Rauvolfia vomitoria Afzel.	1	4	28	SC
Bignoniaceae	*Markhamia lutea* K. Schum.	5	4.80 ± 1.28	80	SC
	Kigelia africana (Lam.) Benth.	3	3.30 ± 1.33	89	SC
Burseraceae	*Canarium schweinfurthii* Engl.	2	2.50 ± 1.50	10	C
Capparidaceae	*Maerua duchesnei* (De Wild.) F. White	3	11.33 ± 1.20	244	SC
Chailletiaceae	*Tapura fischeri* (Engl.) Engl.	5	12.20 ± 3.29	230	SC
Clusiaceae	*Mammea africana* Sabine	4	1.75 ± 0.25	84	SC
	Symphonia globulifera L.f.	3	8.00 ± 1.15	2	C
Ebenaceae	*Diospyros abyssinica* (Hiern) F. White	9	10.56 ± 2.18	125	C
Eurphorbiaceae	*Thecacoris lucida* (Pax.) Hutch.	22	10.50 ± 1.46	1652	SC
	Argomuellera macrophylla Pax Laka	10	4.00 ± 0.47	739	Ss
	Acalypha ornata Hochst. ex A. Rich.	9	4.55 ± 1.07	2587	Ss
	Acalypha neptunica Muell. Arg.	8	6.75 ± 1.19	2691	Ss
	Alchornea laxiflora (Benth.) Pax & K. Hoffm.	7	12.29 ± 3.10	839	SC
	Drypetes ugandensis (Rendle) Hutch.	4	3.25 ± 0.63	100	SC
	Mallotus oppositifolius (Geisel.) Muell. Arg.	4	5.25 ± 1.11	295	SC
	Drypetes gerrardii Hutch. var. *grandifolia*	3	6.00 ± 1.00	87	C
	Euphorbia teke Schweinf. ex Pax	2	3.50 ± 0.50	44	SC
	Antidesma laciniatum Muell. Arg.	1	2	60	SC
	Antidesma venosum E. Mey. ex Tul.	1	5	45	SC
	Bridelia micrantha (Hochst) Baill.	1	2	44	SC
	Claoxylon hexandrum Muell. Arg.	1	5	7	SC
	Croton macrostachyus Hochst. ex Del.	1	4	84	SC
	Croton sylvaticus Hochst. ex Krauss.	1	4	65	SC
	Margaritaria discoidea (Baill.) Webster	1	5	63	SC
	Ricinodendron heudelotii (Baill.) Pierre ex Pax	1	1	17	C
Fabaceae	*Cynometra alexandri* C.H. Wright	46	8.35 ± 0.83	1031	C
	Senna spectabilis (DC.) Irwin & Barneby	29	5.28 ± 0.62	2140	C
	Tetrapleura tetraptera (Schumach & Thonn.) Taub	5	2.80 ± 0.49	53	C
	Albizia glaberrima (Schumach. & Thonn.) Benth.	4	3.00 ± 1.22	50	SC
	Mildbraediodendron excelsum Harms	3	1	20	C
	Dialium excelsum J. Louis ex Steyaert	2	3.00 ± 1.00	11	C
	Albizia grandibracteata Taub	1	3	24	C
	Albizia zygia (DC.) Macbr.	1	2	43	C
	Erythrophleum suaveolens (Guill. & Perr.) Brenan	1	4	45	C
	Piptadeniastrum africanum (Hook. F.) Brenan	1	1	15	C
Flacourtiaceae	*Caloncoba crepiniana* (De Wild. & Th. Dur.) Gilg	7	6.14 ± 1.03	119	SC
	Rawsonia lucida Harv. & Sond.	3	16.33 ± 1.76	245	SC
	Oncoba spinosa Forssk.	2	2.50 ± 0.50	31	SC
	Lindackeria mildbraedii De Wild.	1	1	10	SC
Icacinaceae	*Leptaulus daphanoides* Benth	1	3	3	SC
Loganiaceae	*Strychnos mitis* S. Moore	3	15.67 ± 7.88	104	C
Melastomataceae	*Memecylon jasmonoides* Gilg.	5	3.60 ± 0.87	44	SC
Meliaceae	*Khaya anthotheca* (Welw.) C.DC.	13	2.77 ± 0.50	489	C
	Trichilia drageana Sond.	12	2.17 ± 0.20	187	C
	Trichilia prieureana A. Juss	7	3.71 ± 0.68	293	SC
	Trichilia rubescens Oliv.	6	5.17 ± 0.75	400	SC
	Guerea cedrata (A. Chiev.) Pellegr.	5	2.40 ± 0.68	100	C
	Entandrophragma angolense (Welw.) C.DC.	2	1	39	C
	Entandrophragma utile (Dawe & Sprague) Sprague	2	2.00 ± 1.00	66	C
	Entandrophragma cylindricum (Sprague) Sprague.	1	2	78	C
	Lovoa schweinfurthii	1	3	3	
	Lovoa sywnnertonii Bak. F.	1	2	24	SC
	Lovoa trichilioides Harms	1	11	30	C
Moraceae	*Antiaris toxicaria* (Pers.) Lesch.	14	2.14 ± 0.47	262	C

Appendix A (*Continued*)

Family	Species	No. of stumps (= no. of damaged plants)	No. of sprouts/ stump mean (±S.E.)	No. of undamaged plants	Growth form
	Myrianthus holstii Engl.	6	4.17 ± 0.70	303	SC
	Morus mesozygium Stapf	5	5.80 ± 2.65	81	C
	Ficus exasperata Vahl	4	4.50 ± 1.04	61	C
	Trilepisium madagascariense DC.	3	4.00 ± 0.58	203	C
	Ficus asperifolia Miq.	2	2.50 ± 1.50	12	SC
	Ficus sur Forssk.	2	6.50 ± 1.50	57	C
	Ficus variifolia Warb.	1	1	3	C
Myrtaceae	*Pycnanthus angolensis* (Welw.) Warb.	1	3	35	C
Ochnaceae	*Ouratea densiflora* De Wild. & Th. Dur.	5	1.80 ± 0.20	258	SC
	Ochna holstii Oliv.	4	3.75 ± 0.48	24	SC
Oleaceae	*Linociera johnsoni* Baker	1	4	31	SC
Rhamnaceae	*Lasiodiscus mildbraedii* Engl.	81	8.02 ± 0.58	4548	SC
Rhizophoraceae	*Cassipourea congensis* DC.	1	5	17	SC
Rubiaceae	*Coffea canephora* Pierre ex Froehn	4	4.75 ± 1.55	100	SC
	Belonophora hypoglauca (Welw. ex Hiern) A. Chiev	2	1	149	SC
	Coffea euginoides S. Moore	1	2	39	SC
	Dictyandra arborescens Welw. ex Benth. & Hook. F.	1	7	40	SC
	Galiniera saxifraga Del.	1	2	4	SC
	Pavetta molundensis K. Krausse	1	3	49	SC
	Rothmannia whitfieldii (Lindl.) Dandy	1	1	10	SC
Rutaceae	*Teclea nobilis* Del.	8	7.25 ± 1.26	294	SC
	Zanthoxylum rubescens Hook. F.	2	2.00 ± 1.00	25	SC
	Balsamocitrus dawei Stapf.	1	4	15	SC
	Teclea grandifolia Engl.	1	4	10	SC
Sapindaceae	*Blighia unijugata* Bak.	7	2.43 ± 1.27	187	SC
	Aphania senegalensis (Juss. ex Pior.) Radlk	6	3.00 ± 0.44	27	SC
	Melanodiscus sp.	4	4.25 ± 0.85	113	SC
	Lychnodiscus cerospermus Radlk.	3	4.33 ± 1.20	251	SC
	Pancovia turbinata Radlk.	2	3.50 ± 1.50	36	SC
	Allophyllus dummeri Bak. F.	1	3	21	SC
	Zahna golungensis Hiern	1	2	38	SC
Sapotaceae	*Pouteria altissima* (A. Chiev.) Aubrev. & Pellegr.	14	8.43 ± 1.39	357	C
	Pachystela brevipes (Baker) Engl.	12	5.83 ± 1.48	36	SC
	Chrysophyllum albidum G. Don	10	4.90 ± 0.82	311	C
	Chrysophyllum perpulchrum Hutch. & Dalz	8	5.00 ± 1.07	162	C
	Bequaertiodendron oblanceolatum (S. Moore) Hiene & J.H. Hemsl	7	6.86 ± 1.64	133	SC
	Mimusops bagshawei S. Moore	4	4.50 ± 1.50	72	C
	Manilkara dawei (Stapf.) Chiov.	3	3.00 ± 0.58	33	C
	Bequeartiodendron natelense (Sond.) Hiene & J.H. Hemsl	1	2	24	SC
	Chrysophyllum muerense Engl.	1	8	23	C
Simaroubaceae	*Klainedoxa gabonensis* Pierre ex Engl.	5	7.40 ± 2.04	16	C
	Irvingia gabonensis (Aubry-Lecomte O'Rorke) Baill.	2	4.50 ± 0.50	4	C
Sterculiaceae	*Cola gigantea* A. Chev.	5	2.20 ± 0.58	106	C
Sterculiaceae	*Leptonychia mildbraedii* Engl.	3	5.00 ± 0.58	52	SC
	Sterculia dawei Sprague	1	1	11	C
Tiliaceae	*Desplatsia dawevrei* (De Wild. & T. Dur.) Burret	4	2.75 ± 0.25	79	SC
	Glyphaea brevis (Spreng.) Manachino	1	2	3	SC
Ulmaceae	*Celtis mildbraedii* Engl.	104	8.68 ± 0.55	2472	C
	Celtis zenkeri Engl.	7	14.14 ± 2.44	549	C
	Celtis gomphophylla Baker	1	5	216	C
Violaceae	*Rinorea ardiisiflora* (Welw. ex Oliv.) Kuntze.	25	8.24 ± 0.81	1666	SC
	Rinorea brachypetala (Turcz.) O. Ktze.	10	4.80 ± 0.66	802	SC
	Rinorea dentata (P. Beauv.) O. Ktze.	2	9.00 ± 3.00	26	SC
	Rinorea oblongifolia C. Marquand	1	8	298	SC

SC: sub-canopy species, <25 m tall; C: canopy species, >25 m tall; Ss: shrub.

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