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Intensive tree planting facilitates tropical forest biodiversity and biomass accumulation in Kibale National Park, Uganda

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ABSTRACT

The extensive area of degraded tropical land and the calls to conserve forest biodiversity and sequester carbon to offset climate change demonstrate the need to restore forest in the tropics. Deforested land is sometimes replanted with fast-growing trees; however, the consequences of intensive replanting on biomass accumulation or plant and animal diversity are poorly understood. The purpose of this study was to determine how intensive replanting affected tropical forest regeneration and biomass accumulation over ten years. We studied reforested sites in Kibale National Park, Uganda, that were degraded in the 1970s and replanted with five native tree species in 1995. We identified and measured the size of planted versus naturally regenerating trees, and felled and weighed matched trees outside the park to calculate region-specific allometric equations for above-ground tree biomass. The role of shrubs and grasses in facilitating or hindering the establishment of trees was evaluated by correlating observed estimates of percent cover to tree biomass. We found 39 tree species naturally regenerating in the restored area in addition to the five originally planted species. Biomass was much higher for planted (15,675 kg/ha) than naturally regenerated trees (4560 kg/ha), but naturally regenerating tree regrowth was an important element of the landscape. The establishment of tree seedlings initially appeared to be facilitated by shrubs, primarily *Acanthus pubescens* and the invasive *Lantana camara*; however, both are expected to hinder tree recruitment in the long-term. Large and small-seeded tree species were found in the replanted area, indicating that bird and mammal dispersers contributed to natural forest restoration. These results demonstrate that intensive replanting can accelerate the natural accumulation of biomass and biodiversity and facilitate the restoration of tropical forest communities. However, the long-term financial costs and ecological benefits of planting and maintaining reforested areas need to be weighed against other potential restoration strategies.

1. Introduction

Between 2000 and 2005, the world lost ~7.3 million ha (or ~200 km^2) of forest per day (FAO, 2005). This figure does not include vast areas of forest that are degraded by selective logging or fire, both of which affect huge areas (Chapman et al., 2006). This rapid rate of degradation is caused by a number of socio-economic and political factors, partially due to large increases in human population in most tropical countries (Brown and Pearce, 1994; Myers, 2002; Wright and Muller-Landau, 2006; Jacob et al., 2008). In many regions, widespread commercial logging of tropical forests provides access to previously remote areas and promotes policies for agricultural expansion. For example, in the 1970s the governments of Brazil (Steininger, 2000), Indonesia (Lawrence, 2005), and Uganda (Hamilton, 1984; Struhsaker, 1997) adopted agricultural reforms to expand productive areas. They provided tax incentives to encourage migration from densely populated regions to forested areas that could be converted to agriculture. Unfortunately, many of these formerly forested regions rapidly lost soil fertility; the subsequent decline in crop yield forced settlers to abandon recently cleared land (Brown and Lugo, 1994; Dobson et al., 1997). As a result, it is estimated that there are 350 million ha deforested and another 500 million ha degraded secondary and

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primary tropical forests; many of these areas have since been abandoned (ITTO, 2002; Lamb et al., 2005). The current scale of tropical deforestation and the large areas of degraded and abandoned lands underscore the need for intervention to restore biodiversity and the ecological functions, processes, and goods and services previously provided by these lands (de Groot et al., 2002; Boyd and Banzhaf, 2007).

In many cases, natural succession can cause forest to return to deforested areas within a reasonable time frame (i.e., years to a few decades) (Reiners et al., 1994); however, succession can also occur at a very slow rate (Brown and Lugo, 1994; Chapman and Chapman, 1999) and be considered arrested if it does not proceed within a reasonable time frame (Aide et al., 1996; Shono et al., 2007). Instances of arrested succession from both anthropogenic and natural causes have been reported throughout the tropics, including Brazil (Nepstad et al., 1991), Colombia (Aide and Cavelier, 1994), Panama (Brokaw, 1983), Singapore (Corlett, 1991), Sri Lanka (Ashton et al., 1997), and Uganda (Chapman and Chapman, 1999; Chapman et al., 1999). Arrested succession may reflect a lack of tree seeds or resprouts, high seed or seedling mortality (Nepstad et al., 1996; Ashton et al., 1997), inhospitable abiotic and biotic site conditions (e.g., a lack of mycorrhizae or limited soil nutrients; Janos, 1980; Uhl et al., 1988; Corlett, 1991; Lwanga, 2003; Lawes and Chapman, 2005), or competitive dominance of herbs and shrubs (Denslow et al., 1991; Duncan and Chapman, 1999; George and Bazzaz, 1999a,b; Duncan and Chapman, 2003b).

Seed limitation often inhibits the recovery of tropical forest tree biodiversity when deforested areas are large or far from intact (i.e., non-degraded) forest. The majority of tropical tree species have animal-dispersed fruits (Howe and Smallwood, 1982; Chapman, 1995), but many frugivores avoid deforested areas (DaSilva et al., 1996; Zanne and Chapman, 2001), especially mammals (Chapman and Chapman, 1999). Wind-dispersed seeds may arrive at deforested sites in high numbers; however, since they are small-seeded, the harsh micro-site conditions associated with abandoned lands often limit the establishment of these seedlings. For example, Ingle (2003) found that the stem density of vertebrate-dispersed species outnumbered wind-dispersed species in montane forests of the Philippines, although 15 times more wind-dispersed seeds arrived in these degraded areas. Furthermore, seed dispersal limitation can be severe for large-seeded tree species because in many systems the predominant seed dispersal agents in abandoned areas are small birds and bats that typically only carry small seeds (Nepstad et al., 1996; Duncan and Chapman, 1999). These limitations can be reduced when remnant trees (Guevara et al., 1986) and shrubs (Vieira et al., 1994; Holl, 2002) are present because they attract large seed dispersers and facilitate forest regeneration under their canopies. In some deforested areas grasses invade before primary successional tree species establish. High grass biomass can increase the likelihood and intensity of fire, further arresting natural forest restoration (Nepstad et al., 1990; Lwanga, 2003). In previously forested systems, fire can also impoverish soils, reduce seedling growth (Aide et al., 1996), and impede forest recovery (Buschbacher et al., 1988).

The Uganda Wildlife Authority (UWA) and Face the Future (formerly the Forests Absorbing Carbon Emissions (FACE) Foundation), hereafter UWA–FACE, have a collaborative reforestation program in Kibale. This intensive program was designed to facilitate the rapid restoration of woody vegetation in a large area of the park that was illegally encroached by agriculturalists who cleared forest and grassland areas to plant crops (Chapman and Lambert, 2000; Struhsaker, 2003). The primary objectives of our study were to (1) quantify species richness of naturally regenerating (i.e., non-planted) trees in Kibale National Park, Uganda, and (2) compare the biomass accumulation of planted versus naturally regenerating trees in sites replanted by UWA–FACE.

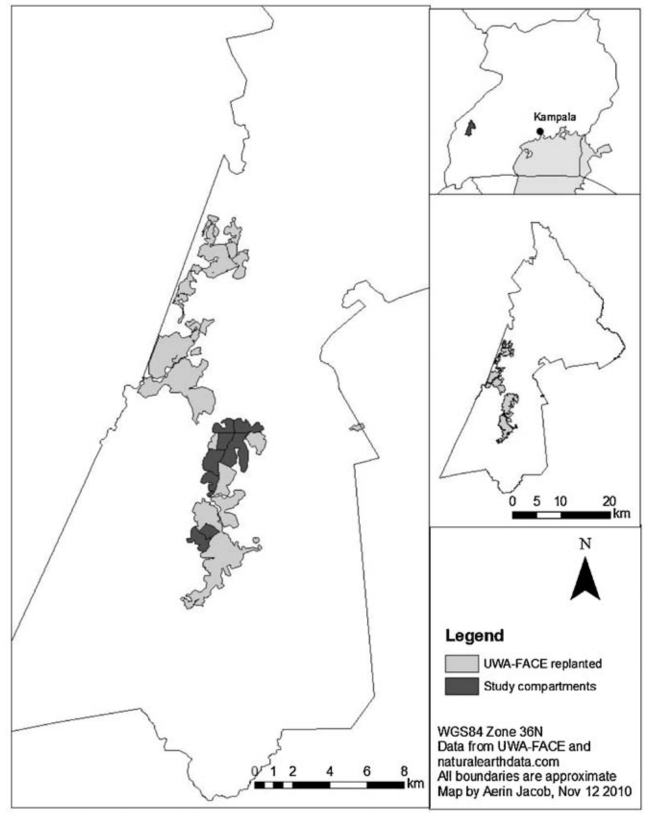

Fig. 1. The location of Kibale National Park within Uganda and the location of the all restoration compartments planted to date (light grey) and the study compartments (dark grey) within Kibale.

2. Methods

2.1. Study area and UWA–FACE field activities and costs

This study was conducted between May 2005 and May 2006 in the southern section of Kibale National Park, Uganda (Fig. 1). The park (795 km^2) is located in western Uganda (0.13–0.41′N and 30.19–30.32′E) near the foothills of the Ruwenzori Mountains (Chapman and Lambert, 2000; Struhsaker, 1997). Kibale is a mid-altitude, moist-evergreen forest that receives 1697 mm of rain annually (1990–2009). Although there are some early successional species in the park (e.g., *Albizia grandibracteata*, *Polysciasfulva*, *Trema orientalis*; Zanne and Chapman, 2005), Kibale is notable for its lack of aggressive colonizers typical of other tropical regions (e.g., *Musanga* spp., *Cecropia* spp.). Within the park, there is a gradual decrease in elevation from north to south, which corresponds to an increase in temperature, decrease in rainfall, and changes in forest composition (Struhsaker, 1997). In the south, the un-encroached forest is dominated by *Cynometra alexandri* and its affiliated species; however, there are also areas of mixed forest along riverine strips and even *Acacia* woodland to the far south.

In 1994, UWA–FACE started a reforestation program to establish carbon offsets on degraded land in Kibale, with tree planting commencing in 1995. The project is based in the southern part of Kibale in an area which was illegally occupied by agriculturalists in the 1970s until their eviction in 1992 (van Orsdol, 1986; Baranga, 1991). Agricultural encroachment adversely affected approximately 120 km^2 (15% of the total area of Kibale), mainly leading to forest destruction and grassland clearing (Chapman and Lambert, 2000). After the eviction, grassland areas became dominated by elephant grass (*Pennisetum purpureum*) because frequent fires set by poachers or that spread into the park from neighboring subsistence farms prevented natural forest regeneration (Struhsaker, 2003).

For the first phase of the replanting program (Phase 1: 1994–1997), the majority of seedlings were raised from seeds or collected from the wild (wildings). A limited number of species survived transplantation into the restoration areas, which were typically dominated by the grass *P. purpureum*. As a result, future replanting phases concentrated on planting *Albizia* spp., *Bridelia micrantha*, *Sapium ellipticum*, *Celtis durandii*, and *Warbugia ugandensis* seedlings. The species were collected from the forest floor in areas that were not affected by agricultural encroachment (one person can collect up to 180 wildings per hour), transferred to a nursery, watered, and kept in plastic covered chambers with high humidity for four weeks until a new root system formed. Special care was taken during collection and acclimatization in the nursery to ensure the roots healed before wildings were planted in the restoration areas. Vegetative propagation by cuttings accounted for 5% of the trees planted. Cuttings were directly set to root in 7 cm × 21 cm poly-bags containing a 1:1 mixture of forest topsoil and sand.

Preparing the site for planting involved clearing the elephant grass along a series of 2-m wide paths spaced in a 5 m × 5 m grid, and digging a small pit every 5 m along the paths for the seedling; thus, 400 tree seedlings were planted per hectare. The replanted area was divided into a series of well mapped compartments to facilitate monitoring. The size and placement of the compartments were done by UWA–FACE and were based on convenience (e.g., the edge of the road formed the compartment border). A total of 16.35 km^2 were replanted in eight compartments during Phase 1 (Fig. 1). After planting, the seedlings were monitored and weeded two to three times a year to protect them from fire and to limit competition, primarily from grasses. Fire breaks were cut between compartments and UWA–FACE staff fought fires and maintained access roads to protect the planted areas. The total cost for these activities was approximately US$120,000 per km^2 (UWA–FACE, 2005).

2.2. Sampling design

The eight study compartments were mapped using GPS units at the time of planting and the corners marked with trenches. We used maps from UWA–FACE to identify the compartments and individual trees that were planted during Phase I. We randomly established ten 10 m × 50 m plots in each compartment using randomly generated locations and directions. If a plot extended beyond the edge of the compartment, it was re-oriented to 180° opposite the original direction. We identified each seedling, sapling, and mature tree in the plot and measured their height, diameter at breast height (DBH), and diameter at ground height (DGH). Diameter at breast height is a commonly used metric that allows comparisons with other studies; diameter at ground height allowed us to evaluate small stems and was used in our allometric analysis to estimate biomass. It was easy to separate planted from naturally regenerating individuals as the seedlings were originally planted in straight lines at set intervals.

We established small (1 m × 1 m) subplots every 5 m next to the path used for planting. We estimated the percentage cover of shrubs, dominant grasses, and average vegetation height (cm) and identified plants using well recognized plant keys (Polhill, 1952; Kingston, 1967; Hamilton, 1991; Katende et al., 1995; Lwanga, 1996).

Species richness and density data were log transformed prior to analysis. We estimated species diversity using the Shannon–Wiener index (Krebs, 1989) and evaluated the effects of grass and shrub cover on species richness, biomass, and tree height using a regression analysis. We selected and measured trees in forested land adjacent to the park to provide a site-specific estimate of dry tree biomass. We chose nine species commonly found in regenerating areas: *Albizia grandibracteata*, *Bridelia micrantha*, *Celtis africana*, *Celtis durandii*, *Clausena* spp., *Maesa lanceolata*, *Funtumia latifolia*, *Milletia dura*, and *Trema orientalis*. Individuals of similar sizes to regenerating trees (both planted and naturally regenerating stems) in the replanted area were selected (i.e., DBH = 1.1–10.0 cm and DGH = 1.6–11.0 cm; dry weight = 0.25–10 kg; total n = 200 stems), and we measured their DBH and DGH. We felled the trees at ground level, removed the branches, and measured the total dry weight of stems and leaves. We cut the tree stems into small sections and air dried them until a constant mass was attained. The dry biomass of trees in the planted areas was predicted by the allometric equation log DGH ($r^2 = 0.653$, $n = 200$, $y = 2.053x + 2.056$).

We measured the seed size of tree species found naturally regenerating in the plots to evaluate the relative role of birds and large mammals in moving seeds into the restoration areas. We measured the longest axis of 20 seeds from six adult trees in the adjacent undisturbed forest. Based on the observations of the foraging activity of birds and mammals (Chapman, unpublished data), we estimated the largest seed typically dispersed by birds in this community to be *Olea capensis* (mean length = 1.39 cm) (excluding black and white casqued hornbills, *Bycanister subcylindrucus*). Seeds larger than 1.39 cm were assumed to be mammal dispersed. Smaller seeds could be dispersed by either mammals or birds, since mammals often disperse both small-and large-seeded species (Wrangham et al., 1994).

3. Results

The mean predicted biomass of planted trees in the eight compartments was 15,657 kg/ha (range: 4120 kg/ha ($n = 76$) to 26,916 kg/ha ($n = 244$); Table 1), while the mean biomass of the naturally regenerating trees was 4560 kg/ha (range: 1126 kg/ha ($n = 30$) to 11,470 kg/ha ($n = 162$); Table 1). In general, the naturally regenerating trees represented 22.5% of the total biomass in the restoration area.

A total of 39 tree species established themselves naturally in the compartments in the ten years since replanting (Table 2). The restoration program introduced only one tree species that did not regenerate naturally in the area (*Sapium ellipticum*), although this species is commonly found in the neighboring forest. Determining what proportion of the species in the adjacent forest these 39 species represent is difficult: many species in Kibale are rare and would require extensive sampling to identify, and the forest composition changes along a north–south gradient in elevation and rainfall. However, species/area curves from our previous sampling suggest that the number of new species found decreases after sampling approximately 2 ha of scattered plots. Sampling 8.6 ha throughout the park resulted in the identification of 74 species (Chapman et al., 1997). This suggests that approximately half the species in the adjacent forest were also present in restoration area.

Tree species diversity and evenness varied among plots: species diversity was highest in compartments 109 (2.36) and 114 (2.32), while evenness was highest in compartment 109 (0.45), followed equally by 101, 103 and 113 (all 0.38; Table 3). Compartment 109 had 23 tree species and the individuals were distributed relatively equally among these species. The contribution of the tree planting to species diversity was negligible (Table 3).

Acanthus pubescens and *Lantana camara* were the dominant shrubs in all compartments. We did not find a relationship between the percentage cover of shrubs and grasses in the subplots and the biomass of naturally established or planted

Table 1
Above ground biomass (kg/ha) and stem densities (per ha) of woody tree species, and percentage coverage of grass and shrubs in the study compartments, Kibale National Park, Uganda.

Compartment	Planted					Natural regrowth		
	Grass	Shrub	Biomass	*N*	No. of spp.	Biomass	*N*	No of spp.
101	27	27	9620	152	5	1154	30	7
102	26	36	20,786	234	5	1126	42	8
103	31	37	15,114	318	5	7318	148	14
107	40	27	4,120	152	5	2496	72	8
108	30	34	14,126	430	5	2626	66	8
109	30	37	12,440	248	5	5060	246	19
113	24	37	22,276	448	5	11,470	162	18
114	37	28	26,916	488	5	5230	134	21
Total			125,398			36,480		
Mean			15,675			4560		
Standard deviation			7362			3534		

Table 2
Tree species, mean seed length (where available) and frequencies for the study compartments Kibale National Park, Uganda. Tree species are arranged according to their frequency of occurrence. Trees marked with an asterisk are considered to be mammal dispersed.

Tree species	Mean seed length (cm)	Not planted	Planted	Total
Bridelia micrantha	0.74	2	173	175
Warbugia ugandensis	0.99	1	57	58
Sapium ellipticum	0.57	0	55	55
Albizia grandibracteata	0.77	4	16	20
Harrisonia abyssinica	0.39	10	0	10
Allophyllus rubifolius	0.64	9	0	9
Combretum molle		*8*	*0*	*8*
Acacia spp.	0.68	7	0	7
**Mimusops bagshawei*	1.65	8	0	8
Tabernaemontana holstii	1.06	7	0	7
Grewia occidentalis	0.75	7	0	7
**Erythrina abyssinica*	1.83	7	0	7
Cassia spectabilis	0.83	6	0	6
Ficus capensis	0.10	6	0	6
Gardenia lanciloba		5	0	5
Rauvolfia vomitoria	1.27	4	0	4
Prunus africana	0.87	2	0	2
Markhamia lutea	1.17	4	0	4
Croton macrostachyus	0.82	0	4	4
Diospyros abyssinica	0.75	3	0	3
Antidesma spp.		3	0	3
Spathodea campanulata	1.00	3	0	3
Funtumia latifolia	0.29	3	0	3
Celtis durandii	0.50	0	2	2
**Chrysophyllum albidum*	2.10	2	0	2
Olea capensis	1.38	1	0	1
Uvariopsis congensis	1.24	1	0	1
Mangifera indica		1	0	1
Carissa edulis		1	0	1
**Pseudospondias microcarpa*	1.47	1	0	1
Maesa lanceolata	0.32	1	0	1
Kigelia africana	1.16	1	0	1
Persea americana		0	0	1
Apodytesdimidiate	0.47	1	0	1
Coffea eugenioides	0.93	1	0	1
Psidium guajava	0.49	1	0	1
Eudenia spp.	0.97	1	0	1
Dovyalis microcarpa	0.90	1	0	1
Dasylepis eggeling	0.73	1	0	1
Blighia unijugata	1.19	1	0	1
		119	305	425

Table 3
Species richness, Shannon diversity index, and evenness of woody tree species naturally growing in the eight study compartments, Kibale National Park, Uganda.

Compartment	All species			Natural regrowth		
	N	Diversity Index	Evenness	Diversity Index	Evenness	*N*
101	180	1.71	0.38	1.71	0.63	15
102	276	1.24	0.25	1.04	0.64	21
103	233	2.09	0.38	2.13	0.49	74
107	224	1.71	0.36	1.71	0.48	36
108	248	1.38	0.25	1.71	0.49	33
109	247	2.49	0.45	2.36	0.49	23
113	305	2.16	0.38	2.22	0.55	81
114	311	2.00	0.35	0.25	0.20	67

trees. However, after combining the planted and the naturally established trees, the percentage of shrub cover was positively correlated to tree biomass ($r^2 = 0.207$, $p = 0.026$), while there was a negative correlation between tree biomass and percentage grass ($r^2 = -0.081$, $p = 0.018$). However, the amount of variation in tree biomass explained by either of these relationships was small.

The largest seed that birds in Kibale have been observed to disperse is *Olea capensis*, which has an average seed length of 1.39 cm (Chapman, unpublished data; Table 2). *Mimusops bagshawei*, *Chrysophyllum albidum*, *Pseudospondias microcarpa*, and *Erythrina abyssinica* were found in the compartments and their seed sizes are longer than 1.39 cm; therefore it is likely that these species were dispersed into the area by mammals (*E. abyssinica* is thought to be a mimetic seed, one that is brightly colored but without any pulp, so it does not provide any nutritional reward for dispersal). *Kigelia africana* seedlings (average seed length = 1.16 cm) were also found in the restoration areas; these seeds were likely dispersed by elephants or large primates (probably baboons or chimpanzees) since the seeds are embedded in a large fruit with a hard rind (average 60 cm long) (Katende et al., 1995). Seeds smaller than 1.39 cm probably do not place a size constraint on the disperser and can be dispersed by both mammals and birds.

4. Discussion

The results of this research have five contributions, they: (1) demonstrate that the replanting program was successful at accumulating biomass of planted trees, (2) show that native trees naturally establish under planted trees, quickly creating a reasonably rich tree species assemblage, (3) quantify the financial costs of enrichment planting, which is considered relative to potential costs of other strategies, such as fire exclusion, (4) consider the role of grasses and shrubs, particularly the invasive *Lantana camera*, in forest regeneration, and (5) provide evidence that large and small-seeded tree species were found in the replanted area, indicating that bird and mammal dispersers were likely using regenerating forest habitat and contributing to natural forest restoration.

First, we demonstrate that the active restoration of the degraded lands in Kibale was relatively successful as indicated by the predicted biomass the planted trees accumulated approximately 10 years after planting. Success should be measured (i) relative to the goals of the program, which in this case was to accumulate biomass, and (ii) relative to other methods, of which there have been many that have been evaluated in Kibale or elsewhere (Chapman and Chapman, 1999; Chapman et al., 2002; Martinez-Garza and Howe, 2007; Vieira et al., 2009). If agricultural land in the Kibale region is abandoned and left to recover without intervention, it will take a very long time for a closed canopy tree-dominated community to regenerate, even if it is close to seed sources (Chapman and Chapman, 1999). Chapman and Chapman (1999) studied such an area and found that it took four years for trees >5 m tall to reach a biomass of 8.9 kg/ha; even 17 years later these areas are still dominated by shrubs and grasses (unpublished data). However, excluding fire from degraded, regenerating agricultural land increases the rate of reforestation (Lwanga, 2003) and fire can be excluded over large areas at relatively low cost (Omeja, unpublished data). Some researchers have advocated using timber plantations, typically with non-native species, as a means to economically reforest areas (Lugo, 1997; Parrotta et al., 1997; Lamb, 1998), since native forests can regenerate underneath the plantations or following timber harvest, and timber sales can help pay for restoration efforts. In Kibale, this management strategy was successful for reforesting areas, despite the considerable damage caused by initial and poorly planned timber extraction (Chapman and Chapman, 1996; Duncan and Chapman, 2003a; Omeja et al., 2009). This use of this plantation strategy of reforestation in Kibale included all functional groups (pioneers, later-seral species and wind and animal dispersed); however, animal dispersed tree species will rarely be found if the plantation is not near native forest (Zanne and Chapman, 2001).

Second, we documented that many tree species will naturally establish under planted trees, creating a reasonably rich tree species assemblage within a period of time that is reasonable for management. The natural establishment of a diverse tree community with accumulating biomass (almost 1/4 of the total biomass) suggests that these initially species-poor areas (i.e., five planted tree species) will quickly and naturally become richer and accumulate woody tree biomass. One of the most important contributions of programs such as the UWA–FACE restoration project is the rapid rate of biomass accumulation of woody trees that sequester carbon (Holl and Howarth, 2000; UWA–FACE, 2005; Coomes et al., 2008). The fact that the diverse community of naturally regenerating trees within these restoration areas has also quickly accumulated biomass suggests that such programs may contribute to the relatively rapid restoration of biodiversity. Furthermore, observations of animal occurrence in the replanted areas suggest that biodiversity of both plants and animals is rapidly recovering (Jacob and Chapman, unpublished data).

Third, this research raises the question of when the ecological gains of enrichment planting are worth the considerable financial costs. Replanting of a mixture of early and late successional tree species has been recommended to restore diversity more rapidly than removing disturbance and waiting for natural regeneration to occur (Yirdaw, 2001). However, the potential application of enrichment planting to facilitate biodiversity restoration is based on the premise that heightened seedling recruitment will lead to greatly enhanced regeneration of mature trees, which are worth the additional investment that replanting programs require (Plumptre, 1995; Chapman and Chapman, 1996). Even though planted trees have a high probability of establishing and growing, especially when planting is timed to optimize survival rates (Duncan and Chapman, 2003a), enrichment planting generally involves costly nursery maintenance and field labor. For example, while enrichment planting depends on the density of the trees planted, forest restoration is estimated to cost \$250,000 US per km^2 on bauxite-mined land in the Amazon (Parrotta and Knowles, 1999). It cost \$120,000 US per km^2 to conduct the enrichment planting and establish and maintain the fire breaks that we evaluated in Kibale (UWA–FACE, 2005). Given the relative success of the restoration management in Kibale, we suggest that fire exclusion be evaluated in more depth as a restoration strategy, given its relatively low cost and ease of protecting an area (see also Lwanga, 2003). To the credit of the UWA–FACE program, they established and maintain an extensive network of fire breaks to protect the planted areas. Anecdotal evidence suggests that this action has helped to protect as yet unplanted areas that are passively regenerating. These areas, plus others studied by Lwanga (2003), have been protected from fire for <1 to ~30 years; together they create a series of natural experiments to evaluate the role of fire prevention in tropical forest reforestation.

Fourth, the positive relationship we found between the combined biomass of planted naturally establishing tree species and the percentage of plots covered by shrubs concurs with results from other tropical forests (Vieira et al., 1994; Aide et al., 1995; Holl, 2002). This suggests that shrubs, in this case primarily *L. camara* which forms 95% of the shrub layer, initially facilitates woody tree species establishment. Shrubs have been found to lower temperatures, increase soil moisture (Bertness and Callaway, 1994; Callaway and Walker, 1997), and buffer seedlings from harsh environmental condition, such as heat from the sun (DaSilva et al., 1996; Nepstad et al., 1996). These shrubs may also be beneficial in that they deter fire (Lwanga, 2003) and reduce browsing (Sharam et al., 2009). Generally, tropical areas with well-established evergreen undergrowth tend to be less susceptible to fire damage than areas with an accumulation of dry grasses (Parrotta, 1992; Lugo et al., 1993; Parrotta, 1993). Exposed grassy sites, on the other hand, have negative effects on site microclimate, with more pronounced temperature fluctuations and differences in humidity and water availability (Bazzaz, 1991) that are extremely stressful for plants (Loik and Holl, 1999). Furthermore, grass-dominated areas are very prone to fire in the dry season and successive fires severely curtail forest succession.

Presently, observations and the correlation that we found suggest that the shrub layer in Kibale appears to be initially helping the regenerating trees acclimatize and form the dominant canopy; however, studies have shown that there may be a shift in the direction of this interaction over the long-term (Callaway, 1997). In the future, the shrub layer, particularly that of the dense *L. camara* shrubs, may not be conducive to a diverse regenerating plant community as it may suppress seedlings from reaching forest canopy layer (Zalucki et al., 2007). Introduced *L. camara* has been reported to have harmful effects on ecosystems in other regions. For example, *Lantana* sp. was ranked as the most significant weed of non-agricultural areas in south-east Queensland, Australia (Zalucki et al., 2007). In Kenya, the replacement of native pastures by *L. camara* is threatening the habitat of the sable antelope (*Hippotragus niger*), and acts as a safe haven for disease transmitting tsetse-flies and a detrimental force to forest and ecosystem regeneration (Zalucki et al., 2007). The impenetrable thickets formed by *L. camara* are also concerning because they restrict the movement of even highly mobile animals, such as elephants (*Loxodonta africana*) and baboons (*Papio anubis*), which likely reduces seed dispersal. The balance between the advantages that establishing seedlings receive from altered microclimate around *L. camara* versus the disadvantages of reduced seed input and potential long-term inhibited growth remains unknown. Thus, if *L. camara* continues to form a dense shrub layer then the regeneration pathway to forest recovery may be diverted to an arrested successional state. This suggests that there is a pressing need to investigate the long-term role of *L. camara* in forest restoration and experimentation involving removal would help clarify its role.

Lastly, the size of seeds of tree species naturally regenerating in the area reflects the presence of different dispersing animals in the restoration area. Most fruit-eating animals only feed on a portion of the fruits that are available in the forest. Fruit selection no doubt depends on a variety of factors such as morphology, nutritional value, color, and the abundance of secondary compounds. However, seed size is a key factor known to influence which frugivores disperse different species of fruits (Herrera, 1985; Wheelwright, 1985; Fischer and Chapman, 1993). A seed cannot be moved away from the adult tree crown if it exceeds the size of gape of a bird (Wheelwright, 1985; Chapman et al., 2003). Given that a number of tree species have seeds too large to be dispersed by birds, and the fact that mammals disperse both large and small seeds, it seems probable that mammals, such as elephants and baboons, have played an important role in the accumulation of tree species richness in the regenerating areas of Kibale. *Bridelia micrantha* (bird dispersed) and *A. grandibracteata* (wind and rodent dispersed) had higher stem densities than other species, and most of these were growing naturally. These are trees species with small seeds, long distance dispersal capability, long persistence in the soil seed bank, and have the ability to colonize gaps within forest canopies (Zanne and Chapman, 2005; Omeja et al., 2009), attributes that allow rapid colonization of disturbed areas.

5. Conclusion

The potential for restoring degraded forests in Kibale National Park is high following intensive planting of only five tree species. We found that 39 tree non-planted species were able to establish and accumulate considerable biomass following the planting program. This regeneration facilitates the recovery of other tree and animal species of conservation concern. There are many limitations to forest restoration, and we speculated that the major future limitation at this site is the heavy presence of *L. camara* that may slow the progress of current restoration efforts. A more detailed understanding on the role of *L. camara* in future restoration needs to be conducted.

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