ROLE OF *ACACIA AND ERYTHRINA* TREES IN FOREST REGENERATION BY VERTEBRATE SEED DISPERSERS IN GRASSLANDS OF KIBALE NATIONAL PARK, UGANDA

BY

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DECLARATION

I Kiwanuka Majid, declare that, this thesis is my original work and has not been submitted for a degree in this or any other University/ institution of higher learning. The information is based on my field observations unless otherwise stated.

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DEDICATION

This work is dedicated to my dear parents who brought me to this world and gave me the gift of education and to my dear loving wife who gave me words of encouragement and children, who missed the love of a father while I was away in the field.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The central question of this study was ‘Do fire-resistant savanna trees such as *Acacia sieberiana* and *Erythrina abyssinica* and frugivorous vertebrates influence forest regeneration in the fire-prone grasslands of Kibale National Park, Uganda?’ In order to address the above question, seed rain and species richness and abundance of seedlings/saplings of forest trees were estimated both below and ten meters away from the crowns of these savanna trees for a period of six months (August 2007- March 2008). In addition, the rate of seed removal by seed predators in both areas below and ten meters away from crowns was estimated. Both areas, below and ten meters away from crowns, received seed rain and contained seedlings/saplings similar to those of the trees in the nearby forest. Species richness and abundance were significantly higher below than ten meters away from the crowns. However this was not the case with regards to seed rain. Although distance from the forest edge had a negative influence on species richness and abundance of seedlings/saplings, crown sizes of savanna trees had a positive influence. It was also found that there was no significant correlation between seed rain and distance from the forest edge. Furthermore the rate of seed removal by seed predators below and ten meters away from the crowns of savanna trees was not significantly different. The results from this study therefore demonstrate that forest regeneration is possible below the crowns of *Acacia sieberiana* and *Erythrina abyssinica* trees in the grasslands of Kibale National park.

Key words: frugivorous vertebrates, seed rain, savanna trees, seed dispersal, seed predation, forest regeneration.

CHAPTER 1

GENERAL INTRODUCTION

1.0: Background to the study

Globally forests cover just 15 percent of the land surface but are very important in that they harbour over 50% of the world’s species (Struhsaker 1987; Mackinnon 1997). There are other benefits associated with forests. For example forests contribute to the preservation of soil fertility, prevention of soil erosion, floods and landslides, and provision of reliable water supplies (Hamilton 1984; Struhsaker 1987). In addition, forests regulate regional and global climate (Hamilton 1984; Struhsaker 1987). Evapo-transpiration from forests contributes merely 2-3% of the global water cycle (Bruenig 1996), but can be enormously essential regionally. For instance, it contributes 48% of rainfall in Amazonia (Shukla *et al.*, 1990). Forests can also lessen the annual net addition of carbon to the atmosphere by carbon-fixing (Bruenig 1996). This consequently underscores the significance of conserving tropical forests for protection and conservation of biodiversity. One way of contributing to tropical forest conservation is through encouraging forest regeneration in habitats that were formerly forested, such as grassland patches enclosed by forests.

In Kibale National Park, grasslands constitute about 40 percent of the entire park (Kingston, 1967). Here, fire has been suggested as one of the most important factors inhibiting forest regeneration in grasslands (Kuper, 1996) and there is some evidence to show that in its absence, forests can recuperate though at a slow rate (Chapman and Chapman, 1997; Chapman *et al.*, 1999; Lwanga, 2003). For example, at Ngogo, Kibale National Park, Lwanga (2003) found that the proportion of stems of climax species in any given area was closely related to the period of fire exclusion. Given the significance of forests in the conservation of biodiversity and the improvement of atmospheric conditions, it is necessary to find ways of accelerating forest regeneration wherever there is room for expansion. In this respect, the fire prone grasslands in Kibale National Park are prime candidates for this exercise.

It would be desirable to restore forests in grasslands using indigenous species but the sheer diversity and lack of adequate knowledge about the biology of most tropical tree species is a major impediment to this undertaking (Hubbell and Foster 1992; Condit *et al.,* 1993). Evidence from Kanyawara some 12 km NE of Ngogo indicates that plantations of pines and cypress have the potential of fostering the establishment of indigenous forest trees (Kasenene, 2007; Zanne and Chapman 2001). Nevertheless, in poverty stricken countries like Uganda, this may not be a viable option because the cost of establishing and maintaining exotic plantations can be high (Kuper, 1996). Realizing the value of increasing the area under tree cover to wildlife, local and global environment, Uganda Wildlife Authority has made an effort to re-establish a tropical high forest in areas formerly deforested by agriculturalists (UWA, 2003). However, this is proving to be a very costly endeavor. For example it was estimated that establishing 12 km of new fire breaks and maintaining 44 km of the already existing ones would cost roughly $16,750 per year, while the annual recurrent costs would be $12,400 excluding salaries and benefits of the fire fighting crew and rangers (Struhsaker 2003). Apparently, even the small area planted so far is only possible because of external funding, without which the government may not be able to uphold.

If we are to augment forest cover using indigenous trees as biologists, we need to innovate inexpensive methods of accelerating forest formation in grasslands. These should attempt to emulate natural processes whereby the re-vegetation process is driven by natural seed dispersing agents. One such attempt is the provision of perches for birds (Uhl *et al.,* 1982;

McDonnell and Stiles 1983; McClanahan and Wolfe 1993). However, this approach may fail in Kibale grasslands because the frequent fires may raze the perches together with the young trees that might have established underneath the perches. Furthermore, the perches may fail to provide appropriate microclimate for the growth of tree seedlings that establish below them because of the inadequate shade (Duncan and Chapman 2002). For example, investigations carried out on recruitment below artificial perches in abandoned pasture in southern Costa Rica found no difference in recruitment below these perches relative to recruitment in nearby treeless areas (Holl 1998).

Thus, the interaction between vertebrate seed dispersers and fire resistant savanna trees as a possible means of reducing the cost of accelerating forest regeneration and expansion was investigated in grasslands of Kibale National Park. For this reason, frugivorous vertebrates such as birds, bats and primates were considered as potential seed dispersers in the Park. Furthermore, two species of savanna trees; *Acacia sieberiana* and *Erythrina abyssinica* were chosen as candidates for the study because they are easily identifiable, are the commonest medium to large savanna tree species scattered in the grasslands, they grow well emerging above the grass or shrub canopy without weeding or other human assistance and are fire resistant (Katende *et al.,* 1995). Using these species in the initial stages of re-aforestation programmes can curtail or eliminate the cost of fire fighting which can be extremely high when forest trees that are vulnerable to fire are established in grasslands at the initial stages as was done in the southern part of the Park (Kuper 1996, Struhsaker, 2003).

1.1: Role of vertebrate seed dispersers in forest regeneration in grasslands

Kibale National Park consists of an array of vertebrate frugivores including primates such as Chimpanzees (*Pan troglodytes*), Baboons (*Papio anubis*), grey-cheeked Mangabeys (*Lophocebus* (*Cercocebus*) *albigena johnstoni*), red-tailed monkeys (*Cercopithecus ascanius*) (Struhsaker 1987; Lambert 1988; Chapman 1995; Lambert 2001; Dominy and Duncan 2005); birds such as black and white casqued hornbills (*Bycanister subcylindricus*), great blue turaco (*Corythaeola cristata*), red-eye dove (*Streptopelia semitorquata*) (Obua 1992; Kalina 1988) and many species of megachiroptera bats (family *Pteropodidae*) (Duncan and Chapman 1999; Kityo, 2008). These have the potential to disperse forest tree seeds. However, very little is known about the contribution of these frugivores towards the dissemination of forest tree seeds into the grasslands.

In Kibale National Park, large bodied frugivores such as Chimpanzees have been observed to play a significant role in the dispersal of seeds to considerable distances away from parent trees (Terborgh 1988; Chapman 1995; Wrangham *et al.*, 1994). Primates vary in the mechanisms by which they process fruits. Whereas some are seed predators, most primates swallow and spit or defecate intact viable seeds, in varied patterns (Chapman, 1995; Lambert, 1997, 1988, 2001; Dominy and Duncan 2005). For example, at Kanyawara, Kibale National Park, red-tailed monkeys (*Cercopithecus ascanius*) were found to spit seeds of *Chrysophyllum*, whereas Chimpanzees (*Pan troglodytes*) swallowed and defecated them (Wrangham *et al.*, 1994; Chapman, 1995; Lambert, 1997, 1999, 2001).

Of the two mechanisms, seed spitting may be a poor means of dispersal for some large-seeded plant species (Dominy and Duncan 2005) most of which are adapted to clumped dispersion (Howe 1989); and may not be important in as far as long distance dispersal of forest trees seeds into the grassland is concerned. Rowell and Mitchell (1991) have presented evidence that shows that seeds swallowed and deposited in feaces occur any where from 200 to 1000 m from parent trees while seeds spat out only travel 30 to 50 m from parent trees.

Similarly, Lambert (1997) reports that, in a single day, Kibale monkeys can disperse the seeds of up to approximately 33,800 fruits per square kilometer and Chimpanzees up to 1,400 fruits per square kilometer-a large number of which may have ecological consequences for forest regeneration dynamics and tree species reproduction. Nevertheless, Chapman (1995) reports that seeds deposited in large numbers directly under trees in which primates repeatedly sleep may have a low probability of survival relative to seeds dispersed while animals are traveling or seeds deposited at sleeping sites used only once. Seeds deposited in large numbers are often subjected to disproportionately high (density-dependent) mortality that usually characterizes the environment beneath parent trees (Janzen 1970; Connell 1971). But Idani (1986), Wrangham *et al.*, (1994) contend that passage of fruit or seeds through the gut can increase germination success and decrease the time to germination for some species.

Consequently a decline in frugivorous primate populations may have deleterious consequences for forest regeneration and or tree species composition. Indeed, an evaluation of seedling recruitment in the protected Kibale forest interior with intact primate populations, compared with that in forest fragments where primate populations have been severely reduced, Chapman and Onderdonk (1998) found that fragments had lower seedling density and fewer species of seedlings than the forest. This suggests a cost of losing primates which extends beyond the loss of the animals themselves. Such findings support the idea that frugivores such as Chimpanzees, Baboons and Mangabeys coming from the forest interior (Olupot *et al*., 1994) have a role to play in the dispersal of forest tree seeds. This could be vital to the survival of fruiting trees in grasslands because the survival of fallen fruit does not appear to be sufficient to maintain populations of many tropical tree species (Howe 1984; Chapman *et al*., 1992) and perhaps very important as a means of reducing the cost of tree planting.

1.2: Role of savanna trees in forest regeneration in grasslands

In Kibale National Park, *Acacia sieberiana* and *Erythrina abyssinica* trees are the commonest medium to large savanna tree species scattered in the grasslands. These trees may offer food, perch or nesting sites to frugivores, and thus are expected to receive more zoochorous seed rain than treeless areas (Olupot *et al*., 1994). Seedling establishment may be better below these trees than nearby treeless areas probably because such trees have the potential of offering a better microclimate (Uhl *et al.*, 1982; Nepstad *et al.*, 1991; Vieira *et al.*, 1994) or lower temperatures and fuel load below savanna trees may protect seeds and seedlings from fire (Kuusipalo *et al.*, 1995).

Furthermore, given that many primates such as Chimpanzees and Baboons use one or a small number of sleeping sites repeatedly over a number of years (Anderson 1984, Chapman 1989b, Chapman *et al.*, 1999, Julliot 1997, Russo and Augspurger 2004); these sites are clearly areas of high seed deposition through defecation. Nevertheless, a similar pattern of repeated defecation may also exist for feeding trees or any other frequently used location (McConkey 2000, Schupp *et al.*, 2002). Therefore defecation at *Acacia sieberiana* and

Erythrina abyssinica trees used as nest sites or locations that offer food or protection from predators indicates that such locations may have a high seed rain or high species richness and abundance of seedlings/saplings of forest trees compared to treeless areas in the grassland. Consequently forest regeneration may proceed faster in such areas than in the treeless areas of the grassland.

However, other factors such as distance of tree from the nearest forest edge, crown size or presence of predators may influence the importance of savanna trees as regeneration nuclei. Distance from the forest edge alone may be particularly important when dispersers have to cross habitat boundaries and disperse seeds to a habitat different from that in which seeds were ingested (Oliveira and Ferrari 2000). Zanne and Chapman (2001) reported that dispersal of most species showed a distance effect. Small-seeded animal dispersed species tended to show a strong distance effect with decreasing density as distance increased. These results can likely be attributed to the fact that animal dispersers inhabiting forests will often not enter deforested areas because of the high energy cost of seed dispersing vertebrates moving out of the forest, the risk of seed dispersers encountering predators could be high or seed dispersing vertebrates would rather concentrate their foraging where food is more plentiful than move to places where food is scarce (Janzen *et al.*, 1976; Aide and Cavelier 1994; Da Silva *et al.*, 1996). Consequently, forest regeneration is likely to occur faster in areas close to the mature forest than areas far away.

Crown size of a tree on the other hand directly translates into the ground area covered by the tree crown. This may in one way or another influence dispersal of forest tree seeds into the grasslands. Trees with large crown sizes have the potential to accommodate large numbers of seed carrying vertebrates. Thus there is a high likelihood of such trees receiving a high amount of seed rain. However, their large shade may be more suitable for the establishment of seedlings/saplings of forest trees and as a result trees with large crown sizes may have a high species richness and abundance of seedlings/saplings of forest trees below them. Others have showed that regression of seedling/sapling density against the log area of forest fragments for animal dispersed species yields a positive slope, indicating lower recruitment in smaller fragments than larger ones (Cordeiro and Howe 1999). These results can likely be attributed to the principles of island biogeography (MacArthur and Wilson 1967) which state that species richness is proportional to the log of habitat area and inversely proportional to increasing distance.

In Kibale National Park, the four most abundant species of rodents include: *Hybomys univittatus, Hylomyscus stella, Mus minutoides* and *Praomys jacksoni* all of which are seed predators (Kasenene 1980; Lwanga 1994). A number of studies have documented the role of rodent seed predators on seed and seedling survival (Chapman 1989a; Forget and Milleron, 1991; Chapman, 1995; Chapman and Chapman, 1996; Russo and Augspurger 2004). For example, Chapman (1995) showed that the probability of disappearance of seeds of *Balanites wilsoniana* was only 10% whereas that of seeds of *Pseudospondias microcarpa* was 100%. Probably the site where seeds are deposited or their nature may influence the rate of seed removal by seed predators. For this matter, Chapman and Chapman (1996) reported that seeds of the Kibale tree species *Uvariopsis congensis* experienced 56% more seed predation when dispersed away versus directly under parent plants.

Other investigators working in Peru found that 99% of seeds of *Virola calophylla* that had been naturally dispersed by spider monkeys (*Ateles paniscus*) or had fallen below the parent tree were preyed upon within 15 months (Russo and Augspurger 2004). At Santa Rosa

National Park, Costa Rica, 98% of the seeds placed at experimental stations were removed or killed within 70 days (Chapman 1989a). Furthermore, Forget and Milleron (1991) investigated the fate of experimentally dispersed *Virola surinamensis* seeds on Barro Colorado Island, Panama and observed that rodents scatter-hoarded *V. surinamensis* seeds that they found both singly and in clumps.

Nevertheless, evidence suggests that seeds dispersed by frugivores and not found by rodents probably are capable of germination if conditions are right (Chapman 1995). Indeed, in a study focusing on forest succession in abandoned gardens near Kibale Forest, Chapman and Chapman (1999) found that large seeded forest tree species were among those establishing in the abandoned gardens in spite of the abundance of seed-eating rodents being nearly twice that found in the mature forest. Therefore, in Kibale seed removal by seed predators is likely to have little influence on seed or seedling survival and hence forest regeneration.

1.3: Statement of the problem

Loss of natural forests is one of the major ecological problems facing Uganda and other tropical countries today. It is estimated that at least 30% of Uganda’s land area used to be forest, but this has now been reduced to barely about 3% (Karlowski, 2006). It is imperative that this trend is stopped and probably reversed. If the trend is not checked, it is apparent that Uganda will lose much of its biodiversity, especially of animals and plants inhabiting these ecosystems. Therefore it is urgent that ways of restoring or accelerating forest regeneration are established wherever there is room.

1.4: Significance of the study

Restoration of deforested lands to their original high diversity forest is expensive in terms of human energy and money. Given that money for conservation is scarce, there is need for inexpensive afforestation methods that restore ecological complexity. One of the methods is by encouraging interplay between fire resistant savanna trees such as *Acacia sieberiana* and *Erythrina abyssinica*, frugivores such as birds or bats, primates and seed sources from forests. If the selected tree species are found to attract seed dispersing vertebrates and improve the microclimate then the results from this study will help forest managers in planning to reduce the cost of forest restoration and fire fighting.

1.5: Scope of the study

The study covered the aspect of primary seed dispersal to areas below crowns of *Acacia sieberiana* and *Erythrina abyssinica* trees involving frugivorous vertebrates such as birds and bats which was done by quantifying the amount of seed rain. Although the study in addition considered Chimpanzee and Baboon seed dispersal, focal observations of the above mentioned vertebrates were not taken but inference were made basing on fruit syndromes of mature forest trees to arrive at conclusions as to whether a particular seed, seedling/sapling was potentially dispersed by vertebrates. The study also quantified and compared the amount of seed rain, rate of seed removal by seed predators, species richness and abundance of seedlings/saplings below and ten meters way from the crowns of *Acacia sieberiana* and *Erythrina abyssinica* trees. Correlation between these parameters and distance from the forest edge or crown size were also investigated. Inspection of growth rates of seedlings/saplings and seed bank analyses were beyond the scope of this study.

CHAPTER 2

POTENTIAL ROLE OF SEED RAIN AND SEED PREDATORS ON SPECIES RICHNESS AND ABUNDANCE OF FOREST TREE SEEDLINGS/SAPLINGS BELOW *ACACIA* AND *ERYTHRINA* TREES IN NGOGO.

2.0: INTRODUCTION

Acacia sieberiana and *Erythrina abyssinica* trees may be used by vertebrate seed dispersers such as birds, bats and primates as nesting or perch sites, locations to watch out for predators or such trees may provide food for these animals (Debussche *et al*., 1982; Uhl *et al*., 1982; McDonnell and Stiles 1983; McDonnell, 1986; Campbell *et al*., 1990; Vieira *et al*., 1994; Duncan and Chapman 2002). Consequently there is a high likelihood of these savanna trees receiving a high amount of seed rain than treeless areas in the grassland. This has conservation implications in that *A. sieberiana* and *E. abyssinica* trees could be important as nuclei for regeneration of forests in grasslands.

Nevertheless, the number of seeds deposited under a tree may be influenced by other factors, such as crown size or distance from the forest edge (Guevara *et al*., 1992; Robinson and Handel 1993; Zanne and Chapman 2001). For instance, trees with larger crown sizes are expected to receive a higher amount of seed rain than trees with smaller crown sizes because larger crown sizes would probably accommodate large numbers of seed dispersers such as Chimpanzees or Baboons that live and move in large groups. However, as distance from the forest edge increases fewer and fewer frugivores are able to venture into the open grassland most likely because of the risk of encountering predators or scarcity of food resources in the grassland (Janzen *et al*., 1976; Aide and Cavelier 1994; Da Silva *et al*., 1996).

In addition, the amount of seed rain received below a tree may also be influenced by presence of seed predators such as rodents. Numerous studies cite the importance of rodent seed predation on the fate of dispersed seeds (Basuta 1979; DeSteven and Putz 1984; Nepstad *et al.*, 1991; Chapman and Chapman 1999). For example, DeSteven and Putz (1984) documented the influence of seed predation on the recruitment of a tropical canopy tree (*Dipteryx panamensis,* Leguminosae) on Barro Colorado Island, Panama. They found that predation of unprotected *D. panamensis* seeds and seedlings exceeded 90% and suggested that predation can be so extensive that even dispersed seeds have little chance of escape.

In Uganda, Shepherd and Chapman (1998) documented that clumps of seeds found in Chimpanzee defecations rarely remain at the site of deposition after a single day. Furthermore, Nepstad *et al.*, (1991), working in the Paragominas (Eastern Amazonia) found that tree seeds that escape predation must overcome additional obstacles during the seedling/sapling stage. For example in their study area, they found that leaf-cutter ants removed leaves, apical meristems and sometimes entire shoots of tree seedlings/saplings and appeared to prefer the seedlings/saplings of tree species over those of grasses and shrubs that dominated the area. Other studies have also shown that incidences of seed removal by seed predators decreases with increase of distance from underneath tree crowns where seeds are deposited (Janzen 1970; Connell, 1971). Furthermore, fire which is regular or sometimes intense, may also influence the survival of seeds to the seedling/sapling stage (Kuusipalo *et al.*, 1995). If all the above findings are true, then it is worth investigating the potential role of seed rain and seed predators on species richness and abundance of forest tree seedlings/saplings below the fire resistant *Acacia* and *Erythrina* trees in Ngogo, Kibale National Park.

2.1: Objectives of the study

The main objectives of this part of the study were:

1. To investigate whether *Acacia sieberiana* and *Erythrina abyssinica* trees have the potential to attract vertebrate seed dispersers from forests to grasslands.
2. To evaluate the potential of the two species of savanna trees as regeneration nuclei.

The specific objectives of this study were:

1. To examine whether seed dispersal actually occurs from forests to grasslands.
2. To identify the main agents involved in seed dispersal.
3. To determine whether there is a relationship between amount of seed rain and distance from the forest edge.
4. To examine the role of seed predators in forest regeneration in grasslands.

2.2: Hypotheses

The hypotheses tested in this study were:

1. Seed dispersal does not occur from forests to the adjacent grasslands.
2. Wind and not vertebrates is the main agent of seed dispersal into grasslands.
3. There is no relationship between amount of seed rain and distance from forest edge.
4. Seed predators have no role in forest regeneration in grasslands.

2.3: METHODS

2.3.1: Study area

This study was conducted in Kibale National Park, which is approximately 766 km^2 in size and is located in western Uganda, within the geographical boundaries: 0°13’- 0°41'N and 30°19'-30°-32'E (Lwanga, 2003). The Park is about 24 km east of the Rwenzori Mountains and it consists of mature, mid-altitude, moist, semi deciduous and evergreen forests (57%), colonizing forest (19%), grassland (15%), woodland (4%), and swamp (4%) (Zanne and Chapman 2001). Altitude within the Park ranges from 1500 m in the North to 990 m in the South. Mean annual rainfall is 1700 mm but typically March-May and September-November are the wettest months; while June-July and December–February are usually dry. Mean daily minimum temperature is 15.5 °C and mean daily maximum temperature is 23.7 °C (Struhsaker, 1997).

The study plots (Fig 1) were located at Ngogo study site in grasslands bordered by mature forest on all sides. The landscape of the area is of undulating hills separated by gently sloping valleys. A motorable track and fire break lines transect the grassland and the forest. These provide access to some parts of the grassland. Dominant grasses in the study area include: *Pennisetum purpureum*, *Imperata cylinderica* and *Cymbopogon afronardus*. *Acathus pubisens* is a common shrub that seems to replace *P.purpureum*, *I. cylinderica* and *C. afronardus* in the succession process. *Acacia sieberiana* and *Erythrina abyssinica* are the commonest medium to large savanna tree species scattered in the grasslands.

Species of birds such as hornbills, turacos and red eyed doves; primates such as Chimpanzees, Baboons and Mangabeys; and megachiroptera bats inhabit the forests.

However some of these occasionally visit the grassland and could be potential dispersers of forest tree seeds. The grassland area studied is among those occupied by people up to the early 1900s when humans were evacuated due to widespread rinderpest and sleeping sickness (Kingston, 1967).

2.3.2: Estimation of amount of seed rain

To examine whether seed dispersal actually occurs from the forest to the adjacent grassland, thirty isolated savanna trees (15 *Acacia sieberiana* and 15 *Erythrina abyssinica*) were used in this experiment. The amount of seed rain below and ten meters away from crowns of the selected savanna trees was estimated using seed traps. One seed trap was placed below and another was placed ten meters away from the edge of the crown of each of the 30 savanna trees. The location of the seed trap placed ten meters away from the edge of the crown was randomly selected from one of the four cardinal compass directions. The four major compass directions were written on pieces of paper which were folded and dropped on the ground. A field assistant was asked to pick one; this determined the location of the sample plot.

Seed traps consisted of square wooden frames, 50 cm by 50 cm; each board was about, 2.5 cm by 2.5 cm thick to which durable transparent plastic sheets were fixed. Trap area was approximately 0.25 m^2. The plastic sheets were fixed to the wooden frame using shoe tacks. To prevent the washing away of seeds by rain, the plastic sheet was pierced with small holes to facilitate drainage (McClanahan and Wolfe, 1993). Seed traps were elevated approximately 0.45 m above ground by 4 wooden stands.

2.3.3: Identification of the main seed dispersing agents

To determine the main agents of seed dispersal, seeds found in the seed traps were identified to species with the help of local expertise, counted and recorded. Seeds that could not be identified in the field were collected in labeled plastic bags and transported to the field station where they were germinated in sterilized soil (Slocum and Horvitz, 2000) and identified from seedlings. Where possible, the type of animal that deposited the seeds into the seed trap was identified (e.g. if the seed was found to have white uric acid it was identified as bird dispersed; Duncan and Chapman 1999).

In addition, fruits where collected from mature forest trees of the same species as the seedlings obtained in the germination trials. Characteristics such as colour, size, nature of pericarp and mesocarp (Whitmore, 1998; Obua, 1992; Kalina, 1988) were employed to determine the means of dispersal for each seed collected in the sample. Dispersal mechanisms were categorized as animal or non-animal (self or wind). Animal dispersed seeds were further subdivided into bird/bat or primate dispersed. Seeds of *A. sieberiana* or *E. abyssinica* trees, if fruiting, were not included in the analysis. The seed traps were inspected four times a week for 180 days.

2.3.4: Determination of distance of seed traps from the nearest forest edge

To determine whether there is a relationship between amount of seed rain and distance from the forest edge, the distance of each savanna tree from the nearest forest edge was determined using a Garmin GPS 12XL unit. The position of each savanna tree was determined by placing the antenna of the GPS against the bole of the tree and marking the position.

All way points were downloaded to a computer using geographic information systems (GIS) software (Arc View GIS v3.1, Environmental Systems Research Institute, Redlands, California) on to the most recent (2006) topographical map of the study site. To determine the nearest distance to the forest edge for each savanna tree sampled, eight distances were measured on the topographical map using Arc View software, following the major and secondary compass directions and the shortest of the distances for each tree was taken as the nearest distance to the forest edge. Since the seed traps were place below or close to the savanna trees under investigation, their distance from the forest edge was assumed to be equal to the distance of the corresponding savanna trees from the forest edge.

2.3.5: Estimation of the rate of seed removal by seed predators

To examine the role of seed predators in forest regeneration in grasslands, seed displacement experiments were setup in the same study plots used for the seed rain experiment. A small portion (approximately 0.25 m^2) of the ground below the crown of each savanna tree was cleared of vegetation and searched for any seeds. This procedure was repeated ten meters away from the edge of the crown. Altogether 60 plots were cleared both below the tree crowns and ten meters away in the nearby grassland.

Each plot received one clump of 20 seeds of *Uvariopsis congensis*. Seeds used in the experiment were collected from Chimpanzee dung in the forest. Clumping was used because primates, such as Baboons and Chimpanzees, the major dispersers of *Uvariopsis congensis* in Kibale, defecate seeds in clumps (Lambert, 1999). The position of the clump of seeds was marked using flagging tape placed approximately 2 m above the seeds. The code for each clump of seeds was inscribed on the flagging tape for easy recognition and inspection. The number of seeds; damaged by fungi, insects, rodents, completely removed by seed predators or germinated were recorded. However, complete seed removal from seed plots was the only form of seed predation considered for the analysis.

Uvariopsis congensis seeds were chosen for the experiment because they were readily available but also its seedlings were among the commonest forest interior species found in the grassland and both the seeds and seedlings are eaten by rodents (Kasenene, 1980).The seeds were also easy to identify, are fairly large (mean seed length = 1.445 ± 0.179 cm, mean seed width = 0.924 ± 0.107 cm) and therefore easy to count. The plots were visited 4 times a week for 126 days.

2.3.6: Data analysis

To examine the differences in seed rain below and ten meters away from crowns of savanna trees, differences in seed rain between the two species of savanna trees as well as differences in the rate of seed removal by predators below and ten meters away from crowns and between the two species of savanna trees; The Mann-Whitney U test was used. Linear regression analysis was used to determine the correlation between seed rain and distance from the forest edge. The rate of seed removal by seed predators was obtained by plotting graphs of number of seeds remaining in the seed plots against time in weeks.

2.4: RESULTS

2.4.1: Amount of seed rain

Very little seed rain was observed during the five months of the study. Fifty seeds were collected from ten out of 30 seed traps located below crowns of both *Acacia* and *Erythrina* trees; the mean being 1.67 ± 0.68, n = 30 compared to fifteen seeds collected from eight out of 30 seed traps located ten meters away in the nearby grassland; the mean being 0.50 ± 0.21, n = 30. Thus, there was no significant difference in amount of seed rain received below and ten meters away from crowns of savanna trees ($P > 0.05$; Table 1). For *Acacia* trees alone, the mean amount of seed rain below the crowns was 1.73 ± 0.84; n = 15 (were 15 is the number of seed traps) compared to 0.53 ± 0.35; n = 15, ten meters away from the crowns ($P > 0.05$). However, for *Erythrina* trees, the mean amount of seed rain below the crowns was 1.60 ± 1.08; n = 15 compared to 0.47 ± 0.24; n = 15, ten meters away from the crowns ($P > 0.05$). Generally there was no significant difference in seed rain when *Acacia* and *Erythrina* trees were compared ($P > 0.05$).

2.4.2: Main seed dispersing agents

Forty-two out of the 50 seeds collected from seed traps located below crowns of savanna trees belonged to seven species, the majority (68%, n= 42) of which were small-seeded bird/bat dispersed species (Table 1). In contrast, 13 out of the 15 seeds collected from seed traps located ten meters away in the nearby treeless areas belonged to four species, the majority (76.92%, n=13) of which were self or wind dispersed (Table 1). The only animal dispersed seed from a seed trap in the treeless area belonged to *Bridelia micrantha*, which probably could have been blown by strong winds into the seed trap from the nearby forest.

Two seeds (*Rubus sp* and *Acanthus sp*) found in seed traps are not from forest trees but scramblers and woody shrubs, respectively. Thus, these were excluded from the analysis.

Ten seeds, eight from seed traps located below crowns of savanna trees and two from seed traps located ten meters away in grass dominated areas were not identified because they did not germinate. Of the eight unidentified seeds collected below the crowns, five were associated with bird excrete indicating that they were bird dispersed. The mode of seed dispersal of the other three seeds was undetermined (Table 1). Similarly the mode of dispersal of the unidentified seeds collected from seed traps in the grass dominated areas was unknown. Seven (four below crowns and three in the nearby grassland area) out of 60 seed traps were damaged by Elephants; these were excluded from the analysis.

2.4.3: Correlation of amount of seed rain and distance from the forest edge

There was no significant correlation between amount of seed rain and distance from the forest edge ($r = -0.607$, $P > 0.05$). Distance alone accounted for almost 37% of the variation observed in the amount of seed rain among savanna trees located at different distances from the forest edge. Furthermore, the correlation between the amount of seed rain and distance from the forest edge for *Acacia* trees was not significant ($r = -0.124$, $P > 0.05$). Distance accounted for less than 2% of the variation observed in amount of seed rain among *Acacia* trees located at different distances from the forest edge. However, a similar correlation between the amount of seed rain and distance from the forest edge for *Erythrina* trees was negative and significant ($r = -0.570$, $P < 0.05$). Distance accounted for almost 33% of the variation observed in the amount of seed rain among *Erythrina* trees located at different distances from the forest edge.

2.4.4: Rate of seed removal by seed predators

On the whole, very little seed removal by seed predators was observed during the five months of the study. Of the seeds placed in locations below crowns of both savanna trees, about 0.2% (n = 600) were completely removed by seed predators as compared to 0.14% (n = 600) of the seeds placed in locations ten meters away from the crowns. Thus there was no significant difference in the rate of seed removal by seed predators below the crowns of savanna trees and ten meters away from such trees ($P > 0.05$; Fig 2). For *Acacia* trees alone, the mean number of seeds removed from locations below crowns by seed predators over the period of study was 4.0 ± 0.53; n = 300 compared to 2.67 ± 0.67; n = 300, ten meters away from the crowns ($P > 0.05$). However, for *Erythrina* trees the mean number of seeds removed from locations below crowns was 2.40 ± 0.43; n = 300 as compared to 3.13 ± 0.57; n = 300, ten meters away from the crowns ($P > 0.05$). Generally there was no significant difference in the rate of seed removal when *Acacia* and *Erythrina* trees were compared ($P > 0.05$; Fig 3).

2.5: DISCUSSION

2.5.1: Amount of seed rain

The lack of a significant difference in the results may be attributed to a number of factors: the number and size of seed traps used. In this experiment, only one seed trap with an area of 0.25 m^2 was used per tree and this could have greatly affected the results. Secondly, very few forest trees may have been in fruit during the period of study (seasonality). Results could also have been affected probably by the design or the short duration of the study. However, the prediction was that there would be a significant difference in amount of seed rain received below crowns of *Acacia* than *Erythrina* trees because most of the *Acacia* trees observed had larger crown sizes as compared to those of *Erythrina* trees and so were anticipated to attract a higher amount of seed rain given that larger crowns probably accommodate larger numbers of frugivores or provide more food resources, nesting or resting sites than trees with smaller crown sizes.

It was also expected that the amount of seed rain would be higher below crowns of trees than in the grass dominated areas. This is because seed carrying vertebrates are more likely to visit trees than treeless areas (Duncan and Chapman, 1999). At Kanyawara, about 10 km NW of Ngogo, Duncan and Chapman (1999) working in abandoned gardens, used between one and five seed traps per tree and reported higher seed rains below than away from crowns of trees. Although not significant, the trend in my results suggests that dispersal actually occurs from the forest to the adjacent grassland, *Acacia* and *Erythrina* trees have the potential to attract vertebrate seed dispersers and such trees could be important as nuclei for regeneration of forests in grasslands.

Although other methods for establishing tropical forests in savannas have been suggested, for example, use of exotic soft wood plantations (Kasenene, 2007; Zanne and Chapman 2001) and outright plantation of forest trees (UWA/FACE Project, see Struhsaker, 2003), they may be constrained by a number of factors ranging from the high cost of establishing and maintaining of plantations, controlling fire, and choosing the appropriate species for each site. Therefore, it may be cheaper and more ecologically sound to encourage the establishment of *Acacia sieberiana* and *Erythrina abyssinica* trees in grasslands and let natural regeneration reforest the area. Because these trees are naturally resistant to fire, there will be little or no need to fight fire. Furthermore, the trees will encourage the dissemination of forest tree seeds into the area through the attraction of animal seed dispersers, and a wide variety of seed species, some of which will be suited to the local conditions will be brought in. However, as Lwanga (2003) noted, for this approach to be successful, seed sources and seed dispersers such as birds/bats and primates must be in the vicinity of the grassland concerned.

2.5.2: Main seed dispersing agents

Most of the seeds collected from seed traps located in the grass dominated areas were either self or wind dispersed. In contrast, the majority of the seeds collected from seed traps located below crowns of *Acacia* and *Erythrina* trees were small-seeded bird/bat dispersed species.

It therefore appears that bird/bat seed dispersal play an important role in the initial stage of forest regeneration in grasslands and that birds/bats are the main seed dispersing agents to *Acacia* and *Erythrina* trees although the role of primates such as Chimpanzees or Baboons in the dispersal process was underestimated. This observation underscores the importance of *Acacia sieberiana* and *Erythrina abyssinica* trees in forest regeneration and where applicable, reforestation programs should mimic this natural process to achieve maximum species diversity at a low cost.

2.5.3: Correlation of amount of seed rain and distance from the forest edge

The lack of a significant correlation between amount of seed rain and distance from the forest edge in the results obtained for all savanna trees combined and for *Acacia* trees alone was most likely due to the nature of the terrain. This made it difficult to sample a large number of trees because most of them were far in the grassland and not easily accessible on foot. Most *Acacia* trees tended to appear close to one another while *Erythrina* trees were fairly scattered within the grassland and a lot of difficulty was met sampling them as compared to the *Acacia* trees. Therefore most of the trees in the sample were those close to the fire break system or motorable tracks. Such trees are usually avoided by most frugivores (Duncan and Chapman 1999).

However, the prediction was that there would be a significant negative correlation between amount of seed rain and distance from the forest edge. Janzen *et al.*, (1976); Aide and Cavelier (1994) observed a negative relationship between seed rain and distance from forest edge. They explained that there could be a high energy cost of seed dispersing vertebrates moving out of the forest, the risk of seed dispersers encountering predators could be high or seed dispersing vertebrates would rather concentrate their foraging where food is more plentiful than move to places where food is scarce. This situation is likely to result into a higher number of forest tree seeds being deposited closer to the forest edge than away. Such an observation has conservation implications in that forest regeneration is likely to progress from close to the forest edge into the grassland (Myster and Pickett 1992).

2.5.4: Rate of seed removal by seed predators

The lack of significance in the results could be attributed to a number of factors: probably the study area lacks seed predators such as rodents but it is also possible that grassland-dwelling rodents do not recognize forest tree seeds as food. Other factors could be seasonal variation or that the duration was not long enough for seed predators to come across the piles of the experimental seeds. It is also possible that there are plenty of food resources in terms of seeds for the predators such that a sufficient proportion escapes predation. For example, in a study focusing on forest succession in abandoned gardens near Kibale Forest, Chapman and Chapman (1999) found that large seeded forest tree species were among those establishing in the abandoned gardens in spite of the abundance of seed-eating rodents being nearly twice that found in the mature forest.

This finding further suggest that seed dispersers deposit more seeds than seed predators can consume hence, some seeds escape and contribute to forest regeneration. However, it must be emphasized that other factors beyond differences in seed predation may also influence forest regeneration. For example Chapman *et al* (1999) observed that most of the tree species in the Kibale Forest are not adapted to establishing in large openings. The influence of crown size on seedling survival and growth was beyond the scope of this study but is worth investigating.

2.6: CONCLUSIONS

- Seed dispersal actually occurs from forest to grasslands. Therefore *Acacia sieberiana* and *Erythrina abyssinica* trees could be important as nuclei for colonization of grasslands by forest. Although *Acacia sieberiana* trees could be more important than *Erythrina abyssinica* trees.
- Birds/bats are the main seed dispersing agents to *Acacia* and *Erythrina* trees although the role primates as seed dispersers was underestimated.
- Areas close to the forest edge are likely to receive a higher amount of seed rain than those further away in the grasslands. Therefore forest regeneration is expected to progress faster near the forest edge than away.
- Seed predators seem to a meager role in forest regeneration in grasslands.

2.7: RECOMMENDATIONS

- More *Acacia sieberiana* or *Erythrina abyssinica* trees should be encouraged to establish in the grasslands but close to the forest edge because such trees have the potential to attract seed dispersing vertebrates.
- More effort should be directed towards the conservation of forest dwelling frugivores especially primates because these animal have an important role as seed dispersers to grasslands. This could save on the cost of direct tree planting.

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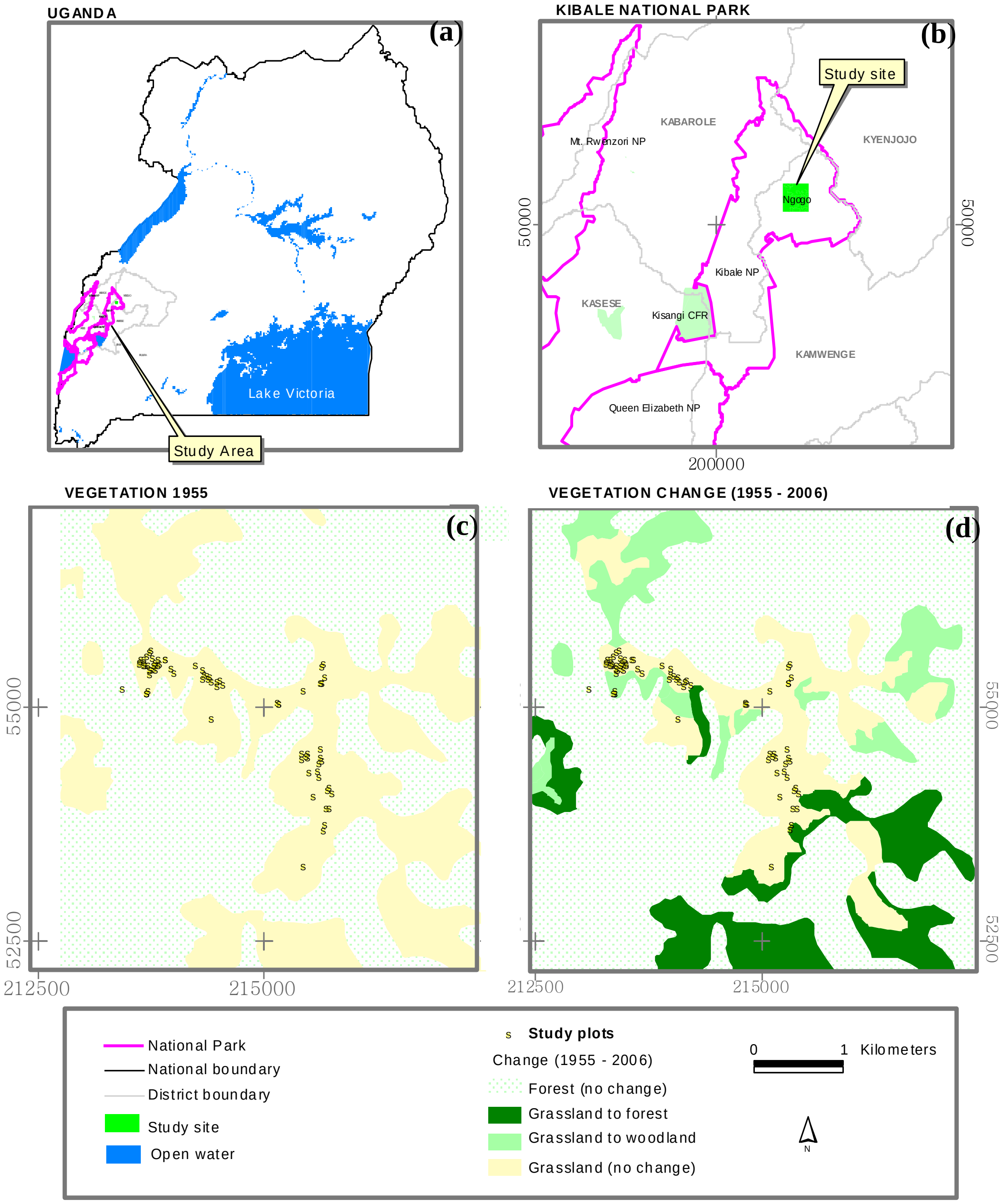

Figure 1: (a) Position of Kibale National Park in Uganda, **(b)** Position of Ngogo study area in Kibale National Park, **(c)** Location of the study plots on the map of the study area showing the vegetation change of 1955 and **(d)** Location of the study plots on the map of the study area showing the vegetation change of 1955 to 2006.

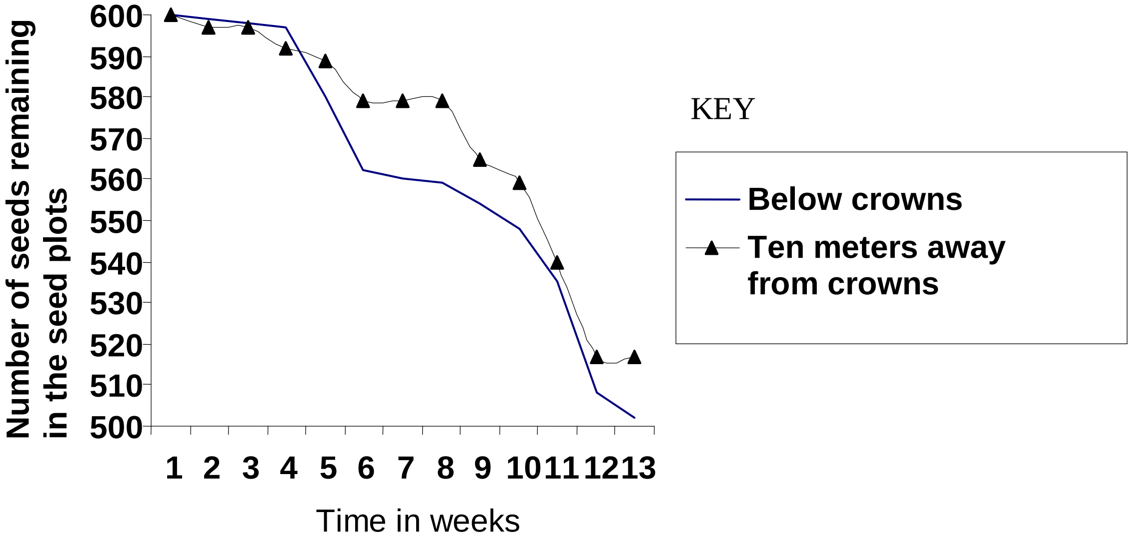

Figure 2: Comparing the rate of seed removal by seed predators below crowns of savanna trees and ten meters away from crowns in the nearby grassland.

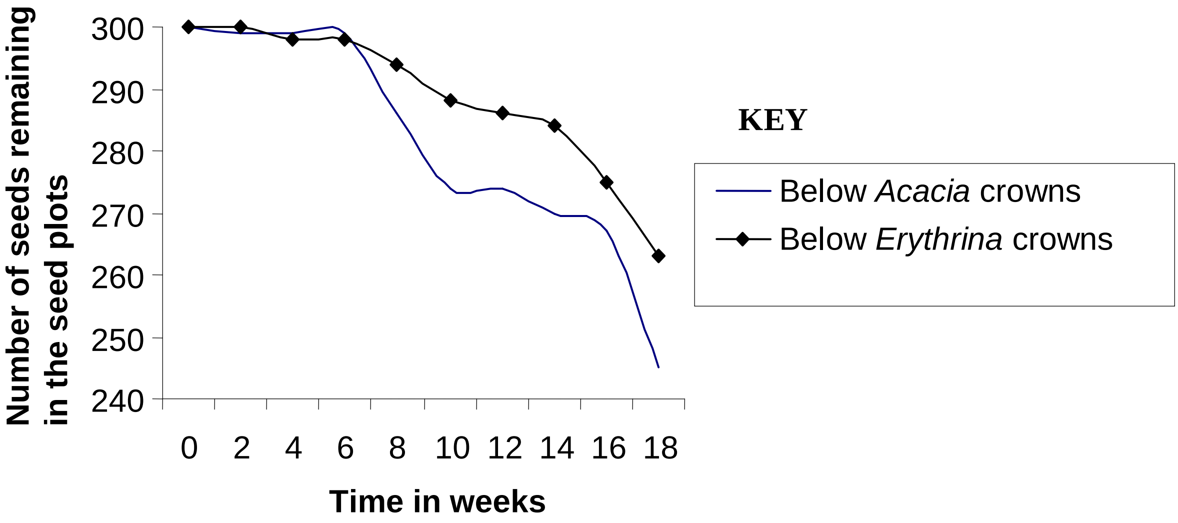

Figure 3: Comparing the rate of seed removal by seed predators below crowns of *Acacia* and *Erythrina* trees

Table 1: Total number of seeds found within seed traps below and ten meters away from crowns of savanna trees, showing plant species and potential disperser.

	Below crowns		Ten meters away from crowns		
Plant species	Seeds	Disperser	Plant species	Seeds	Disperser
Albizia grandibracteata	15	Wind	*Albizia grandibracteata*	9	wind
Harrisonia abyssinica	5	unidentified	*Pterygota mildibraedii*	1	wind
Techlea nobilis	5	primate	*Bridelia micrantha*	1	bird
Diospyros abyssinica	7	bird	*Acanthus sp**	2	explosive
Celtis durandii	5	bird	Unknown	2	unknown
Rauvolfia oxyphylla	2	bird			
*Rubus sp**	3	bird			
unidentified	5	bird			
unidentified	3	unknown			
Grand total	50			15	

* Not tree seeds

CHAPTER 3

SPECIES RICHNESS AND ABUNDANCE OF SEEDLINGS/SAPLINGS BELOW AND TEN METERS AWAY FROM CROWNS OF *ACACIA* AND *ERYTHRINA* TREES IN NGOGO.

3.0: INTRODUCTION

Dispersal of seeds of forest trees to grasslands by frugivorous vertebrates can facilitate forest regeneration, particularly when dispersed seeds meet the right condition required for seedling/sapling establishment. However, reforestation of grasslands is extremely difficult due to compact and nutrient-deficient soil, hydrologic instability, grass competition and allelopathy and large variation in surface temperatures of the soil (Soerianegara 1980; Ohta 1992; Parrotta 1993). Natural succession processes may also be prevented by the frequent fires, which, together with other conditions listed above, destroy plant propagules and seedlings (Kuusipalo *et al*., 1995). Therefore reforestation of grasslands to their original vegetation seems feasible only if environmental conditions are improved. An important option for reforestation programmes is to encourage the establishment of savanna trees such as *Acacia sieberiana* and *Erythrina abyssinica* in grasslands.

Kibale National Park consists of grassland patches surrounded by forest on all sides. These grasslands are dotted with savanna trees such as *Acacia sieberiana* and *Erythrina abyssinica*. An interesting phenomenon that has been observed is the rapid spontaneous emergence of seedlings/saplings under the crowns of *A. sieberiana* and *E. abyssinica* trees. It is likely that most of these plants must have been dispersed to areas below the crowns of these savanna trees from the nearby forest. A few propagules were of forest tree species potentially dispersed by wind but most of them were potentially dispersed by birds, bats or primates.

This therefore suggests that *Acacia sieberiana* and *Erythrina abyssinica* trees could promote the regeneration process by not only providing roosting habitats for seed-dispersing vertebrates but also a suitable microclimate for the establishment of seedlings/saplings of forest trees unable to germinate in the treeless areas of the grassland. Others have also shown that seedling recruitment is greater below than away from crowns of trees (Lugo *et al*. 1993; Parrotta, 1993; Kuusipalo *et al*., 1995; Toh *et al*., 1999).

The high proportion of evergreen woody vegetation observed below the crowns of savanna trees may reduce the risk of fire and grass competition and thus may enhance secondary succession towards natural forest (Kuusipalo *et al*., 1995). Areas below crowns of savanna trees will therefore have improved physical properties and nutrient status of the top soil, the microclimate below crowns of such trees favours woody undergrowth at the expense of more light-demanding grass-dominated vegetation because light, instead of nutrients, becomes a limiting factor for the under storey, and species richness and abundance of seedlings/saplings therefore increases due to the more heterogeneous and limited light availability created by the shade of these trees (Tilman 1982).

Treeless areas on the other hand are dominated by grasses such as *Pennisetum purpureum, Imperata cylinderica* and *Cymbopogon afronardus*. These grasses seem to be strong competitors for water, light and nutrients; they could also have allelopathic effects on tree seeds or seedlings/saplings (Ohta 1992). The grasses can take advantage of the alternation of moist and not too long and severe dry seasons. The regular fires may hamper any succession (Eussen and Wirjahardja 1973, Delacruz 1986). Natural regeneration of forest trees in treeless areas of the grassland may therefore be retarded or impossible.

Although areas below crowns of trees may have the potential to offer a more suitable microclimate for the establishment of seedlings/saplings, other factors such as distance of a tree from the nearest forest edge or crown size may have an influence on the species richness and abundance of seedlings/saplings (Janzen *et al*., 1976). Due to the fact that seed dispersing vertebrates tend to concentrate their foraging in the forest where food is more plentiful (Aide and Cavelier 1994), such a situation is likely to result in a higher number of forest tree seeds being deposited closer to the forest edge. Consequently species richness and abundance of seedlings/saplings of forest trees is expected to be negatively correlated with distance from the forest edge.

However, other than trees with large crown sizes having the potential to accommodate large numbers of seed carrying vertebrates, their large shade may be more suitable for the establishment of seedlings/saplings of forest trees consequently species richness and abundance of seedlings/saplings is expected to be positively correlated with crown size. The aim of this part of the study was therefore to show that forest regeneration is possible below the crowns of *Acacia sieberiana* and *Erythrina abyssinica* trees.

3.1: Definitions

Seedlings were defined as all young forest trees < 0.3 m high while saplings were defined as all young forest trees > 0.3 m to < 1.3 m high (Chapman and Chapman, 1996). Any young forest tree measuring >1.3 m high was categorized as a pole (Kasenene, 2007). However, in this study, young trees in the category of seedling or sapling size classes combined constituted as much as 87% (n = 11090) of all young forest trees enumerated while the proportion of the pole size class was merely 13% (n = 11090). Therefore for matters of simplicity, only seedlings/saplings will be mentioned throughout the text.

3.2: Objectives of the study

The main objectives of this part of the study were:

1. To investigate whether *A*cacia *sieberiana* and *Erythrina abyssinica* trees have the potential to offer a better microclimate for the establishment of seedlings/saplings of forest trees.
2. To evaluate the potential of *Acacia* and *Erythrina* trees as regeneration nuclei in the grasslands.

The specific objectives were to:

1. To examine whether there is a difference in species richness and abundance of seedlings/saplings below and ten meters away from the crowns of savanna trees.
2. To determine whether there is a relationship between species richness and abundance of seedlings/saplings and crown size of savanna trees
3. To determine whether there is a relationship between species richness and abundance of seedlings/saplings and distance from the forest edge.

3.3: Hypotheses

The hypotheses being tested in this study were:

1. There is no difference in species richness and abundance of seedlings/saplings below compared to ten meters away from crowns of savanna trees

2. There is no difference in species richness and abundance of seedlings/saplings between savanna trees with larger crown sizes and those with smaller ones.
3. Species richness and abundance of seedlings/saplings is not correlated to distance from the forest edge.

3.4: METHODS

3.4.1: Study area

For details on study area see Chapter 2.

3.4.2: Selection of savanna trees used in the study

From August 2007 to September 2007, 70 and 50 *Acacia sieberiana* and *Erythrina abyssinica* trees respectively were mapped, coded and tagged using flagging tape. The numbers followed the sequence in which the trees were encountered. Out of these, 35 *Acacia* and 30 *Erythrina* were randomly selected to the sample using computer generated random numbers. For each savanna tree species, crown size, diameter at breast height (dbh), and distance from the nearest forest edge were recorded.

3.4.3: Estimation of species richness and abundance of seedlings/saplings

All seedlings/saplings of forest woody trees and shrubs below the crowns of each savanna tree were enumerated; identifying each individual to species level following Hamilton (1981) and Katende *et al.*, (1995). Before counting the seedlings/saplings of forest trees, the area covered by the crown as projected vertically on to the ground surface for each savanna tree was divided into four pies. The edges of each pie were marked using flagging tape tied onto the ends of one-meter poles which were then driven into the ground. With the help of local field assistants and one researcher, vegetative characteristics such as leaf arrangement, margins, hairiness, smell of crushed leaves, colour of young leaves, presence or absence of thorns and presence or absence of sap; were used for species identification. Specimens of seedlings/saplings that could not be identified in the field were collected and transported to the field station for later identification. Height for seedlings/saplings was measured using measuring tape. This was done to assist in assessing the relative age of seedlings/saplings of forest trees. The sampling procedure was repeated in a plot with an area equal to the crown size of the corresponding tree located ten meters away from the edge of the crown into the treeless area of the grassland. The location of the plot was randomly selected from one of the four cardinal compass directions (See Chapter 2).

3.4.4: Estimation of crown sizes and diameter at breast height of savanna trees

Crown size of each savanna tree was estimated using the formula Πr^2, where ‘r’ is the mean of four distances measured along cardinal compass directions from the bole of the tree to the edge of the crown. Before measuring the four distances, a Magellan compass was used to determine the four major directions i.e. North-South and East-West while standing against the bole of the tree. With the help of a field assistant, a tape measure was stretched out from the bole of the tree along each direction to the edge of the crown to obtain the ‘r’ value. Diameter at breast height (Dbh) was measured at 1.3 m following Kennard (2002), and Zhuang and Corlett (1997). For trees that forked below 1.3 m, diameter was measured just below the point of branching (Lwanga, 2003). The aim of measuring diameter at breast height was to determine whether there is a correlation between Dbh and crown size of the savanna trees (Chapman *et al*., 1992).

3.4.5: Determination of distance of savanna trees from the nearest forest edge

For details on determination of distance of savanna trees from the forest edge see Chapter 2

3.4.6: Data analyses

To examine whether there are differences in species richness and abundance between areas below and ten meters away from crowns of each savanna trees as well as difference in species richness and abundance between areas on the ground covered by the crowns of *Acacia* and *Erythrina* trees, The Mann Whitney U test was used. The same test was also used to determine differences in crown sizes, Dbh and distances from forest edge of the two species of savanna trees. To determine whether there is a correlation between crown sizes and species richness and abundance of seedlings/saplings of forest trees as well as a correlation between distance from the forest edge and species richness and abundance, a linear regression analysis was used.

The seedlings/saplings encountered during this study were divided into various categories with respect to potential dispersing agents (i.e. animal, bird or bat, primate, Elephant and self or wind dispersed species). The Mann-Whitney U test and linear regression analyses were carried out on these.

3.5: RESULTS

3.5.1: Species richness and abundance of seedlings/saplings of forest trees

Species richness was significantly higher below crowns of savanna trees compared to ten meters away from the crowns ($P < 0.05$; Table 2, 3). Similarly, when the two savanna tree species were compared, species richness of seedlings/saplings was significantly higher below *Acacia* than *Erythrina* tree crowns ($P < 0.05$; Table 4).

Overall abundance of seedlings/saplings was significantly higher below savanna tree crowns than ten meters away from the crowns ($P < 0.05$; Table 2, 3). Comparison of the two species of savanna trees revealed that overall abundance of seedlings/saplings was significantly higher below crowns of *Acacia* than below crowns of *Erythrina* trees ($P < 0.05$; Table 4). When all seedlings/saplings of forest trees in the sample were assigned to their potential dispersal agents, abundance of seedlings/saplings potentially dispersed by animals was significantly higher below crowns of savanna trees than ten meters away ($P < 0.05$; Table 2, 3). Comparison of the two species of savanna trees revealed that abundance of seedlings/saplings potentially dispersed by animals was significantly higher below *Acacia* than below *Erythrina* tree crowns ($P < 0.05$; Table 4).

However, when seedlings/saplings potentially dispersed by animals were further categorized the abundance of seedlings/saplings potentially dispersed by birds/bats and primates were significantly higher below crowns of savanna trees than ten meters away from crowns ($P < 0.05$; Table 2, 3). Comparison of the two species of savanna trees revealed that abundance of seedlings/saplings potentially dispersed by birds/bats was significantly higher below crowns of *Acacia* than *Erythrina* trees ($P < 0.05$; Table 4) but this was not the case for seedlings/saplings potentially dispersed by primates ($P > 0.05$; Table 4). However, when analysis was restricted to seedlings/saplings potentially dispersed by Elephants, there was no significant difference in abundance of such seedlings/saplings below crowns of savanna trees and ten meters away from the crowns ($P > 0.05$; Table 2, 3). Comparison of the two species of savanna trees revealed that abundance of seedlings/saplings potentially dispersed by Elephants was significantly higher below crowns of *Acacia* than *Erythrina* tree crowns ($P < 0.05$; Table 4).

Lastly, it was observed that there was no significant difference in abundance of seedlings/saplings potentially dispersed by non-animal mechanisms (self/wind) below savanna tree crowns and ten meters away ($P > 0.05$; Table 2, 3). This was also true when the two species of savanna trees were compared ($P > 0.05$; Table 4).

3.5.2: Correlation between species richness and crown size

On the average, the *Acacia* trees sampled had larger crown sizes than *Erythrina* trees; mean crown size (m^2) for *Acacia* and *Erythrina* trees were 194.03 ± 16.53, n = 35 and 57.43 ± 5.65, n = 30; respectively. When this parameter was compared using The Mann-Whitney U test, there was a significant difference in crown sizes of *Acacia* and *Erythrina* tree species ($P < 0.05$). The correlation between species richness of seedlings/saplings and crown size of *Erythrina* trees was positive and significant ($P < 0.05$; Table 5). Crown size explained 47.3% of the variation in species richness. Nevertheless, this relationship was not significant for *Acacia* trees although it was positive ($P > 0.05$; Table 5).

3.5.3: Correlation between abundance and crown size

A strong positive relationship between crown size and the abundance of seedlings/saplings of forest trees below the crowns of *Acacia* trees did exist (P < 0.05; Table 5); crown size explained about 31% of the variation in abundance of seedlings/saplings of forest trees. Similarly for *Erythrina*, abundance of seedlings/saplings of forest trees was positively significantly correlated with crown size (P < 0.05; Table 5); crown size explained 35.5% of the variation in abundance of seedlings/saplings of forest trees. When seedlings/saplings of forest trees were categorized with respect to potential dispersing agents, a strong positive relationship between abundance of seedlings/saplings of forest trees predominantly dispersed by animals and crown size for both *Acacia* and *Erythrina* trees was detected (P < 0.05; Table 5); with crown size alone explaining 31.5% and 34.6% respectively of the variation in the abundance of seedlings/saplings of forest trees dispersed by animals.

Similarly, abundance of seedlings/saplings of tree species predominantly dispersed by birds or bats was positively correlated with tree crown sizes for both *Acacia* and *Erythrina* trees (P < 0.05; Table 5). However, for this dispersal category, the relationship was stronger for *Erythrina* than *Acacia* trees; 25% of the variation in the abundance of seedlings/saplings of forest trees was explained by crown size for *Erythrina* while this was merely 14% in the case of *Acacia* trees. A similar positive relationship was also found between crown size and the abundance of seedlings/saplings of forest trees predominantly dispersed by primates below the crowns of both *Acacia* and *Erythrina* trees (P < 0.05; Table 5). In this case, crown size explained even a bigger proportion (49.1%) of the variation in abundance of seedlings/saplings of forest trees dispersed by primates; but this accounted for only 15% in case of *Erythrina* trees.

Although Elephants do not use savanna trees as perches, field observations indicated that they use *Acacia* or *Erythrina* trees as food sources or objects for scratching their skins. In so doing they sometimes deposit seeds of forest trees when they defecate. From this study, there is evidence that suggests that crown size influenced the use of the savanna trees: the abundance of seedlings/saplings of forest trees that are predominantly dispersed by Elephants was significantly positively correlated with crown size for both *Acacia* and *Erythrina* ($P < 0.05$; Table 5). In both cases, crown size explained about 19% of the variation in the abundance of seedlings/saplings of forest trees predominantly dispersed by Elephants.

Lastly, a relatively weak and possibly spurious positive relationship between abundance of seedlings/saplings of wind or self dispersed forest trees and crown size was detected for *Erythrina* ($P < 0.05$; Table 5). Crown size alone explained 15.2% of the variation in the abundance of seedlings/saplings of forest trees. For *Acacia*, abundance of wind or self dispersed species was not related to crown size ($P > 0.05$; Table 5).

3.5.4: Correlation between species richness and distance from the forest edge

The mean distance in meters from the nearest forest edge to both *Acacia* and *Erythrina* trees was 171.71 ± 10.58, $n = 35$ and 161.07 ± 6.70, $n = 30$; respectively. However, there was no significant difference in mean distance from the forest edge to both *Acacia* and *Erythrina* ($P > 0.05$); suggesting that any differences in species richness and abundance of seedlings/saplings of forest trees below the crowns of the two species were not artifacts of distances from the nearest forest edge. A significant negative relationship between species richness and distance from the forest edge was detected for *Erythrina* ($P < 0.05$; Table 6). Distance alone explained about 56% of the variation in species richness of seedlings/saplings of forest trees below the crowns of *Erythrina* trees. For *Acacia* trees, this relationship was positive but not significant (P > 0.05; Table 6).

3.5.5: Correlation between abundance and distance from the forest edge

The relationship between overall abundance of seedlings/saplings of forest trees and distance from the forest edge was strongly negative for both *Acacia* and *Erythrina* trees (P < 0.05; Table 6), with distance alone explaining 40.1% and 37.4% respectively of the variation in the abundance of seedlings/saplings of forest trees below the crowns of *Acacia* and *Erythrina* trees.

When seedlings/saplings of forest trees were categorized with respect to potential dispersers, a strong negative relationship between abundance of seedlings/saplings of forest trees predominantly dispersed by animals and distance from forest edge for both *Acacia* and *Erythrina* trees was detected (P < 0.05; Table 6); with distance alone explaining 40.1% and 36.5% respectively of the variation in the abundance of seedlings/saplings of forest trees dispersed by animals. The relationship between distance from forest edge and abundance of seedlings/saplings of forest trees predominantly dispersed by birds or bats below the crowns of *Acacia* trees was negative but not significant (P > 0.05; Table 6). For *Erythrina*, this relationship was strong and negative (P < 0.05; Table 6). Distance alone explained 29.4% of the variation in abundance of seedlings/saplings of forest trees dispersed by bird or bat below the crowns of *Erythrina*.

However, when this analysis was restricted to seedlings/saplings predominantly dispersed by primates, a strong negative relationship between abundance of seedlings/saplings and distance of *Acacia* trees from forest edge was detected (P < 0.05; Table 6); with distance alone explaining 55.8% of the variation in the abundance of seedlings/saplings dispersed by primates below the crowns of *Acacia*. For *Erythrina*, the relationship was negative but weak for seedlings/saplings of forest trees predominantly dispersed by primates ($P > 0.05$; Table 6). When only seedlings/saplings of forest trees predominantly dispersed by Elephants were considered, a strong positive relationships between distance from forest edge and abundance of seedlings/saplings below crowns of both *Acacia* and *Erythrina* were established ($P < 0.05$; Table 6), with distance alone explaining 35.4% and 34.4% respectively of the variation in abundance of seedlings/saplings. Lastly, there was no relationship between distance from forest edge and abundance of wind or self dispersed seedlings/saplings below the crowns of both *Acacia* and *Erythrina* trees ($P > 0.05$; Table 6).

3.6: DISCUSSION

3.6.1: Species richness and abundance of seedlings/saplings

The observation that species richness and abundance of seedlings/saplings was higher below than ten meters away from crowns of *Acacia* and *Erythrina* trees, suggests that the microclimate below the crowns of savanna trees may be more suitable for seedling/sapling establishment than areas dominated by grasses (Nepstad *et al*., 1991; Guevara *et al*., 1992). However, suitable microclimate alone may not be sufficient to explain the exceptionally high species richness and abundance of seedlings/saplings below tree crowns. Indeed Lambert (2001) reported that there is marked decrease in fungal attack and survival increases when seeds are passed through the gut or cleaned by monkeys. For example, 83% of seeds spat out by red-tailed guenons germinated, while only 12% of unprocessed seeds survived to germinate. Of the processed seeds that germinated, 60% survived to seedling establishment, while only 5% of unprocessed seeds survived to seedling establishment. Unprocessed seeds were more likely to be attacked and damaged by seed predators than seeds with pulp removed; 20% of processed seeds were either damaged or removed, in contrast to 58% of fully fleshed seeds. Only 2% of the processed seeds were infected with fungus, in contrast to 96% of seeds with intact fruit pulp.

Further more, Lieberman *et al.*, (1977) were able to germinate seeds from 59 plant species collected from Baboon dung in Ghana. They found that ingestion improved germination success over that of fresh seeds in 3 of the 4 species tested. In studies carried out by Wrangham *et al.*, (1996), 15.5% of seeds collected from Chimpanzee dung germinated, whereas control seeds did not. Therefore, the passage of seeds through frugivore gut and their subsequent deposition in places where they are more likely to germinate and establish as future trees is beneficial to forest regeneration. This differential processing of seeds and deposition coupled with suitable microclimate may explain the higher species richness and abundance of seedlings/saplings of forest trees below the crowns than ten meters away (Vieira *et al.*, 1994; Uhl *et al.*, 1982; Kuusipalo *et al.*, 1995).

Nevertheless, the lack of a significant deference in abundance of primate dispersed seedlings/saplings below the crowns of *Acacia* and *Erythrina* trees was surprising. One would have expected more seedlings/saplings below the crowns of the larger *Acacia* trees than *Erythrina* because trees with larger crowns should provide better shade to protect seedlings/saplings from the hot sun or fire. In addition, *Acacia* trees also provide more sleeping sites for Baboons or food in form of ripe pods. However, during this study *Erythrina* trees were not in fruit, it is possible that Baboons could also eat *Erythrina* pods if they were present and that the crowns of *Erythrina* trees were large enough to accommodate Baboon troops, hence the lack of a difference in the abundance of seedlings/saplings dispersed by primates below the crowns of the two species of savanna trees.

There was however, one exception, the abundance of seedlings/saplings of forest trees predominantly dispersed by Elephants was not affected by presence of savanna trees. Lack of a significant difference in abundance of Elephant dispersed seedlings/saplings ten meters away and below crowns of savanna trees seems to suggest that Elephants do not have particular preference for savanna trees over treeless areas; but it may also reflect Elephants' short stay at any one location. It therefore appears that the two savanna tree species are most important in attracting birds, bats and primates (Chapter 2). Most primate species in Kibale are adapted to the forest habitat with Chimpanzees and Red tailed Monkeys occasionally venturing into grasslands (Lwanga 2003). However, the predominantly savanna species, Baboons (Wrangham *et al*., 1994), frequently visit the forest; these appear to be the most important dispersers of primate-dispersed forest tree species into grasslands. During this study, Baboons were encountered frequently in *Acacia* trees where they fed on ripe pods (Figure 5).

3.6.2: Correlation between species richness and abundance and crown size

Results from this study strongly suggest that savanna trees in grasslands can play a major role in forest regeneration and thus, could be used in reforestation programmes that aim at transforming grasslands into forests. The observation that species richness and abundance of seedlings/saplings of forest trees were strongly positively correlated to crown sizes of both savanna tree species; suggests that savanna trees with larger crown sizes have the potential to offer a better microclimate for the establishment of seedlings/saplings of forest trees.

Results from this study can be applied directly in this forest. In the southern part of the park, UWA/FACE project is attempting to reforest anthropogenic-induced grasslands that resulted from agricultural encroachment during the 1970s (Hamilton 1984) by direct planting of forest tree seedlings (Kuper 1996, UWA 2003). This is however proving to be very expensive; approximately five million US dollars were used in nine years to plant only 32 km^2 of forest (Struhsaker, 2003). It must be emphasized that the cost is higher than this, because the trees still need to be protected from fire. Another shortcoming with attempts to re-establish natural forests by planting tree seedlings is that only a few species can be used and these may not be representative of the natural forest, a situation is not good for conservation (Struhsaker, 2003). This study has clearly demonstrated that under *Acacia sieberiana* and *Erythrina abyssinica* trees forest regeneration can be possible and most especially under *Acacia sieberiana* trees. Furthermore, the forest that will establish under these savanna trees will be more diverse than that established by direct planting of seeds or seedlings. In addition, once the *Acacia* trees are established, the colonizing forest may need no manual fire protection because it will be naturally protected by the *Acacia sieberiana* trees.

Another pathway that has been suggested for re-establishing tropical forests in grasslands is by allowing indigenous trees establish under plantations of exotic tree species (Parrotta, 1993; Kuusipalo *et al.*, 1995). However, the high cost of establishing a plantation may render this approach impractical. Furthermore, in a place like Kibale with populations of large herbivores, establishment of a plantation may not be appropriate as it can lead to conflict between the plantation managers and wildlife. Therefore, in Kibale, and elsewhere where conditions favoring the natural pathway of forest regeneration, i.e. presence of a nearby forest to serve as source of seeds and seed dispersers (Lwanga, 2003) the cheapest and probably more ecologically sound way to establish a forest in a grassland is to foster the establishment of fire resistant trees and let seed dispersers facilitate the regeneration process.

3.6.3: Correlation between species richness and abundance and distance from forest edge

The observation that the relationship between species richness and distance from the forest edge was significant and negative for *Erythrina* while for *Acacia*, this relationship was positive but not significant was rather surprising. The most probable explanation for this observation was that most *Acacia* trees tended to appear close to the forest edge and to one another while *Erythrina* trees were fairly scattered within the grassland. Therefore this could have led to a false positive relationship between species richness and distance for *Acacia* trees. However, the prediction was that species richness should be negatively correlated with increase in distance away from the forest edge.

Others have observed that some of the forest dwelling vertebrate seed dispersers may avoid treeless areas of grasslands to reduce the risk of predation or concentrate their foraging in the forest where food is more abundant (Janzen *et al*., 1976). In this case, species richness and abundance of seedlings/saplings should be negatively correlated with distance from the forest edge. From a management viewpoint, this implies that, should the use fire resistant savanna trees be adopted in afforestation programs, it is necessary to encourage their establishment close to the forest edge, lest animal seed dispersers may not find them. To attract seed dispersers into the grassland interior, savanna trees that establish at relatively short distances to the forest edge will be more important in facilitating the movement of seed dispersers between neighbouring trees. In Mexico, Graham (2001) found that Kill-billed toucans moved more frequently between patches separated by low cost-distance values; suggesting that distance between neighboring trees has an influence on the movements of seed dispersers which in turn can influence the forest regeneration.

3.6.4: Variation in characteristics of savanna trees

The observation that the number of Elephant dispersed seedlings/saplings below crowns of *Acacia* was nearly three times that below *Erythrina* trees suggests that Elephants are probably more attracted to *Acacia* than *Erythrina* trees. It is well known that Elephants browse on *Acacia* trees (Chiyo, 2000; Cochrane 2001), probably Elephants visit trees to meet dietary requirements but the large crowns of *Acacia*s may also provide suitable shelters from the hot sun. As they rest, they deposit forest tree seeds. Some tree species such as *Balanites* are dispersed solely by Elephants (Ghiglieri *et al*., 1982; Chiyo, 2000; Cochrane 2001); therefore the presence of *Acacia* in grasslands may accelerate the colonization of grasslands by *Balanites*. However, it remains to be tested whether *Balanites* establishes better under the shade than in the open grassland; should this be the case, then dispersal in a suitable microclimate is an added advantage.

Nevertheless, the more than double the number of bird or bat dispersed seedlings/saplings of forest trees below *Acacia* than *Erythrina* crowns; suggest that the former species not only attract more seed dispersers but may provide a more suitable microclimate for the establishment of seedlings/saplings than the latter. *A. sieberiana* could be very effective in suppressing light-demanding grass and herb vegetation, mainly due to its dense crown, which also creates a moister and cooler microclimate, and abundant litter fall (Anon. 1983). It is evergreen even during a prolonged dry season in climatic conditions typical of humid tropics (Anon. 1983). *A. sieberiana* could also be a nitrogen-fixing legume; nitrogen-rich litter increases the amount of organic input into the soil maintaining its biological activity and improving the nutrient status (Sanchez & Miller 1986). Phosphorus uptake is efficient due to the symbiosis with compatible vesicular-arbuscular (VA) mycorrhizal fungi (Malloch et al. 1980). All in all, *A. sieberiana* seems to favour shade-tolerant, relatively nutrient and moisture demanding forest tree species at the expense of light-demanding herbs and grasses below its crown.

However, below crowns of *Erythrina* the light intensity is seemingly much higher than below crowns of *Acacia* trees. The poor shading and vigorous competition by grasses may also inhibit the germination and survival of the forest tree seedlings/saplings. Therefore successful establishment of *Acacia sieberiana* trees seem to be able to act as an initial step in the secondary succession of grasslands back to natural forests by allowing many indigenous forest tree species to colonize the sites within a relatively short period of time.

Acacia sieberiana could be a particularly more suitable species because it seems to turn the resource supply ratio into a more favourable one for woody perennial undergrowth: light becomes a more limiting resource than nitrogen, moisture and other soil resources. Grasses and herbs cannot take advantage from improved soil conditions due to their generally higher light demand compared to woody perennials which, in turn, can only establish on an improved soil (Tilman 1982). The more woody, evergreen undergrowth, the lesser susceptibility to fire damage (see Figure 4). This is a rule of thumb which has, for a long time, been appreciated by foresters and forest scientists working elsewhere in the tropics (Lugo et al. 1993; Parrotta 1993). *A. sieberiana* seems to provide an alternative which creates suitable conditions for an abundance of under storey trees. The Nitrogen-fixing species such as *Albizia lebbek* used by Parrotta (1993) in Costa Rica, or *Acacia sieberiana* in the present study, can have a dramatic effect on soil fertility through their production of decomposable, nutrient-rich litter and turnover of fine roots and nodules. In general, the comparisons between *Acacia sieberiana* and *Erythrina abyssinica* suggest that the former could be better at enhancing forest regeneration in grasslands.

Nevertheless, understanding of seed ecology, including dispersal characteristics and habitat requirements for germination and seedling development is of particular importance in forest restoration design. Many important tree species predominating Kibale forests have large seeds that require large bodied vertebrate dispersers and subsequently spread very slowly into areas where mother trees have completely disappeared. Therefore dispersal of primary forest species within the shelter of crowns of *Acacia sieberiana* trees could speed up the restoration process considerably.

3.7: CONCLUSIONS

- Based on the observation that species richness and abundance were higher below *Acacia sieberiana* and *Erythrina abyssinica* trees than in the nearby treeless areas, it implies that such trees have the potential to provide a better microclimate for the establishment of seedlings/saplings of forest trees.
- Savanna trees with large crown sizes and at short distance to the forest edge will be more important at enhancing the establishment of seedlings/saplings than such trees with smaller crown sizes and far away from the forest edge.

3.8: RECOMMENDATIONS

- More fire resistant savanna trees especially *Acacia sieberiana*, which were found to have high levels of species richness and abundance of seedlings/saplings below their crowns; should be encouraged to establish in all areas that require reforestation such as deforested lands. Furthermore, since they are fire resistant their establishment in the grassland will reduce the cost of fire fighting.
- It would be more suitable to encourage the establishment of such trees close to the forest and to one another so as to facilitate movements of vertebrate seed dispersers from the forests and from one tree to the next.

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Figure 4: Intact vegetation below the crown of an *Acacia* tree and grass (fore ground) in the nearby treeless area recovering shortly after burning.

Figure 5: Baboons resting on top of an *Acacia* tree.

Table 2: The Mann Whitney U test comparing species richness and abundance of seedlings/saplings for the overall and for the various modes of dispersal below and ten meters away from the crowns of *Acacia sieberiana* trees.

	Below crowns of *Acacia*	Ten meters away from crowns	
	Mean and SE	Mean and SE	p
Species richness	21.57 ± 1.11 (65)	6.80 ± 0.75 (43)	<0.05
Overall abundance	185.37 ± 23.93 (6488)	33.31 ± 5.37 (1166)	<0.05
Animal dispersed	182.86 ± 23.82 (6400)	29.71 ± 4.96 (1040)	<0.05
Bird or bat dispersed	17.83 ± 4.33 (624)	1.06 ± 0.35 (37)	<0.05
Primate dispersed	40.80 ± 8.38 (1428)	2.22 ± 0.80 (78)	<0.05
Elephant dispersed	8.74 ± 2.0 (306)	8.29 ± 3.02 (209)	>0.05
Wind/self dispersed	2.51 ± 0.76 (88)	3.60 ± 1.18 (126)	>0.05

Table 3: The Mann Whitney U test comparing species richness and abundance of seedlings/saplings for the overall and for the various modes of dispersal below and ten meters away from the crowns of *Erythrina abyssinica* trees.

	Below crowns of *Erythrina*	Ten meters away from crowns	
	Mean and SE	Mean and SE	p
Species richness	14.63 ± 1.17 (56)	4.80 ± 0.63 (29)	<0.05
Overall abundance	94.20 ± 15.94 (2826)	20.33 ± 3.50 (610)	<0.05
Animal dispersed	92.47 ± 15.75 (2774)	16.63 ± 3.10 (499)	<0.05
Bird or bat dispersed	5.60 ± 1.63 (168)	0.30 ± 0.20 (9)	<0.05
Primate dispersed	35.23 ± 10.39 (1057)	1.40 ± 0.55 (42)	<0.05
Elephant dispersed	3.73 ± 1.21 (112)	3.03 ± 1.12 (91)	>0.05
Wind/self dispersed	1.73 ± 0.60 (52)	3.70 ± 1.20 (111)	>0.05

Table 4: The Mann Whitney U test comparing species richness and abundance of seedlings/saplings for the overall and for the various modes of dispersal below the crowns of *Acacia sieberiana* and *Erythrina abyssinica* trees.

	Below crowns of *Acacia*	Below crowns of *Erythrina*	
	Mean and SE	Mean and SE	p
Species richness	21.57 ±1.11 (65)	14.63 ± 1.17 (56)	<0.05
Overall abundance	185.37 ± 23.93 (6488)	94.20 ± 15.94 (2826)	<0.05
Animal dispersed	182.86 ± 23.82 (6400)	92.47 ± 15.75 (2774)	<0.05
Bird and bat dispersed	17.83 ± 4.33 (624)	5.60 ± 1.63 (168)	<0.05
Primate dispersed	40.80 ± 8.38 (1428)	35.23 ± 10.39 (1057)	>0.05
Elephant dispersed	8.74 ± 2.0 (306)	3.73 ± 1.21 (112)	<0.05
Wind/self dispersed	2.51 ± 0.76 (88)	1.73 ± 0.60 (52)	>0.05

Table 5: The linear regression between crown sizes and species richness and abundance of seedlings/saplings for the overall and for the various modes of dispersal below crowns of *Acacia sieberiana* and *Erythrina abyssinica* trees.

	Crown size (*Acacia*)			Crown size (*Erythrina*)		
	r	R^2	p	r	R^2	p
Species richness	+0.163	0.027	>0.05	+0.688	0.473	<0.05
Overall abundance	+0.559	0.312	<0.05	+0.596	0.355	<0.05
Animal dispersed	+0.561	0.315	<0.05	+0.588	0.346	<0.05
Bird +bat dispersed	+0.376	0.141	<0.05	+0.503	0.253	<0.05
Primate dispersed	+0.701	0.491	<0.05	+0.393	0.155	<0.05
Elephant dispersed	+0.436	0.190	<0.05	+0.439	0.193	<0.05
Wind/self dispersed	-0.011	0.000	>0.05	+0.390	0.152	<0.05

Table 6: The linear regression between distance from the forest edge and species richness and abundance of seedlings/saplings for the overall and for the various modes of dispersal below crowns of *Acacia sieberiana* and *Erythrina abyssinica* trees.

	Distance (*Acacia*)			Distance (*Erythrina*)		
	r	R^2	p	r	R^2	p
Species richness	+0.289	0.084	>0.05	-0.746	0.557	<0.05
Overall abundance	-0.633	0.401	<0.05	-0.612	0.374	<0.05
Animal dispersed	-0.633	0.401	<0.05	-0.604	0.365	<0.05
Bird +bat dispersed	-0.392	0.153	>0.05	-0.542	0.294	<0.05
Primate dispersed	-0.747	0.558	<0.05	-0.423	0.179	>0.05
Elephant dispersed	+0.595	0.354	<0.05	+0.587	0.344	<0.05
Wind/self dispersed	-0.187	0.035	>0.05	-0.398	0.158	>0.05

CHAPTER 4

GENERAL DISCUSSION

4.1: Seed rain, species richness and abundance of seedlings/saplings

This study has demonstrated that forest regeneration is possible below crowns of *Acacia sieberiana* and *Erythrina abyssinica* trees in grasslands of Kibale National Park. Although investigations on the seed rain lasted a short duration and may not be entirely representative of the long-term scenario, data on seedlings/saplings of forest trees recorded in the grassland lend support to this inference. However, since the seedlings/saplings observed are as a result of seed rain that has accumulated over a longer period compared to the duration of this study, they more or less represent the role played by the different mechanisms of seed dispersal in this area. The large proportion of animal dispersed seeds and seedlings/saplings of trees encountered below the crowns of savanna trees in the grassland during this study strongly suggest that interventions that increase use of grasslands by frugivorous vertebrates will facilitate forest regeneration. Indeed there are studies (Uhl, 1987; Vieira *et al*., 1994; Duncan and Chapman, 1999) that lend support to this idea. For example, at Kanyawara, about 10 km NW of Ngogo, Duncan and Chapman (1999) working in abandoned gardens reported higher seed rains below crowns of trees than in treeless areas. Their findings suggest that *Acacia sieberiana* and *Erythrina abyssinica* trees can enhance forest regeneration in grasslands.

Although other methods for establishing tropical forests in savannas have been suggested, for example, the provision of perches (McClanahan and Wolfe 1993; Robinson and Handel 1993), use of exotic soft wood plantations (Kasenene, 2007; Zanne and Chapman 2001) and outright plantation of forest trees (UWA/FACE Project, see Struhsaker, 2003), they may be constrained by a number of factors; ranging from the high cost of establishing and maintaining of plantations, controlling fire, and choosing the appropriate species for each site. Therefore, it may be cheaper and more ecologically sound to encourage the establishment of these savanna trees in grasslands and allow natural regeneration reforest the area. Because the savanna trees are naturally resistant to fire, there will be little or no need to fight fires. Furthermore, *Acacia sieberiana* and *Erythrina abyssinica* trees will encourage the dissemination of forest tree seeds into the area through the attraction of animal seed dispersers, and a wide variety of seed species, some of which will be suited to the local conditions will be brought in. However, as Lwanga (2003) noted, for this approach to be successful, seed sources and animal dispersers must be in the vicinity of the grassland concerned.

4.2: Correlation between species richness and abundance and crown size

Crown size among other actors can influence species richness and abundance of seedlings/saplings of forest trees. The fact that both species richness and abundance of seedlings/saplings of forest trees were strongly positively correlated to crown size of both *Acacia sieberiana* and *Erythrina abyssinica* tree species; lends support to the hypothesis that seedling/sapling survival will be better below savanna trees with larger crown sizes than those with smaller ones. These results can be applied directly to this forest. In the southern part of the Park, UWA/FACE project is attempting to reforest anthropogenic induced grasslands that resulted from agricultural encroachment during the 1970s (Hamilton 1984) by direct planting of forest tree seedlings (Kuper 1996, UWA 2003). This is however proving to be very expensive; approximately five million US dollars were used in nine years to plant only 32 km^2 of forest (Struhsaker, 2003). It must be emphasized that the cost is higher than this, because the trees still need to be protected from fire. Another shortcoming with attempts to re-establish natural forests by planting tree seedlings is that only a few species can be used and these may not be representative of the natural forest, which situation is not good for conservation (Struhsaker, 2003). This study has revealed that species richness and abundance of seedlings/saplings was greater below savanna trees with larger crown sizes, *Acacia siberiana* in particular. This observation suggests that the forest that establish under the savanna trees will be more diverse than that established by direct planting of seeds or seedlings. In addition, once the *Acacia* trees are established, the colonizing forest may need no manual fire protection because it is naturally protected by the *Acacia*.

Although the use of exotic tree plantations for re-establishing tropical forests in grasslands has been suggested (Kuusipalo *et al*., 1995; Parrotta, 1993), the high cost of establishing a plantation may render this approach impractical. Furthermore, in a place like Kibale with populations of large herbivores, establishment of a plantation may not be appropriate as it can lead to conflict between the plantation managers and wildlife. Therefore, in Kibale, and elsewhere where conditions favoring the natural pathway of forest regeneration, i.e. presence of a nearby forest to serve as source of seeds and seed dispersers (Lwanga, 2003) the cheapest and probably more ecologically sound way to establish a forest in a grassland is to foster the establishment of fire resistant savanna trees and let seed dispersers facilitate the regeneration process.

4.3: Correlation between seed rain, species richness and abundance and distance from the forest edge

Results from this study show that the relationship between species richness and abundance of seedlings/saplings of forest trees and distance from the forest edge was strongly negative and statistically significant. Nevertheless, the relationship between seed rain and distance from forest edge was negative though not significant. However, Janzen *et al*., (1976); Aide and Cavelier (1994) observed a strong negative relationship between seed rain and distance from forest edge. They explained that there could be a high energy cost of seed dispersing vertebrates moving out of the forest, the risk of seed dispersers encountering predators could be high or seed dispersing vertebrates would rather concentrate their foraging where food is more plentiful than move to places where food is scarce. This situation is likely to result into a higher number of forest tree seeds being deposited closer to the forest edge than away.

The negative relationship between seed rain, species richness and abundance of seedlings/saplings of forest trees and distance from the forest edge has ecological and management implications. From a management viewpoint, this implies that, should the use of *Acacia sieberiana* and *Erythrina abyssinica* trees be adopted in afforestation programmes, it is necessary to encourage their establishment at relatively short distances to the forest edge and to one another, lest animal seed dispersers may not find them.

4.4: CONCLUSIONS

- *Acacia sieberiana* and *Erythrina abyssinica* trees with large crown sizes that establish at relatively short distances to the forest edge could be important as nuclei for colonization of grasslands by forest because significantly high species richness and abundance of seedlings/saplings of forest trees were observed below these trees compared to the treeless areas. However, *Acacia sieberiana* trees could be more important than *Erythrina abyssinica* trees.
- Birds, bats and primates have an important role to play in forest regeneration in the grasslands. However, seed predators have a limited role in forest regeneration.

4.5: RECOMMENDATIONS

- More fire resistant savanna trees especially *Acacia sieberiana* should be encouraged to establish in grasslands of Kibale National Park, and elsewhere where conditions favoring the natural pathway of forest regeneration, i.e. presence of a nearby forest to serve as source of seeds and seed dispersers (Lwanga, 2003). However, it would be more suitable to foster their establishment close to a forest and to one another as Graham (2001) suggested, so as to reduce the cost of movement by frugivores out and back to the forest; thereby facilitating seed dispersal and forest regeneration.
- Future studies should investigate other fire resistant savanna trees such as *Albizia grandibracteata* for their suitability as potential candidates in enhancing forest regeneration in grasslands.

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APPENDICES

1: The code number of study plots, distance (meters) of study plots from forest edge, seed trap number, number of seeds collected in traps below and ten meters away from crowns of savanna trees, seed station number, number of initial seeds placed at each seed station and number of seeds removed by predators below and ten meters away from crowns of savanna trees.

Code	Dist (m)	S/T No	Seed rain (crown)	Seed rain (ten meters away)	S/S No	Initial no. seeds	Pred (crown)	Pred (away)
AC1	187	30	0	0	4	20	4	6
AC10	138	28	8	2	30	20	6	0
AC16	163	16	5	0	14	20	4	1
AC17	110	17	0	1	13	20	3	0
AC20	135	18	1	0	12	20	7	6
AC22	136	14	0	0	22	20	3	0
AC23	161	29	2	0	29	20	3	4
AC25	186	26	0	0	27	20	4	1
AC28	135	25	10	5	28	20	4	7
AC3	187	9	0	0	16	20	7	2
AC4	176	11	0	0	21	20	4	7
AC48	132	6	0	0	18	20	2	1
AC7	75	23	0	0	25	20	7	1
AC8	158	24	0	0	26	20	0	2
AC9	174	27	0	0	5	20	2	2
ER1	134	7	2	0	19	20	1	4
ER10	201	10	0	0	15	20	2	2
ER12	167	12	0	1	24	20	3	7
ER13	126	15	0	0	23	20	3	1
ER2	186	19	0	0	11	20	5	5
ER25	119	1	0	3	1	20	0	1
ER28	147	2	5	0	2	20	3	3
ER29	177	13	0	0	17	20	1	6
ER30	172	3	0	0	3	20	4	0
ER32	168	4	0	1	6	20	6	5
ER35	169	5	0	0	7	20	2	6
ER4	174	20	0	0	10	20	1	2
ER5	137	21	1	2	9	20	3	1
ER6	107	22	16	0	8	20	1	2
ER9	159	8	0	0	20	20	1	2
			50	15		600	96	87

2: List of all species of seedlings/saplings of forest trees encountered below and ten meters away from crowns of savanna trees; including their families and potential dispersers.

Species	Family	Dispersers
Aeglopsis eggelingii	*Rutaceae*	Elephants
Afrosersalisia cerasifera	*Sapotaceae*	Primates, Birds
Albizia grandibracteata	*Mimosaceae*	Wind
Aningeria altissima	*Sapotaceae*	Primates, Bats
Antiaris toxicaria	*Moraceae*	Birds, Primates
Aphania senegalensis	*Sapindaceae*	Primates, Elephants
Balanites wilsoniana	*Balanitaceae*	Elephants
Bersama abyssinica	*Melianthaceae*	Birds
Blighia unijugata	*Sapindaceae*	Birds, Elephants
Bridelia micrantha	*Euphorbiaceae*	Birds, Primates
Cassine buchananii	*Celastraceae*	Primates
Cassipourea ruwensorensis	*Rhizophoraceae*	Birds
Celtis africana	*Ulmaceae*	Birds, Primates
Celtis durandii	*Ulmaceae*	Birds, Primates, Elephants
Chaetacme aristata	*Ulmaceae*	Primates, Elephants
Chrysophyllum albidum	*Sapotaceae*	Primates, Elephants
Clausena anisata	*Rutaceae*	Birds
Coffea eugenioides	*Rubiaceae*	Primates, Bats
Cola gigantea	*Sterculiaceae*	Birds, Primates
Cordia millenii	*Boraginaceae*	Primates, Birds, Elephants
Croton macrostachyus	*Euphorbiaceae*	Birds
Dasylepis eggelingii	*Flacourtiaceae*	Primates, Elephants
Diospyros abyssinica	*Ebenaceae*	Primates, Birds, Elephants
Dovyalis macrocalyx	*Flacourtiaceae*	Primates, Elephants
Dovyalis spinossisima	*Flacourtiaceae*	Elephants
Drypetes ugandensis	*Euphorbiaceae*	Primates
Fagaropsis angolensis	*Rutaceae*	Birds
Ficus mucoso	*Moraceae*	Primates, Birds, Bats
Ficus sur	*Moraceae*	Primates, Birds, Bats
Flueggea virosa	*Euphorbiaceae*	Birds, Primates
Funtumia latifolia	*Apocynaceae*	Wind
Harrisonia abyssinica	*Simaroubaceae*	Birds, Primates
Kigelia moosa	*Bignoniaceae*	Elephant, Primates
Lindackeria bukobensis	*Flacourtiaceae*	Birds
Maesa lanceolata	*Myrsinaceae*	Birds, Primates
Millettia dura	*Papilionaceae*	Self
Mimusops bagshawei	*Sapotaceae*	Primates, Birds, Elephants
Monodora myristica	*Annonaceae*	Primates, Elephants, Birds
Morus mesozygia	*Moraceae*	Birds, Primates
Olea capensis	*Oleaceae*	Birds
Oncoba spinosa	*Flacourtiaceae*	Elephants
Pancovia turbinata	*Sapindaceae*	Primates
Phoenix reclinata	*Palmae*	Birds, Primates
Piptadeniastrum africanum	*Mimosaceae*	Wind
Premna angolensis	*Verbenaceae*	Birds

Prunus africana	*Rosaceae*	Elephants
Pseudospondias microcarpa	*Anacardiaceae*	Primates, Birds, Elephants
Psychotria lauracea	*Rubiaceae*	Birds, Bats
Pterygota mildbraedii	*Sterculiaceae*	Wind
Rauvolfia oxyphylla	*Apocynaceae*	Birds
Rothmania malleifera	*Rubiaceae*	Primates, Elephants
Rothmania urcelliformis	*Rubiaceae*	Primates, Elephants
Rytigynia beniensis	*Rubiaceae*	Birds
Sapium ellipticum	*Euphorbiaceae*	Birds, Primates
Senna spectabilis	*Caesalpiniaceae*	Self
Spathodea campanulata	*Bignoniaceae*	Wind
Tabernaemontana holstii	*Apocynaceae*	Primates
Tabernaemontana ventricosa	*Apocynaceae*	Birds
Tarenna pavettiodes	*Rubiaceae*	Birds, Primates
Teclea nobilis	*Rutaceae*	Primates, Birds, Elephants
Treculia africana	*Moraceae*	Primates, Elephants
Trichilia splendida	*Meliaceae*	Birds
Trimeria grandifolia	*Flacourtiaceae*	Birds
Turraea floribunda	*Meliaceae*	Birds
Uvariopsis congensis	*Annonaceae*	Primates, Birds, Elephants
Vangueria apiculata	*Rubiaceae*	Primates, Birds
Warburgia ugandensis	*Canellaceae*	Primates, Elephants
Zanha golungensis	*Sapindaceae*	Primates, Birds