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Tree gap dynamics and their influence on chimpanzee food tree regeneration in Kalinzu Forest Reserve, south-western Uganda

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Abstract

The chimpanzee (*Pan troglodytes schweinfurthii*) community in Kalinzu Forest Reserve, South Western Uganda is relatively stable and ranks third in the country with a total population density of 1.55 Km^{-2} compared to Kibale in western Uganda at 2.32 Km^{-2} and Bugoma at density 1.9 Km^{-2}. This is attributed to sustainable existence of chimpanzee food trees in Kalinzu Forest Reserve. Like many Ugandan forests, Kalinzu Forest Reserve displays a lot of gaps due to timber harvesting and other disturbances, yet it is not clear how the introduced tree gaps affect regeneration of chimpanzee food trees. The objective of this study was to document the effect of forest gap dynamics on regeneration of chimpanzee food trees in a natural rain forest in south-western Uganda. Results indicate occurrence of about 115 gaps, distributed throughout the habitat. The leading causes of forest gaps in both production and research zones of Kalinzu Forest Reserve were tree and/or branch falls (34.8%), charcoal burning (18.3%), gold mining (18.3%), selective logging (15.7%) and other causes (13%). In terms of size, gaps located in the production zone were medium (8.45 - 518.86 m^2); whereas gaps in the research zone were bigger (13.58 - 855.10 m^2). Tree regeneration in gaps was much higher than in the forest understory, an indication that gaps favour regeneration of chimpanzee food trees in this forest. Gaps in the production zone regenerated trees faster than their counterparts in the research zone. This study concludes that without human induced disturbance, regeneration of chimpanzee food tree species continues to occur in gaps created by natural causes. It is also clear that with regulated forest use, chimpanzees in Kalinzu may continue to have a sustainable food source.

Key words: Forest disturbance, *Pan troglodytes schweinfurthii,* selective logging, tree regeneration, understory

Introduction

Kalinzu Forest Reserve, located in southwestern Uganda, is a natural rainy forest and home to approximately 230 chimpanzees, owing to its endowment with tree species suitable for chimpanzee nutrition. Unfortunately, the trees are also used for timber, charcoal production; and for construction and the craft industry (Aine-omucunguzi, 2015). Unplanned deforestation due to tree harvesting is responsible for the occurrence of forest gaps, whose structure, distribution and effect on chimpanzee food tree regeneration are yet to be documented. This change in space and time in the pattern, frequency, size and successional processes of the food trees following gap formation is known as gap dynamics (Uriarte *et al*., 2005).

Gaps are defined as holes in the forest stand structure created by disturbances, natural or humanly induced (Sarkar and Devi, 2014). Gap formation induces significant changes in microclimate, for instance soil temperature and moisture, compared to forest understory, resulting into increased germination, establishment, growth and reproduction of many pioneer and secondary tree species (Babaasa *et al.*, 2004). However, the species diversity of non-pioneer and shade tolerant trees appears not to be properly maintained by the gaps (Uhl *et al*., 1992; Hubbell and Foster, 2002; Muller-Landau *et al*., 2002).

The pattern of plant growth and other ecological processes are thought to vary as a function of gap size, because light directly affects soil micro-climate in gaps such as solar radiation, moisture content, nutrient availability (Canham *et al*., 1990) and space, which is subsequently occupied by regenerating trees as a result of seedling recruitment from the buried or dispersed seed propagules (Irwin *et al*., 2010). Within the gaps, new trees grow up and a mature canopy is eventually attained (Vodde, 2004). Therefore, gaps are a critical phase in the forest cycle because what grows determines the future floristic forest stand.

Several studies have shown that the rate of closure of gaps depends on forest gap size (Babaasa *et al*., 2004; Muhanguzi *et a*l., 2005). Small gaps are most likely to close through lateral growth and branching; whereas large gaps close by in-growth of saplings (Babaasa *et al.*, 2004). This implies that regeneration also varies locally as a result of human induced disturbances, especially logging.

These human disturbances pose a great concern, particularly in terms of whether the formed gaps enhance regeneration of chimpanzee food trees within the forest, since studies conducted in Kalinzu Forest Reserve have documented that fruit trees contribute 75% of the total chimpanzees diet (Kagoro *et al.*, 2015).

Performance of seedlings and saplings of the trees whose fruits constitute the most chimpanzee diet has not been documented in the two zones that form the chimpanzee M-group ranging area. The objective of this study was to document forest gap dynamics and regeneration characteristics of chimpanzee food trees in forest gaps and understory, caused by natural and introduced gaps in the Kalinzu Forest Reserve in south western Uganda.

Materials and methods

Study area

This study was conducted in the Kalinzu Forest Reserve, located in south-western Uganda (0°17'S and 30°07'E) at an altitude of 700–1840 m above sea level (Howard, 1991; Hashimoto, 1995). It is classified as a medium altitude moist ever-green tropical rain forest (Howard, 1991), and covers approximately 137 Km^2, over an exceptional altitudinal range which combined with its geographical, climatic and geological diversity, and its location in the Albertine rift valley close to the Pleistocene forest refugia gives rise to the great variety of forest habitats.

The forest occupies a shallow saucer-shaped depression in the rift valley escarpment, with its floor at about 1463 m above sea level; from which rise a few grassy hills that reach up to 1845 m (Hashimoto, 1999). The rainfall pattern has two peaks in April and October. The June-July dry season is more severe than the one in January. Temperatures of Kalinzu Forest Reserve range from the minimum of 13 °C to the maximum of 28 °C.

Vegetation sampling and data analysis

This study was done in the production and research zones of Kalinzu Forest Reserve, with consideration of the ranging area of the chimpanzee M-group that is the research group on which the basis of ecotourism started. The production zone has a history of having been heavily mechanically pit-sawn for a long time, and has remained under human pressure; while the research zone has a history of minimal disturbance in the 1970s, and is currently not experiencing human disturbance and is a main ranging area for the chimpanzee M-ranging group since 1992 (Hashimoto, 1998; Fig. 1).

Ten parallel transects 5 Km long and 500 m wide, marked transect 100 to transect 1000 running east to west in all the five blocks of the upper research zone in which the M-group of the chimpanzees range (M-ranging group area); and the adjacent five blocks in the production zone of Kalinzu Forest Reserve, were purposively selected. Plots of 50 m x 50 m, separated by a distance of 500 m, were alternately set up along these transects and were used to collect data of the regeneration of

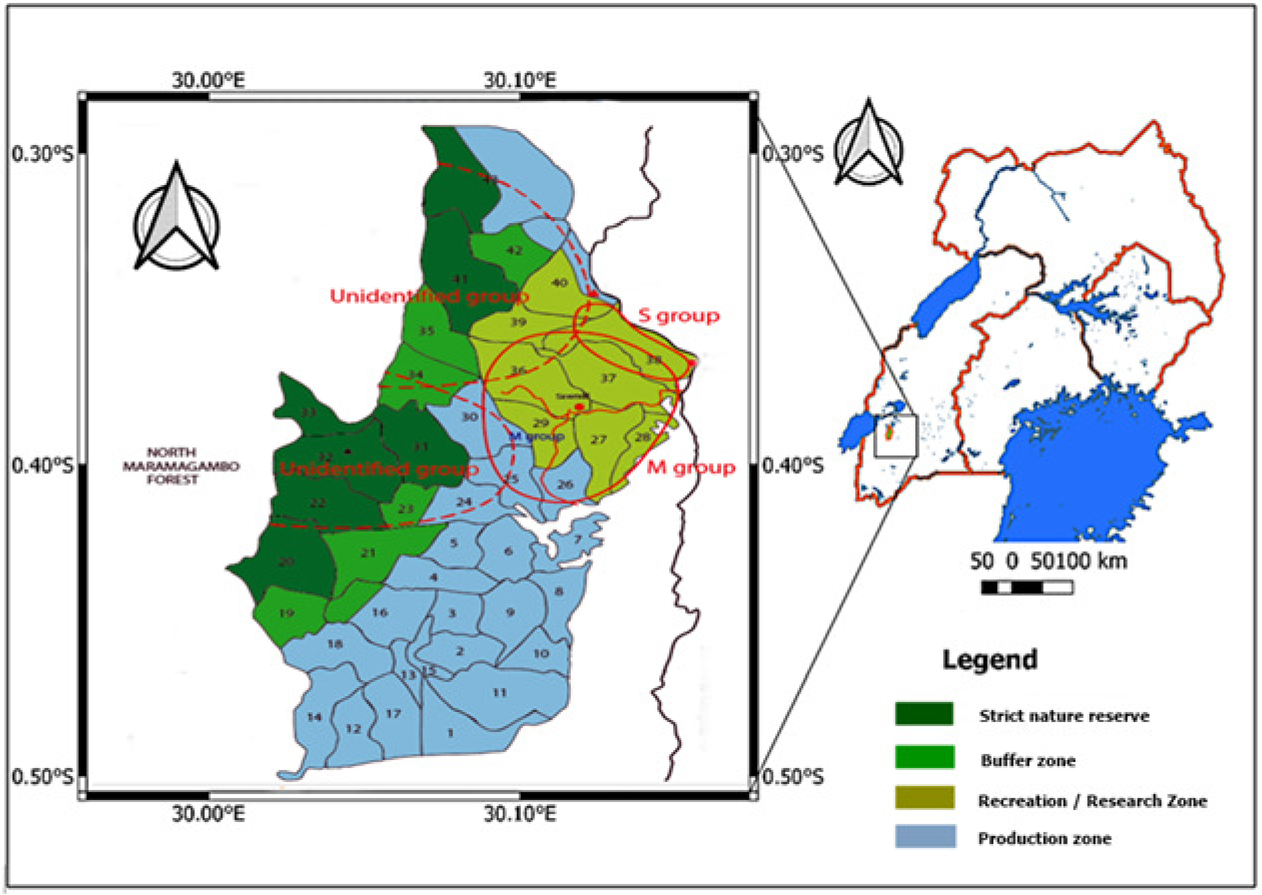

Figure 1. Location of Kalinzu Central Forest Reserve, in south-western Uganda. Map also shows management zones and different habituated chimpanzee groups.

Chimpanzee food trees. Each of these plots was divided into nested plots of 20 m x 20 m and 10 m x 10 m. In the 50 m x 50 m, large trees (diameter >10 cm) were identified, counted and the diameter at breast height (DBH) measured at 1.3 m above the ground using a DBH meter. The diameter of trees with buttress roots was measured at a point just above the buttresses. In the 20 m x 20 m plot, saplings (DBH 5-10 cm) were identified and counted. In the 10 m x 10 m plot, seedlings (DBH 0-4 cm) (Lejju, 2004) were identified and counted.

Forest regeneration was determined by establishing the number of seedlings, saplings and then adult trees by measuring their DBH using a DBH meter. To assess the influence of gaps on tree germination and establishment, the rate of regeneration was determined in both forest gaps and understory of both zones. Gap dynamics determined in this study included numbers, distribution and size; and the possible causes of these gaps. Gap size and position (hence distribution) were recorded using the Global Positioning System (GPS). The causes of gaps within study plots were identified by direct observation and through interviews with all the six National Forestry Authority staff officials at the Kalinzu forest station.

Data collected were analysed using Statistical Package for Social Sciences (SPSS) edition 20. Treatment means were separated using independent t-test at 5% level of significance to compare regeneration of chimpanzee food trees in gaps and understory of both production zone and research zone as well as general regeneration in the two forest zones.

Results

Gap dynamics

Estimates of gap dynamics in both production and research zones of Kalinzu Forest Reserve are presented in Table 1. More gaps per unit area were encountered in the production zone (heavily disturbed) (67 gaps) than in the research zone (undisturbed) (48 gaps). Values for the fraction of the total area of the forest covered by gaps showed that the production zone had a lower percentage (0.05%) than the research zone (0.06%). In terms of size, gaps in the research zone were larger than those in the production zone (Table 1). The gap size range for the research zone was larger (13.58-855.10 m^2) than that in production zone (8.45-518.86 m^2). Larger gaps were mainly located along or near river valleys, especially in the northern part of the study area (research zone) and along steep slopes in both the research zone and production zone (southern part).

The main causes of gaps in both production and research zones of Kalinzu Forest Reserve, based on reports from the study area, are as shown in Table 2. In the

Table 1. Gap dynamics in the Production Zone and Research Zone of Kalinzu Forest Reserve in South-western Uganda

Characteristic	Production zone	Research zone
Number of gaps per site	67.00	48.00
Number of gaps (ha^{-1})	0.27	0.19
Gap area as a percentage of the total area inventoried	0.05	0.06
Mean gap size (m^2)	95.19	151.37
Range gap size (m^2)	8.45-518.86	13.58-855.10

production zone, the highest mean gap size arose from selective logging (127.46 ± 33.83 m^2); followed by charcoal burning (55.15 ± 12.96 m^2), tree fall and branch fall (50.16 ± 3.86 m^2) and other causes (14.57 ± 3.33 m^2). In the research zone, gold mining contributed to the highest gap size (225.58 ± 33.50 m^2); followed by tree and branch fall (36.73 ± 7.63 m^2), charcoal burning (21.80 ± 11.32 m^2), selective logging (18.73 ± 12.98 m^2) and other causes (6.75 ± 3.55 m^2).

In terms of frequency, the most causative of forest gaps in the production zone were tree and branch fall (34.32%); followed by both charcoal burning and selective logging (22.39%), and other causes (16.42%). Gold mining was the least cause of gaping in this zone, having caused a total of 4.48%. In the research zone, most of the gaps were often caused by gold mining (37.50%), tree falls and branch falls (35.42%), charcoal burning (12.50%), other causes and selective logging were the least, with each contributing four (8.33%) and three gaps (6.25%) (Table 2).

Chimpanzee food tree regeneration

Gaps in the production zone showed a higher seedling and sapling density per m^2 than gaps in the research zone (Figures 2 and 3, respectively). In gaps of the production zone, *Celtis durandii* had the highest number of seedlings per m^2 (0.48±0.07), followed by *Musanga leo-ererrae* (0.44±0.07), *Craterispernum laurinum* (0.44±0.11), *Dryptes bipidensis* (0.34±0.07), *Beilschmeida ugandensis* (0.30±0.05), *Myrianthus holstii* (0.23±0.05), *Pseeudospondius microcapa* (0.12±0.03) and *Prunus africana* (0.09±0.05). Regeneration in gaps of production zone was poorest for *Ficus species* and *Uvariopsis congensis* (0.02±0.01). There was no regeneration for *Monodora myristica* and *Ficus vallis choudae* in gaps of production zone.

Table 2. Causes of gaps in the Kalinzu Forest Reserve in south-western Uganda

Gap cause	Production Zone			Research Zone		
	n	Gap size (Mean ± SE)	Gap size range (m^2)	n	Gap size (Mean ± SE)	Gap size range (m^2)
Charcoal burning	15	55.15 ± 12.96	69.85 - 191.30	6	21.80 ± 11.32	58.71 - 229.12
Gold mining	3	0	491.52	18	225.58 ± 33.50	101.09 -754.01
Selective logging	15	127.46 ± 33.83	108.43 - 518.86	3	18.73 ± 12.98	104.70 - 243.68
Tree / branch fall	23	50.16 ± 3.86	19.48 - 57.49	17	36.73 ± 7.63	15.47 - 121.74
Others*	11	14.57 ± 3.33	12.612 - 53.881	4	6.75 ±3.55	13.58 - 71.85

*Other causes included encroachment, firewood, construction materials, lightning and heavy debarking of trees

Results of the mean seedling density further showed that *Craterispernum laurinum* had the highest regeneration per m^2 (0.44±0.12) in gaps of research zone, followed by *Celtis durandii* (0.40±0.07), *Musanga leo-ererrae* (0.39±0.08), *Dryptes bipidensis* (0.36±0.10) and *Beilschmeida ugandensis* (0.24±0.06). Like in gaps of the production zone, *Ficus species* showed the poorest seedling regeneration in gaps. There was no seedling regeneration of *Ficus vallis choudae* and *Uvariopsis congensis* in gaps of research zone (Fig. 2). Results indicated that all chimpanzee food tree seedlings were found in gaps of both the production and research zones and were not significantly different, except for *Ficus vallis choudae,* which was absent in both zones. *Monodora myristica* was absent in gaps of production zone, but present in gaps of research zone. Generally, most chimpanzee food trees had a higher seedling density (per m^2) in gaps of production zone than in gaps of research zone, except for *Dryptes bipidensis, Monodora myristica* and *Prunus africana. Pseudospondius microcapa* and *Uvariopsis congensis* showed a significant difference in regeneration in gaps of production zone and research zone (P = 0.01 and 0.042, respectively; Fig. 2).

Results for saplings showed that the mean sapling density (per m^2) in gaps of the production zone was highest for *Craterispernum laurinum* (0.34±0.08), followed by *Celtis durandii* (0.31±0.05), *Musanga leo-ererrae* (0.17±0.04), *Dryptes bipidensis* (0.15±0.03), and *Beilschmeida ugandensis* (0.12±0.01). There was

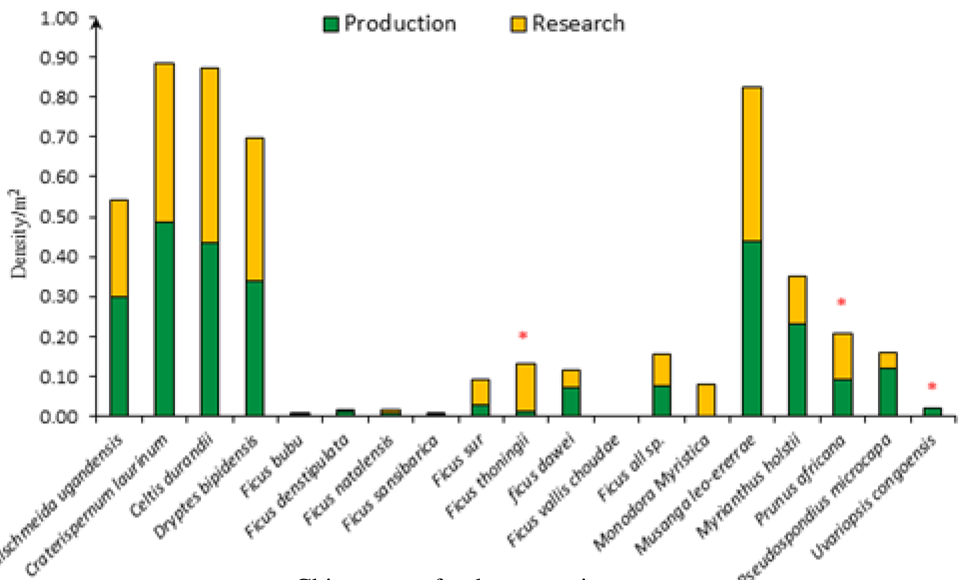

Figure 2. Mean seedling density per m^2 in forest gaps the two forest types of Kalinzu forest in south-western Uganda. * = Significant difference at P≤005.

no regeneration of *Ficus* species and *Uvariopsis congensis* in the production zone. However in gaps of the research zone, mean sapling density (per m^2) was highest for *Musanga leo-ererrae* (0.23±0.06), followed by *Beilschmeida ugandensis* (0.17±0.03), *Celtis durandii* (0.17±0.08), *Craterispernum laurinum* (0.12±0.04), *Dryptes bipidensis* (0.12±0.03). *Ficus species* and *Uvariopsis congensis* had no saplings in gaps within the research zone. *Monodora myristica* (0.01±0.01), *Prunus africana* (0.02±0.01), *Myrianthus holstii* (0.07± 0.03) had the least mean sapling number per m^2. Results further revealed that no significant difference between the saplings per m^2 in gaps of production zone and research zone, except for *Celtis durandii* (P = 0.020; Fig. 3).

Regeneration in the forest understory

The mean seedling density (per m^2) of chimpanzee food trees in the understory of the production zone for all the species was higher than that of the corresponding understory of research zone (Fig. 4). There was a significant difference in the regeneration of chimpanzee food trees in the understory of the production zone and that of research zone. However, there was no regeneration of *Ficus species* in the understory of both zones of Kalinzu CFR.

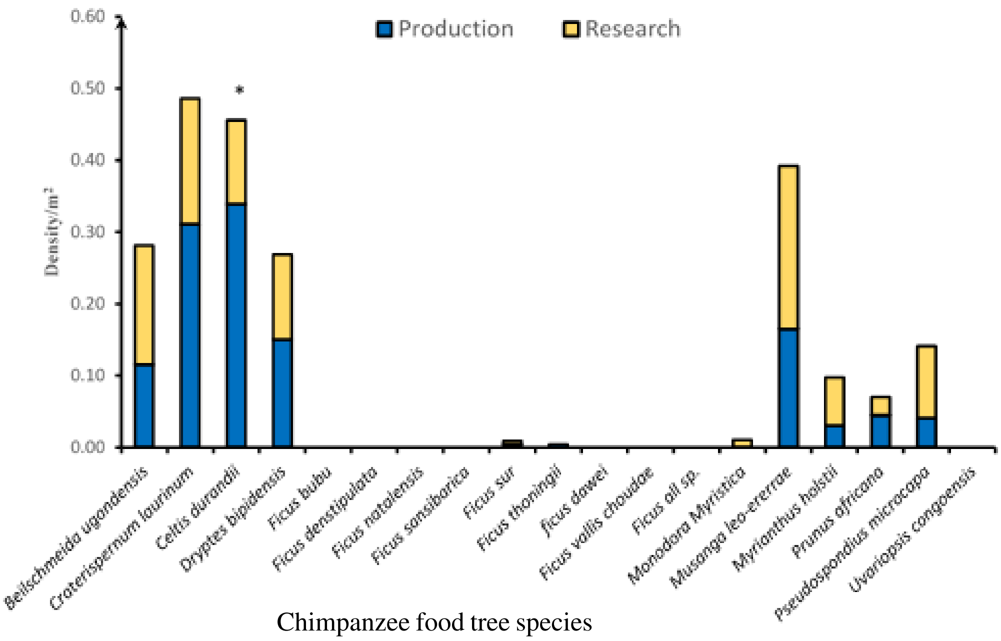

Figure 3. Mean sapling density of chimpanzee food trees in gaps of production and research zones of Kalinzu Forest Reserve in south-western Uganda. * = significant difference at $P \leq 0.05$.

There was no regeneration of *Uvariopsis congensis* in the understory of production zone; while *Monodora myristica* did not regenerate in the forest understory of the research zone (Fig. 4). In the understory of production zone, regeneration as established by mean seedling density per m^2 was highest in *Celtis durandii* (0.35±0.02), *Dryptes bipidensis* (0.32±0.02), *Musanga leo-ererrae* (0.24±0.02), *Myrianthus holstii* (0.22±0.02), *Prunus africana* (0.21±0.02) and *Beilschmeida ugandensis* (0.15±0.02) and *Pseudospondius microcapa* (0.08±0.02). In the understory of research zone, regeneration was highest for *Celtis durandii* and *Craterispernum laurinum* (0.09±0.02), *Prunus africana* (0.09±0.02), *Beilschmeida ugandensis* (0.08±0.02), *Dryptes bipidensis* (0.08±0.01), *Monodora myristica* and *Uvariopsis congensis* (0.02±0.01).

Results further showed that like mean seedling density per m^2, the mean sapling density (per m^2) in the understory of the production zone was generally higher than that in the understory of research zone, except for *Myrianthus holstii*, whose sapling density was higher in the understory of research zone than that in production zone understory (0.19±0.03 and 0.13±0.02, respectively). However, there was no significant difference between mean sapling density in the research zone and production zone understory (Fig. 5). Sapling density was nil for all *Ficus species*, *Monodora*

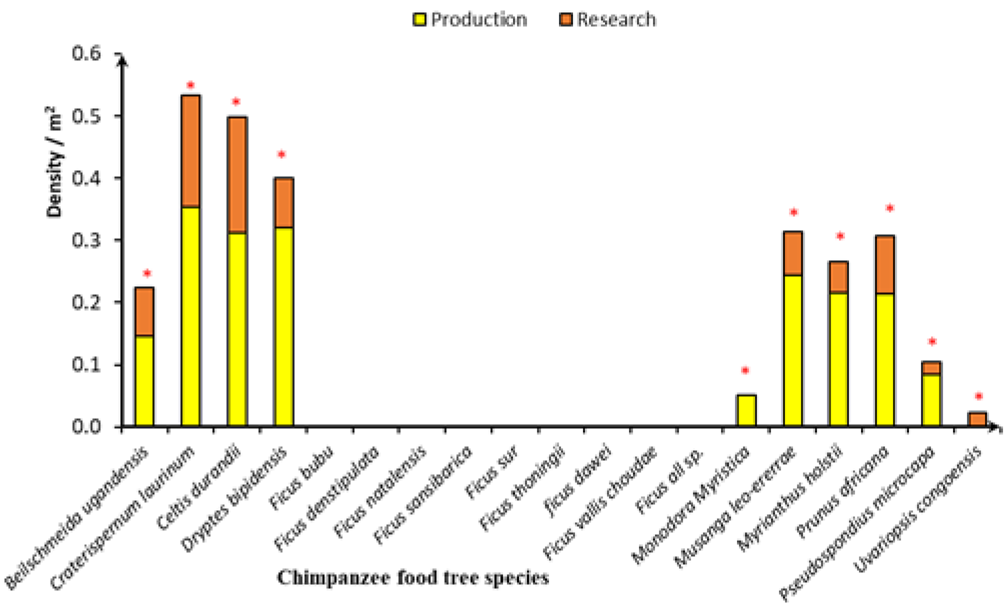

Figure 4. Mean seedling density per m^2 in research zone and production zone forest understory of Kalinzu Forest Reserve in south-western Uganda. * = significant difference at P≤0.05.

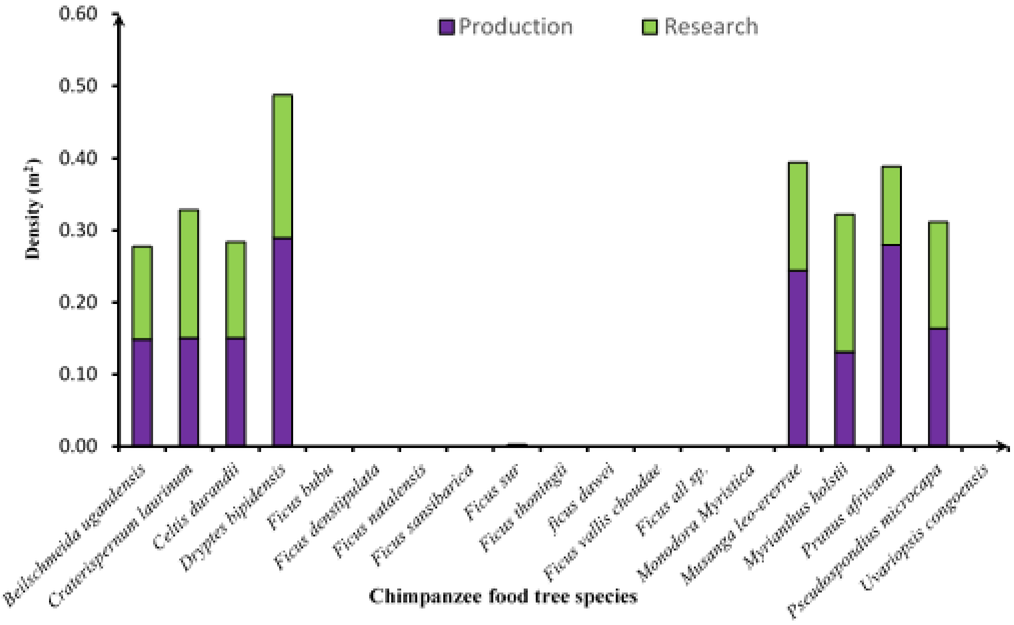

Figure 5. Mean sapling density per m^2 of chimpanzee food trees in forest understory of production and research zones of Kalinzu Forest Reserve in south-western Uganda.

myristica and *Uvariopsis congensis* in the understory of both production and research zones of the forest.

Regeneration of chimpanzee fruit trees

Results show interspecific variations in germination and establishment of various chimpanzee food tree species seedlings, within the gaps of the production and research zones, and understory of the Kalinzu Forest Reserve as presented in Table 3. Data for regeneration of chimpanzee food tree species in gaps and understory of both production and research zones of Kalinzu Forest Reserve are presented in Table 4. Mean seedling density per m^2 for all chimpanzee food tree species in the production zone were generally higher in forest gaps than in forest understory; except for *Prunus africana* and *Monodora myristica* which were significantly different ($P<0.001$). Results further showed a significant difference between the seedling density in gaps and forest understory of production zone in Kalinzu Forest Reserve for *Beischmeida ugandensis* ($P=0.02$), *Ficus sur* ($P=0.04$), *Ficus thoningii* ($P=0.05$), and other *Ficus species* ($P=0.00$), *Ficus dawei* ($P=0.02$) and *Musanga leo-errerae* ($P<0.001$).

In gaps of the production zone, there was no regeneration of *Ficus bubu*, *Ficus sansibarica*, *Ficus vallis choudae* and *Monodora myristica*. No *Uvariopsis congoensis* was observed to regenerate in the understory of the production zone.

Table 3. Interspecific variations in establishment (Mean ± SE seedling density per m²) in gaps and understory of both production and research zones Kalinzu forest in south-western Uganda

Species name	Gaps			Understory		
	Production	Research	P value	Production	Research	P value
Beilschmeida ugandensis	0.30±0.05	0.24±0.06	0.454	0.15±0.02	0.08±0.02	0.004
Celtis durandii	0.48±0.07	0.40±0.07	0.998	0.35±0.02	0.19±0.02	0
Craterispernum laurinum	0.44±0.11	0.44±0.12	0.398	0.31±0.02	0.19±0.02	0
Dryptes bipidensis	0.34±0.07	0.36±0.10	0.904	0.32±0.02	0.08±0.01	0
Ficus bubu	0.003±0.002	0.0020±0.002	0.84	0	0	-
Ficus denstipulata	0.01±0.01	0.003±0.002	0.181	0	0	-
Ficus natalensis	0.01±0.00	0.01±0.01	0.742	0	0	-
Ficus sansibarica	0.004±0.00	0.01±0.004	0.782	0	0	-
Ficus sur	0.03±0.01	0.06±0.02	0.12	0	0	-
Ficus thoningii	0.01±0.005	0.12±0.05	-	0	0	-
Ficus dawei	0.07±0.02	0.04±0.02	0.181	0	0	-
Ficus vallis choudae	0	0	-	0	0	-
Ficus all sp.	0.08±0.02	0.08±0.02	0.856	0	0	-
Monodora myristica	0	0.08±0.04	0.061	0.05±0.02	0	0.005
Musanga leo-ererrae	0.44±0.07	0.39±0.08	0.621	0.24±0.02	0.07±0.01	0
Myrianthus holstii	0.23±0.05	0.12±0.02	0.053	0.22±0.02	0.05±0.01	0
Prunus africana	0.09±0.05	0.11±0.02	0.533	0.21±0.02	0.09±0.02	0
Pseudospondius microcapa	0.12±0.03	0.04±0.01	0.014	0.08±0.02	0.02±0.01	0.002
Uvariopsis congoensis	0.02±0.01	0	0.042	0	0.02±0.01	0.122

Table 4. Regeneration (Mean +SE seedling density per m^2) in gaps and understory of production and research zones of Kalinzu forest in south-western Uganda

Species	Production zone		P value	M-ranging research zone		P value
	Gaps	Understory		Gaps	Understory	
Beilschmeida ugandensis	0.30 ± 0.05	0.15 ±0.02	0.02	0.24±0.06	0.08 ±0.02	0.02
Celtis durandii	0.44 ± 0.11	0.31 ± 0.02	0.39	0.44 ±0.12	0.19 ±0.02	0.09
Craterispernum laurinum	0.48 ± 0.07	0.35 ± 0.02	0.13	0.40 ±0.07	0.18 ±0.02	0.01
Dryptes bipidensis	0.34 ± 0.07	0.32 ± 0.021	0.82	0.36 ±0.10	0.08 ±0.01	0.03
Ficus bubu	0	0	-	0	0	-
Ficus denstipulata	0.01 ± 0.01	0	0.11	0	0	-
Ficus natalensis	0.01 ± 0.00	0	0.18	0.01 ±0.01	0	0.4
Ficus sansibarica	0	0	-	0.01 ±0.003	0	0.26
Ficus sur	0.03 ±0.01	0	0.04	0.06 ±0.02	0	0.01
Ficus thoningii	0.01 ± 0.00	0	0.05	0.12 ±0.05	0	0.04
Ficus dawei	0.07 ±0.02	0	0.02	0.04 ±0.02	0	0.03
Ficus vallis choudae	0	0	-	0	0	-
Ficus all sp.	0.08 ± 0.02	0	0	0.08 ±0.02	0	0.01
Monodora Myristica	0	0.05 ±0.02	0	0.08 ±0.04	0	0.14
Musanga leo-ererrae	0.44 ± 0.07	0.24 ± 0.02	0.03	0.39 ±0.08	0.07 ±0.01	0
Myrianthus holstii	0.23 ± 0.05	0.22 ±0.02	0.81	0.12 ± 0.02	0.05 ±0.01	0
Prunus africana	0.09 ± 0.02	0.21 ± 0.02	0	0.11 ± 0.03	0.09 ± 0.02	0.63
Pseudospondius microcapa	0.12 ± 0.03	0.08 ± 0.02	0.36	0.04 ±0.01	0.02 ± 0.01	0.24
Uvariopsis congoensis	0.02 ± 0.01	0	0.09	0	0.02 ±0.01	0.07

In the research zone, the seedling density (number per m^2) in gaps was higher than that in the forest understory (Table 4). However, seedling density in both gaps and understory was lower than that in the production zone gaps and understory. Results also showed that the mean seedling density was significantly different for *Beilschmeida ugandensis* (P=0.02), *Craterispernum laurinum* (P=0.01), *Dryptes bipidensis* (P=0.03), *Ficus natalensis* (P=0.04), *Ficus sur* (P=0.01), and other *Ficus species* (P=0.01), *Musanga leo-errerae* (P<0.001) and *Myrianthus holstii* (P<0.001). There was no regeneration of *Ficus bubu, Ficus denstipulata*, *Ficus vallis choudae* and *Uvariopsis congoensis* in gaps of research zone. All *Ficus species* did not regenerate in the forest understory as shown in Table 4.

Generally, for all chimpanzee food tree species, combined results showed no significant difference between mean seedling density (per m^2) in gaps of the production zone and research zone (P = 0.818) (Fig. 6). Results further showed that seedling density in the forest understory of the production zone was higher than that in the research zone. Thus, there was a significant difference between mean seedling density in forest understory of production zone and the research zone (P = 0.000). Similarly, there was no significant difference for mean sapling density in gaps of the research zone and production zone (P = 0.407). Results further indicated a significant difference between mean sapling density in the forest understory of the research and production zones of Kalinzu Forest Reserve (P= 0.005; Fig. 6).

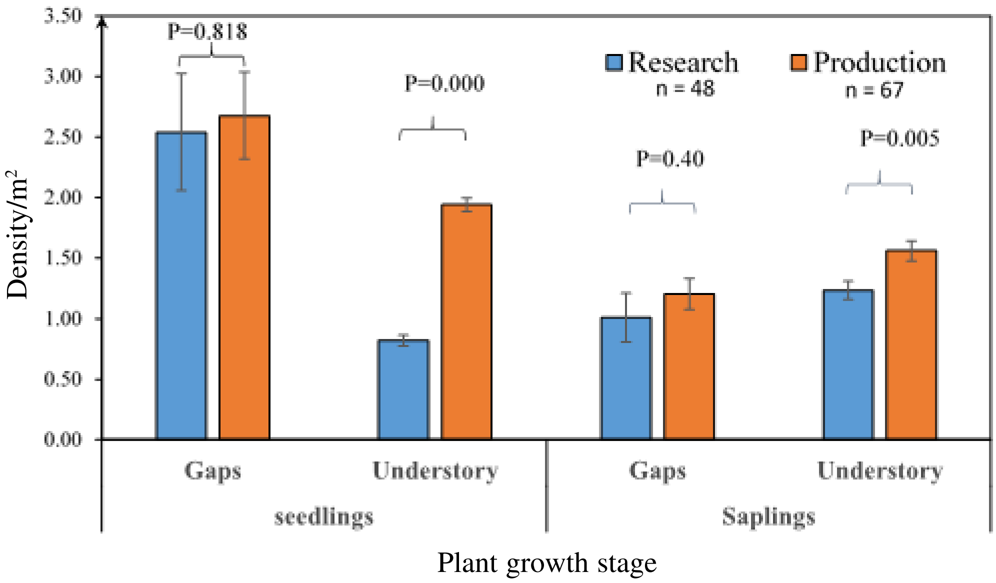

Figure 6. Mean density of all chimpanzee food tree seedlings and saplings in gaps and forest understory of both the production and research zones of Kalinzu forest in south-western Uganda.

Generally, irrespective of production or research zone, results showed that seedling density for all chimpanzee food tree species was greater than of the sapling density, which was also greater than the chimpanzee food adult tree species' density. Results further showed that for chimpanzee food tree species, seedling and sapling density was higher in the production zone than in the research zone. However, the adult chimpanzee food tree density in the research zone was greater than that in the production zone. Results also showed that most of the chimpanzee food trees were in seedling stage, followed by saplings and trailed by adult trees (Fig. 7).

Discussion

Gap dynamics

Most gaps in Kalinzu Forest Reserve were small (<1000 m^2), which was on the lower side compared to most logged medium altitude forests like Kibale and Bwindi (Babaasa, 2004). The gaps were mainly due to frequent tree and/or branch falls on steep slopes in some areas in those zones; and susceptibility of soils and selective logging which creates canopy gaps instead of extended gaps. The slight difference in gap characteristics of the two forest zones reflects the management history of Kalinzu Forest Reserve. There were more gaps in the production zone than the research zone in Kalinzu Forest Reserve because the production zone experienced a lot of human disturbance in the form of selective logging in the past compared to the research

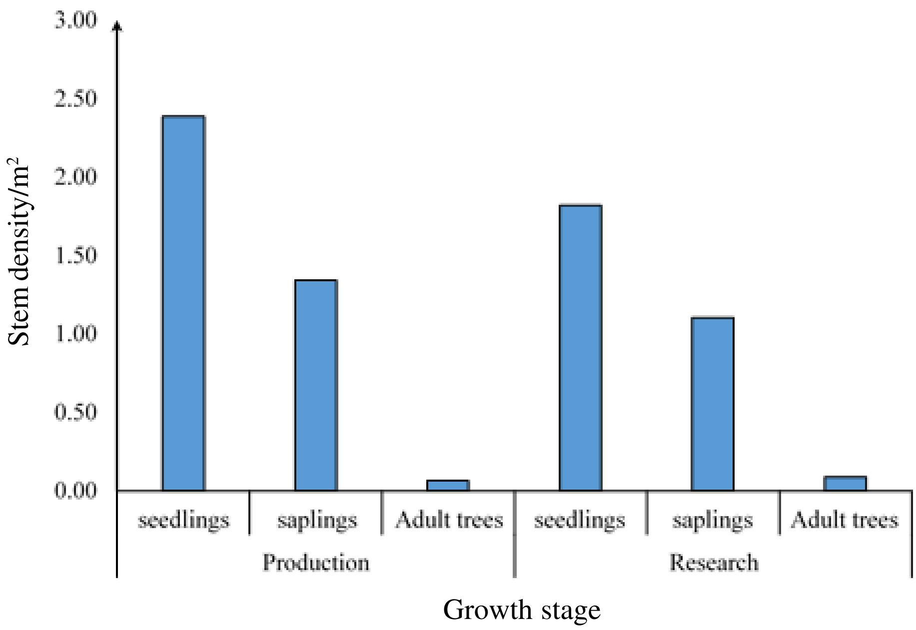

Figure 7. Population structure of chimpanzee food trees in production and research zones in Kalinzu forest in south-western Uganda.

zone where there has never been selective logging. However, gaps in the research zone were larger and covered a greater portion of forest area than those in the production zone. This is attributed to the causes of these gaps, with gaps in the production zone primarily caused by selective logging and other post logging activities; and gaps in the research zone primarily attributed to gold mining, which was observed to cause bigger gaps than any other cause.

From this study, the causes of forest gaps which affect regeneration of chimpanzee food trees in Kalinzu Forest Reserve were grouped into five categories as observed during the study. The number of gaps caused by each of the categorised factors differed in the two zones of the forest. Single or multiple tree and/or branch falls were observed to cause the most forest gaps. This is in agreement with studies by Kasenene (1991) that suggested that in a medium altitude forest, tree and or branch falls account for 74- 90% of tree mortality, and thus causing forest gaps. Tree and branch falls can be attributed to several factors, which can be sudden events or slow progressive die-back processes or a combination of both. In Kalinzu Forest Reserve, the severity of tree and/or branch fall was high; following a rainy session as observed during the study. External factors that accounted for this cause included topography, soil conditions and stand structure. Tree and branch falls were observed to be the leading cause of forest canopy gaps in the production zone; but were ranked as the second cause of forest canopy gaps in the research zone. Trees that surround canopy gaps are more likely to fall than other trees because creation of forest gaps may have destabilised or damaged surrounding trees, thus enhancing the chances that trees will fall in future. This mostly applies where there is creation of canopy gaps following human induced disturbance such as selective logging (Purtz and Milton, 1985).

Charcoal burning, a post logging activity was observed to be the second leading cause of forest gaps in Kalinzu Forest Reserve, especially in the production zone, where most selective logging for valuable timber species occurred. In the research zone, it was observed to be the second least cause of forest canopy gaps, being cited only in forest blocks of the research zone neighbouring the production.

Gold mining was ranked the third cause of forest gaps in M- ranging area of Kalinzu Forest Reserve, and the leading cause of forest gaps in the research zone, especially along river valleys (Table 2). However, it was ranked the least in the production zone; probably due to the difference in the gold deposits which are reportedly to be more concentrated in the research zone than in the production zone (Plumptre, 2002). The abundance of gold deposits, which appeared near the surface in the research zone, attracted many artisan miners around 1999. Their activities, especially along river valleys created a lot of depressions which led to creation of numerous canopy gaps. Furthermore, in this zone, gold mining created bigger gaps than any other cause.

Selective logging was ranked the second cause of forest canopy gaps in the production zone, but the least cause of forest gaps in the research zone of Kalinzu Forest Reserve. This was possibly attributed to the management history of the two zones. The history of selective logging in the production and research zones of Kalinzu Forest Reserve started in the 1970's with the Nkombe saw mill, a logging company, which mechanically logged in the production zone of Kalinzu Forest Reserve (Hashimoto, 1998). *Parinari excelsa* was mainly selectively harvested. Currently, creation of many gaps in the production zone is as a result of activities of the local people that have been logging some useful timber tree species such as *Funtumia africana* and *Carapa grandiflora*.

Other causes of forest gaps, other than those mentioned above included debarking of trees for medicinal purposes, lightning, firewood collection and collection of building materials from the forest and creation of illegal paths within the forest (Table 2). Heavy debarking of trees, like *Prunus africanana,* for medicinal purposes was also observed. The local communities neighbouring the forest harvested medicinal plants from the forest to treat both human and animal diseases (Aine-omucunguzi *et al*., 2009). Fire wood collection was observed in both zones of the forest. In addition, the neighbouring communities harvested building materials in form of tree species and grasses. The harvest of plant resources like *Prunus africana* and *Craterispernum laurinum* has opened up the forest canopy creating forest gaps

Regeneration of chimpanzee food trees

Generally, the density of all chimpanzee food tree species considered in the study was higher in gaps than in the inner forest understory (Fig. 6). This is probably because the gaps in the canopy allowed more light to reach the forest floor, creating a microclimate that favours germination of seeds of the species with a higher seedling density in gaps (Denslow, 1995; Aine-omucunguzi, 2015); unlike in the forest understory where the relatively closed canopy limits the amount of light reaching the forest floor; hence having fewer seeds are germinating. Studies have documented that light strongly influences regeneration of many tropical tree species (Muhanguzi *et al.,* 2002; Augspurger, 2019). According to Benítez-Malvido *et al.* (2003), secondary tree species usually germinate and establish in gaps. Taylor and Metcalfe (2007) noted that many tropical rainforest tree species that colonise open and disturbed habitats, often demand for light for germination and are inhibited by far-red light, which is often present in the understory.

On the other hand, seedlings of some shade tolerant species can establish in either gaps or forest understory (Forget, 1991). Slik *et al.* (2015) noted that many tropical tree species fall between the two limits (pioneer and shade tolerant), thus combining rapid regeneration following increased light availability due to canopy opening. The higher abundance of *Celtis durandii, Craterispernum laurinum, Musanga leo-errerae, Dryptes bipidensis* and *Beilschmeida ugandensis* in gaps of both the production and research zones of Kalinzu Forest Reserve than the forest understory, suggest that they are pioneer tree species with positively photoblastic seeds (Muhanguzi *et a l.*, 2005). *Celtis durandii* had the highest mean seedling density in gaps. These results agree with studies by Kwamba *et al.* (2015), which suggested that *Celtis durandii* was a pioneer tree species without seed dormancy, which makes it possess the highest colonising advantage within gaps. In addition, the higher composition of *Celtis durandii* compared to others, is possibly due to the many lighter seeds, which are easily dispersed as observed during the study. Furthermore, studies by Muhanguzi (2005) indicated that regeneration of *Musanga leo-errrerae*, *Craterispernum laurinum* was promoted by incident solar radiation and soil disturbance in gaps, as the case is with most gaps in production where charcoal burning had opened up the soil exposing many seeds to light and promoting their regeneration.

The absence of *Ficus species* in forest gaps and forest understory is possibly due to the fact that most *Ficus species* often start their life as epiphytes in branches of trees, and eventually send down their earial roots, which once they reach the ground floor provide extra nutrients (Katende, 2000). The occurrence of seedlings of pioneer species under forest understory is inconsistent with the findings of other studies (Chapman, 1997; Burslem and Whitmore, 2008;) which showed that seeds of early successional tree species usually germinate and establish in high light conditions such as clearings and big forest gaps. This can possibly be attributed to the quick closure of smaller canopy gaps that may be primarily caused by branch or tree falls by lateral growth of branches from the surrounding trees.

In both production and research zones of Kalinzu Forest Reserve, seedlings had the highest density; followed by saplings. This resulted into a characteristic inversed J-shaped distribution pattern for each forest type reflecting a regeneration population for most of the chimpanzee food tree species population.

The overall regeneration of all chimpanzee food trees in gaps and forest understory of the production zone was found to be higher in gaps and forest understory than in the research zone. This is because Kalinzu Forest Reserve has experienced a lot of disturbance in the past, with the production zone undergoing more selective logging than the research zone. Also, the study noted more post-logging activity such as charcoal burning, firewood collection and collection of construction materials carried out in the production zone than in the research zone. This influences habitat characteristics such as degree of canopy openness, the abundance and distribution of leaf litter and soil disturbance, which influence tree seedling emergence and establishment.

Pugnaire and Lozano (1997) also noted that soil disturbance influences germination and seedling emergence because it exposes some of the formerly buried seeds to incident light, which may induce some of them to germinate. Previous studies have also documented that soil disturbance improves aeration and soil temperature, thus enhancing seed germination and establishment (Muhanguzi *et al*., 2005).

Furthermore, the amount and distribution of leaf litter within the two forest zones was observed to be different with the research zone having a more forest stand structure was observed to have more leaf litter than that in the production zone. The presence of leaf litter of different depths creates many different microsites for plant establishment, by influencing microclimate such as light availability to the soil, soil temperature, soil aeration, moisture content, nutrient recycling, allelopathic interactions or the physical barrier created by leaves themselves (Augspurger, 2019). This can influence the pattern of chimpanzee food tree establishment and regeneration in both forest understory and gaps.

Studies have documented that in most tropical medium altitude rainforests, regeneration following logging can be affected by herbivory, especially by large mammals, which have been reported in some Ugandan tropical medium altitude rain forests like Kibale and Bwindi (Park and Chapman, 2019). The occurrence of large mammals was not noticed in Kalinzu Forest Reserve and this is possibly the reason for high regeneration of chimpanzee food trees in forest gaps.

Results of the present study revealed that forest gaps seem to favour germination and emergence of chimpanzee food tree species in Kalinzu Forest Reserve, compared to closed canopy habitats (Fig. 6). In addition, the emergence of seedlings of pioneer tree species, like *Celtis durandii, Musanga leo-errerae, Craterispernum laurinum, Beilschmeida ugandensis* and *Dryptes bipidensis*, occured in both forest gaps and forest understory, with gaps having a higher seedling density. Otherwise, many seeds of these species may still be dormant in the soil until such forest light conditions prevail.

Conclusion

This study has revealed that gaps in the M-ranging area of Kalinzu Forest Reserve are mainly small compared to other selectively logged forests like Bwindi and Kibale. The production zone of Kalinzu Forest Reserve had more gaps than the research zone. However, regeneration of chimpanzee food tree species was higher in the production zone than in the research zone, and gaps generally favoured regeneration than the forest understory in the two forest zones. Most chimpanzee food trees were regenerating in gaps and forest understory, implying that regeneration of these chimpanzee food tree species would continue naturally within the forest offering chimpanzees with a sustainable food supply. Of all the chimpanzee food tree species, *Ficus species* and *Uvariopsis congensis* had the least regeneration in both gaps and forest understory of the two forest zones in Kalinzu Forest Reserve. Thus, there is need to study and document the germination and seedling establishment requirements of these rarely regenerating species, since they have been documented to be valuable food sources for chimpanzees.

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