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Biomass accumulation in tropical lands with different disturbance histories: Contrasts within one landscape and across regions

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ABSTRACT

Large areas of tropical forests have been converted to agricultural land and subsequently abandoned. If restoration can occur on these abandoned lands, it offers great potential for biodiversity recovery, carbon sequestration, and enhanced ecosystem services. To understand the interaction between different forms of anthropogenic degradation and restoration strategies we examined biomass accumulation at two different scales. First, using small scale comparisons where the tree species pool, climate, and dispersers were similar, we quantified regeneration in degraded sites in Kibale National Park, Uganda subjected to different restoration strategies. Second, we contrasted biomass accumulation for 57 tropical studies where the nature and time since disturbance differed. The above ground biomass of 10–32 year old forest in Kibale ranged from 15,675 to 34,294 kg/ha and was a function of the type of the management strategy used to promote regeneration. The above ground biomass accumulation from other tropical sites ranged extensively; from 470 kg/ha in an 8 year old abandoned pasture in Brazil to 272,000 kg/ha in a 16 year old abandoned agricultural field in Mexico. Overall, the time since abandonment was a good predictor of biomass accumulation. This review demonstrates that once left to regenerate, secondary forests accumulate above ground biomass in a very positive manner; however, the speed of biomass accumulation can be facilitated by site-specific restoration strategies. Both the cost and efficiency of different restoration strategies vary dramatically and our research in Kibale suggests that making larger financial investments does not necessarily result in more positive biomass accumulation.

1. Introduction

Degraded forest lands and secondary forests cover significant areas throughout the tropics. In fact, in most countries they now exceed areas covered by primary forests (FAO, 2005). It is estimated that, during the 1990s, 16.1 million ha of forest was lost globally each year to deforestation, of which 15.2 million ha was lost in the tropics (Achard et al., 2004; FAO, 2005). This corresponds to annual forest losses of 0.4% globally and 0.8% in the tropics. Of the 15.2 million ha of natural forest lost annually in the tropics, 14.2 million ha were converted to other land uses primarily agriculture and pasture lands (Myers et al., 2000). Outside tropical countries, 0.9 million ha of natural forest were lost per year, of which 0.5 million ha were converted to forest plantations and 0.4 million ha were converted to other land uses (Achard et al., 2002, 2004; DeFries et al., 2002; Fearnside and Laurance, 2003; FAO, 2005). The root causes underlying these changes are a complex combination of interrelated factors that include population growth (Pearce and Brown, 1994; Bawa and Dayanandan, 1997), economic growth and house hold resource consumption (Lui et al., 2003), poverty (Naughton et al., 2011), and land tenure insecurity (Gardner-Outlaw and Engelman, 1997). For example, DeFries et al. (2002) and FAO (2005) argued that, since 1950, the world's population has more than doubled with the compounding result that, in many regions, forests have to be cleared to grow food and to make way for new settlements. Such demographic changes typically go hand in hand with increasing demands for resources by each household (Lui et al., 2003).

These trends in deforestation signify that a greater proportion of the world's primary forests will be replaced by secondary and degraded forests. Wright and Muller-Landau (2006) estimated that secondary forests have replaced at least one of each 6 ha of primary forest deforested in the 1990s and Emrich et al. (2000) estimated that secondary forests represent 35% of all existing tropical forests in the world. In addition, a number of researchers have predicted that in the future many areas of tropical forests will be secondary

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forests regenerating after previous clearing (Wright and Muller-Landau, 2006; Jacob et al., 2008). In Costa Rica, for example, 1800 km^2 are estimated to be under primary forest cover, while secondary forests cover up to 4250 km^2 ha (Berti, 2001). Likewise, in Puerto Rico, the area of secondary forest is much greater than the area in primary forests (Lugo and Helmer, 2004), which results from a combination of slowing population growth rate and urbanization.

Today less than 70,000 km^2 (28%) remains of East Africa's original forests (FAO, 2005). Furthermore, in Uganda, the country in which part of this research focuses, tropical forest covered 20% of the country (39,942 km^2) in the early part of the 19th century, but deforestation has reduced this to just 3% (5991 km^2; Howard et al., 2000). The most recent estimate suggests that the annual rate of loss of tropical forest in Uganda is 7% although this rate is slowing down (Pomeroy and Tushabe, 2004) as there are few forests remaining that are not in protected areas.

There are many reasons why forests in different parts of the world that were cleared for agriculture are abandoned soon after clearing. First, unsustainable shifting agricultural practices in these cleared forests result in lands being abandoned within a few years of cultivation due to loss of productivity (Harwood et al., 1993). This often occurs when populations in particularly in regions rise and there is not enough land remaining to allow adequate fallow times or in frontiers of agricultural expansion where new migrants that have not traditionally been shifting agriculturalists move into an area (Naughton et al., 2011). Second, changing patterns of human settlement resulting from decline in fertility rates and an intense urbanization in many tropical countries (United Nations, 2004) can cause large tracts of agricultural land to be abandoned. If developing countries follow similar socio-economic and demographic changes as has been witnessed in developed countries, this will lead to migration of rural population into urban centers (Aide and Grau, 2004; Wright and Muller-Landau, 2006; Jacob et al., 2008), which could potentially leave large areas of secondary forests in the rural areas. This prediction rests on the assumption that a large portion of the rural population will be attracted to urban centers where they can get relatively well-paying jobs and be offered better social services.

National policy makers and conservationists rarely consider the value of secondary forests. This oversight ignores the fact that these forests have resources that, when properly managed, can alleviate pressure on the remaining primary tropical forests. For example, secondary forests are known for faster accumulation of woody biomass because of the fast growth of pioneer trees species (Silver et al., 2000; Guariguata and Ostertag, 2001) and with the larger areas being abandoned, they could provide many valuable ecosystem services (Lugo and Helmer, 2004), biodiversity conservation, improve water quality, and wood and non-timber forest products (Naughton and Chapman, 2002). In addition, they have the potential to sequester carbon from the atmosphere (Chazdon et al., 1998; Aide et al., 2000; Silver et al., 2000; Lugo and Helmer, 2004; Maass et al., 2005).

The research reported here uses biomass accumulation as a measure of forest regeneration and we contrast regeneration on two scales. (1) First, we report on 48 months of research at a relatively small scale by quantify above-ground biomass of woody trees in secondary forests that have been subjected to different restoration strategies in Kibale National Park, Uganda. Fine-scale contrasts may be more sensitive for evaluating the effectiveness of restoration strategies than comparisons made on larger, more course grained scales. At small spatial scales, phylogeny is largely controlled for, since contrast can often be made within a set of tree species, and un-measured ecological parameters (e.g., climate, soil type) are less likely to differ between neighboring sites than is the case if contrasts were made between widely-separated sites. (2) Secondly, we review rates of biomass accumulation throughout the tropics after different types of human disturbances. Making comparisons at this large spatial scale provides a large data set which can be used to start to understand what forms of anthropogenic degradation results in faster regeneration.

2. Materials and methods

2.1. Small scale comparison of regeneration at sites within Kibale National Park, Uganda

The study was conducted between May 2002 and May 2006 in Kibale National Park, Uganda. 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. Kibale is a mid-altitude (920–1590 m), moist-evergreen forest. It received a mean annual rainfall of 1707 mm between 1990 and 2010, falling mainly during the two rainy seasons and the mean daily minimum temperature is 15.5 °C and the mean daily maximum temperature is 23.8 °C (Chapman and Lambert, 2000; Stampone et al., 2011). We quantified forest regeneration at three sites, which each employed a different strategy to restore tropical forest on areas that were once forest, but became dominated by tall grasses.

Site One was located in former pine plantations (*Pinus caribaea*, *Pinus patula*, *Cupressus lusitanica*) that were planted in Kibale between 1953 and 1977 on grasslands that were previously forested. These lands were abandoned when a rinderpest epidemic devastated the livestock in the area shortly after 1900 (Osmaston, 1959; Kingston, 1967; Wing and Buss, 1970). Active fire exclusion was initially important to protect young pine seedlings, but became less important as the plantation matured (Zanne and Chapman, 2001; Lwanga, 2003). Once the plantations matured, native tree species and shrubs invaded the understory and were not removed (Chapman and Chapman, 1996; Zanne and Chapman, 2001; Duncan and Chapman, 2003b; Omeja et al., 2009). The study was conducted in the Mikana plantation that was harvested in 1998.

In May 2002, two 200 × 100 m (2 ha) plots were established in the harvested pine plantation and each plot was divided into fifty 20 × 20 m sub-plots (Omeja et al., 2009). The plots were adjacent to one another and separated by approximately 20 m. One plot was randomly assigned as the enrichment planting plot. At the time of planting both areas were dominated by a variety of grasses, primarily *Pennisetum purpureum* and *Hyparrhenia* spp., and no seedlings/saplings could be seen emerging from the grass. These grasses are flammable during the dry season, thus the area needed to be protected from fire and fire lanes were maintained in the regenerating area for 5 years, after which time it was viewed that the tree community had developed sufficiently so that the area would not easily burn. Dispersed throughout the grasses were small stands of native trees that had grown up under the pines and had not been harvested. The control plot had eight trees > 30 cm DBH/ha and the experimental plot had 25 trees/ha of this size. This is in comparison to approximately 110 trees/ha of this size in the intact forest. These established trees are excluded from biomass evaluations, but the presence of the larger number of trees in the experimental plot could have enhanced regeneration.

In the enrichment planting plot, 400 seedlings of fast-growing species that colonize disturbed areas (*Albizia grandibracteata, Celtis africana, Celtis durandii*, and *Milletia dura*) were planted, with two of each of these species being planted in each 20 × 20 m subplot. To space the seedlings, each subplot was divided into four sections and two seedlings of one of the four species were planted in the middle of these sections, 2 m apart. The area around the planted seedling was weeded removing competitors. If a seedling died, a new seedling was planted in its place and this replacement continued until the end of the monitoring. If a seedling survived past the first month following planting, the probability of surviving to the end of the 4 years was high. The four species were selected because they were species that typically colonize disturbed areas and were easily available under mature trees, which reduced the cost and time of raising seeds under nursery conditions. The remaining plot was the control; however, we established similar sub-plots to aid in quantifying regeneration and to ensure that each area received similar treatment.

Site 2 is the Ngogo grassland which is situated at the center of the park and has been protected from fires since the 1970s, although some sections have occasionally been burnt by poachers. When Ngogo camp was established 33 years ago, the grassland around the camp and within the trail system started receiving fire protection (Lwanga, 2003). We studied two 0.5 ha plots. The 12-year plot was bordered by a motorable track on the western side and firebreak on either side and it most recently burnt in 1996. The 32-year plot (0.5 ha) was open grassland in 1984 and has not burned since the area began to be monitored in 1975.

Site 3 has a longer and more intense history of land use. This is an area in the southern part of Kibale that was illegally occupied by agriculturalists in the 1970s until their eviction in 1992 (van Orsdol, 1986; Baranga, 1991). The encroachment adversely affected approximately 120 km^2, leading to forest destruction and the suppression of forest restoration. After the eviction, the area was mainly fire maintained grassland, covered by elephant grass because of frequent fires that spread into the park from neighboring gardens (Struhsaker, 2003; Omeja et al., 2011). At this site, the Forest Absorbing Carbon Emission (FACE) Foundation is engaged in a carbon offset reforestation program in collaboration with the Uganda Wildlife Authority (UWA). This program involved assistance to restore 10,000 ha of formerly settled and degraded lands within the park. Eight compartments were established in the first phase of the replanting project. Twelve years later, we randomly established ten 10×50 m plots in each compartment using randomly generated locations and directions. 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). This regenerating area was protected by a series of maintained fire lanes, people in fire watchtowers, and crews available to put out fires soon after they started. Given the investment in the planting, the fire lanes are still maintained, but it seemed likely that after 10 years, the areas would not easily burn.

In each of these three sites we quantified above-ground tree biomass as an index of the speed of forest restoration. Most published allometric relations are site-specific, reflecting the original objective for which they were developed (Girgal and Kernik, 1984; Pastor et al., 1984) and are not developed for regenerating forest. Since, this area was a young regenerating forest, we developed our own allometric regression equations of biomass of woody trees species, by selecting a sample of early successional trees of varying sizes for harvest and to determine their dry weight (Omeja et al., 2011). These, allometric relationships were developed between stem diameter and above-ground biomass. This follows methods that rely on the combination of regression equations to produce either species-specific allometry or allometry for groups of species (Keith et al., 1999; Jenkins et al., 2003). Therefore, we identified trees in forest lands adjacent to the park, measured their diameter at breast height (DBH) and ground height (DGH), and the trees were felled and their total lengths measured. Individual trees were selected so that they were of similar size to those regenerating in the study sites (i.e., DBH 1.1–10.0 cm and DGH 1.6–11.0 cm; within the weights of 0.25–10 kg; $n = 200$). Choice of tree species for biomass estimation was made based on survey of the common tree species in the study sites. In total, 200 stems (20 stems per species) were harvested. The species included*A. grandibracteata, Brideliamicrantha, C. africana, C. durandii, Clausena* spp, *Maesa lanceolata, Funtumia latifolia, M. dura*, and *Trema orientalis*. First, the branches were removed and the total dry weight of stems and leaves was determined. Second, the stems were cut into small sections and air dried until constant mass was attained. Once all components had reached a constant dry weight, the total dry weight of the tree was quantified.

For each site, we identified all the woody tree species, measured their heights, diameter at breast height (DBH) if above 1.3 m, and diameter at ground height (DGH) 0.3 m above the ground. From the DGH measurements, we calculated the biomass per hectare of each site based on the DGH and biomass relationships. The dry biomass of trees was predicted by log DGH ($R^2 = 0.653$, $n = 200$, $y = 2.053x + 2.056$).

2.2. Large scale comparison of biomass accumulations around the world

To compare the generality of patterns quantified in Kibale, we reviewed the available literature on similar studies conducted in any type of closed-canopy forest in the tropics. The results reported here only consider those studies that were undertaken in areas that had undergone the same general kinds of human disturbance regimes as those in Kibale. Making comparisons at this large spatial scale provides a large data set which can be used to start to understand what forms of anthropogenic degradation results in different speeds of regeneration or what restoration efforts are most effective. To compare restoring lands that had received different treatments before abandonment (i.e., agriculture versus pasture), we conducted a regression analysis contrasting biomass accumulation versus the number of years since abandonment. Subsequently, we contrasted the residuals of these treatments with a t-test. If a single paper reported above ground biomass from sites in the same general region, we considered them independent because the biomass within a study among sites was often highly variable.

3. Results

3.1. Small scale assessment of total aboveground biomass

Total aboveground biomass of the woody tree species was highly variable between the areas of Kibale receiving different restoration treatments, ranging from 15,675 kg/ha in a 12 year old secondary forest in the replanted area to 34,294 kg/ha also in a 12 year old forest in fire protected area (Table 1). Surprisingly, the age since abandonment of the land did not proportionately affect the rate of biomass accumulation. This is clearly documented at Ngogo, where the 12 year old fire-protected forest had higher aboveground biomass (34,294 kg/ha) than the 32 year old forest (29,860 kg/ha). This implies that the younger secondary forest species were accumulating biomass at a relatively higher rate (2858 kg/ha/year) than the older secondary forest species in the same location (933 kg/ha/year; Table 1). This reflects the replacement of pioneers with later successional species.

Equally surprising was that despite receiving large financial investment, the area that was intensively reforested (Site 3) was not able to accumulate as much tree biomass (15,675 kg/ha; 1306 kg/ha/year) as the area that received fire protection after the same 12 years. The fire protected area was more than double (34,294 kg/ha; 2858 kg/ha/year) that of intensively reforested area.

In the former pines, the mean aboveground biomass accumulation of woody indigenous trees after 10 years was 22,124 kg/ha (rate = 2212 kg/ha/year; Omeja et al., 2009), while in the area that was intensively reforested aboveground biomass was (15,675 kg/ha; 1306 kg/ha/year; Omeja et al., 2011).

Table 1
Above ground biomass of woody tree species at Kibale National Park, and 57 other tropical sites following different periods since abandonment and different types of land use practices, vegetation types, and species. The Kibale sites described in this study are in bold.

Years	Past land use	Dry biomass (kg/ha)	Source site	Recovery rates (kg/ha/year)
8	Pasture and heavy use	470	Buschbacher et al. (1992), Brazil	59
3.5	Pasture and moderate use	830	Buschbacher et al. (1992), Brazil	237
3	Cut and burnt	870	Uhl et al. (1982), Venezuela.	290
2.5	Pasture and heavy use	760	Buschbacher et al. (1992), Brazil	304
8	Pasture	3000	Uhl et al. (1988), Amazon	375
8	Pasture and moderate use	3280	Buschbacher et al. (1992), Brazil	410
4	Pasture and moderate use	1700	Buschbacher et al. (1992), Brazil	425
3	Cut forest	1291	Uhl et al. (1982), Venezuela	430
3.5	Pasture and moderate use	1680	Buschbacher et al. (1992), Brazil	480
7.5	Pasture and moderate use	3700	Buschbacher et al. (1992), Brazil	493
6	Pasture and heavy use	2994	Naughton and Chapman (2002), Uganda	499
9	Slash and burn; agriculture	5130	Saldarriaga et al. (1988); Columbia/Venezuela	570
2.5	Pasture and heavy use	1550	Buschbacher et al. (1992), Brazil	620
15	Slash and burn; agriculture	10,000	Toky and Ramakrishnan (1983), India	667
4	Mixed species fallow	2771	Tergas (1965), Guatemala	693
4	Slash and burn	2861	Uhl (1987), Venezuela	715
4	Slash and burn	2888	Uhl and Jordon (1984), Venezuela	722
20	Slash and burn; agriculture	15,000	Toky and Ramakrishnan (1983), India	750
6	Slash and burn	4609	Nye and Greenland (1960), Nigeria	768
3.5	Pasture and light use	2940	Buschbacher et al. (1992), Brazil	840
32	**Grassland, fire control**	**29,860**	**Site 2, Kibale, Uganda**	**933**
4	Slash and burn	3796	Ewel (1971), Panama	949
8	Pasture and light use	8610	Buschbacher et al. (1992), Brazil	1076
8	Pasture and light use	8890	Buschbacher et al. (1992), Brazil	1111
4.5	Pasture and light use	5340	Buschbacher et al. (1992), Brazil	1187
4	Slash and burn	4839	Gamble et al. (1969), Colombia	1210
12	**Intensive replanting**	**15,675**	**Site 3, Kibale, Uganda**	**1306**
9	Premontane wet – Atlantic forest in Costa Rica.	12,000	Cifuentes-Jara (2008), Costa Rica	1333
4	Slash and burn	5361	Naughton and Chapman (2002), Uganda	1340
5	Cutting with burning and 6 years cultivation	7100	Uhl (1987), San Carlos del Rio Negro, Venezuela	1420
5	Slash and burn	7669	Bartholomew et al. (1953), DR Congo	1534
80	Agriculture	134,000	Saldarriaga et al. (1988), Columbia	1675
10	**Pine harvested, no planting**	**17,347**	**Site 1 (Control), Kibale, Uganda**	**1735**
30	Agriculture	54,000	Saldarriaga et al. (1988), Columbia	1800
80	Agriculture	144,000	Saldarriaga et al. (1988), Venezuela	1800
60	Agriculture	116,000	Saldarriaga et al. (1988), Venezuela	1933
20	Agriculture	44,000	Saldarriaga et al. (1988), Columbia	2200
60	Agriculture	138,000	Saldarriaga et al. (1988), Columbia	2300
10	**Pine harvested, planted**	**27,202**	**Site 1 (experimental), Kibale, Uganda**	**2720**
8	Agriculture	22,000	Hughes et al. (1999), Mexico	2750
12	**Grassland, fire control**	**34,294**	**Site 2, Kibale, Uganda**	**2858**
15	Abandoned pasture	46,000	Chacón et al. (2007), Costa Rica	3067
20	Agriculture	62,000	Saldarriaga et al. (1988), Columbia	3100
8	Pasture	25,000	Uhl et al. (1988), Paragominas; Amazon	3125
20	Agriculture	64,000	Saldarriaga et al. (1988), Venezuela	3200
14	Abandoned pasture	51,000	Cifuentes-Jara (2008), Costa Rica	3643
14	Abandoned pasture	51,000	Vargas et al. (2008), Mexico	3643
14	Agriculture	53,000	Saldarriaga et al. (1988), Venezuela	3786
9	Abandoned pasture	37,000	Vargas et al. (2008), Mexico	4111
20	Agriculture	83,000	Saldarriaga et al. (1988), Venezuela	4150
16	Abandoned pasture	67,000	Cifuentes-Jara (2008), Costa Rica	4188
15	Abandoned pasture	67,000	Vargas et al. (2008), Mexico	4467
20	Agriculture	98,000	Saldarriaga et al. (1988), Columbia	4900
25	Short and extended landuse	130,000	Steininger (2000), Bolivia	5200
5	Cutting with burning and 3 years cultivation	26,500	Uhl (1987), Venezuela	5300
50	Agriculture	274,000	Hughes et al. (1999), Mexico.	5480
11	Pasture	63,000	Alves et al. (1997) Rondonia, Amazon	5727
10	Slash and burn; agriculture	58,000	Toky and Ramakrishnan (1983), India	5800
8	Pasture	50,000	Uhl et al. (1988), Paragominas, Amazon	6250
12	Agriculture	82,000	Saldarriaga et al. (1988), Columbia	6833
5	Cutting and no burning or cultivation	35,200	Uhl (1987). San Carlos del Rio Negro, Venezuela	7040
26	Agriculture	199,000	Hughes et al. (1999), Mexico	7654
18	Pasture	143,000	Alves et al. (1997), Rondonia, Amazon	7944
25	Short and extended landuse	200,000	Steininger (2000), Brazil	8000
30	Agriculture	241,000	Hughes et al. (1999), Mexico	8033
8	Pasture	97,000	Hughes et al. (1999), Mexico	12,125
16	Agriculture	272,000	Hughes et al. (1999), Mexico	17,000
			Average biomass	2931

Note: The characters in bold are results from this study or other studies conducted in KNP or the surrounding areas.

3.2. Small scale assessment of woody tree species richness

The total number of woody tree species regenerating in all the areas was promising, considering the relatively shorter time that the restoration initiatives have been operating. After 12 years of fire control, the area had 23 tree species in 0.5 ha and after 32 years post-fire control the number of tree species rose to 48 in 0.5 ha. Ten years after pine harvesting, the area had 40 trees species in

2 ha, while the replanted area had a total of 40 tree species 12 years after the onset of restoration program in 4 ha.

3.3. Large scale aboveground biomass throughout the tropics

The aboveground biomass from the data obtained from other areas of the tropics ranged from 470 kg/ha (59 kg/ha/year) in an 8 year old heavily used abandoned pasture in Brazil to 272,000 kg/ha (17,000 kg/ha/year) in a 16 year old abandoned agricultural field in Mexico (Table 1, Fig. 1). This variation was not surprising considering the variation in locations, climate, and land uses. We found that, there was no significant difference between the aboveground biomass accumulation of formerly agricultural or pasture lands (i.e., the residuals of agricultural land and those of pastures did not differ $t = 0.910$, $p = 0.139$).

When we considered the entire data set, the time since abandonment was a good predictor of biomass accumulation despite the fact that they had received different land use treatments, had different climatic regimes, and were found in locations throughout the tropics ($r^2 = 0.663$, $p < 0.001$).

4. Discussion

4.1. Small scale assessment of total aboveground biomass

In tropical forest, human activities are typically destructive. However, this study and a number of related studies (Table 1; Fig. 1) demonstrate that tropical forests have the capacity to recover from even intensive human destruction if they receive protection or some sort of reforestation effort. A major question that remains is: are some forms of management interventions more effective than others? With the data evaluated in our study, this question can be best answered by first examining the results of different management interventions in Kibale where conditions are relatively homogeneous and second by examining the generality of these findings to elsewhere.

Considering the restoration efforts in Kibale, the highest rate of biomass accumulation was at the site that received 12 years of fire protection (2858 kg/ha/year). It is interesting that the site receiving 32 years of fire control had a lower rate of biomass accumulation (933 kg/ha/year). There did not seem to be any physical differences between the two sites (e.g., slope, orientation) and the two areas were in very close proximity, thus soils and climate would not differ. What we believe is happening is that some of the early successional species that first colonized the area, often in high densities, are dying and are being replaced by later successional or old growth species. This is supported by the many dead stems found on the ground at this site. The restoration at the pine site and the intensively reforested site appeared to follow similar patterns; however, since the intensively reforested site had species planted, such *C. durandii* and *Warbugia ugandensis* that are common in old growth forest, the decline following the die-off of the pioneers may not be as severe as the fire protected sites.

The sites regenerating after the harvest of pines planted in grasslands had reasonably high rates of biomass accumulation (1735–2720 kg/ha/year). The planting of the pines is likely of a similar cost to that seen at site which planted native trees at a cost of US$ 120,000 per km^2. However, when the plantations are harvested the sale of the timber can pay for the initial costs of planting. As long as there are natural forest fragments in the vicinity to provide a seed source (Parrotta et al., 1997; Zanne and Chapman, 2001), numerous studies have demonstrated the catalytic effect of plantations in fostering the regeneration of native tree species in their understory (Parrotta, 1992; Chapman and Chapman, 1996; Chapman et al., 2002; Duncan and Chapman, 2003a). Whether such plantations could create unintended consequences (Struhsaker et al., 1989) should be evaluated by conservation managers.

When evaluating a restoration project, one must not only consider the ecological successes or failures, but also consider so-

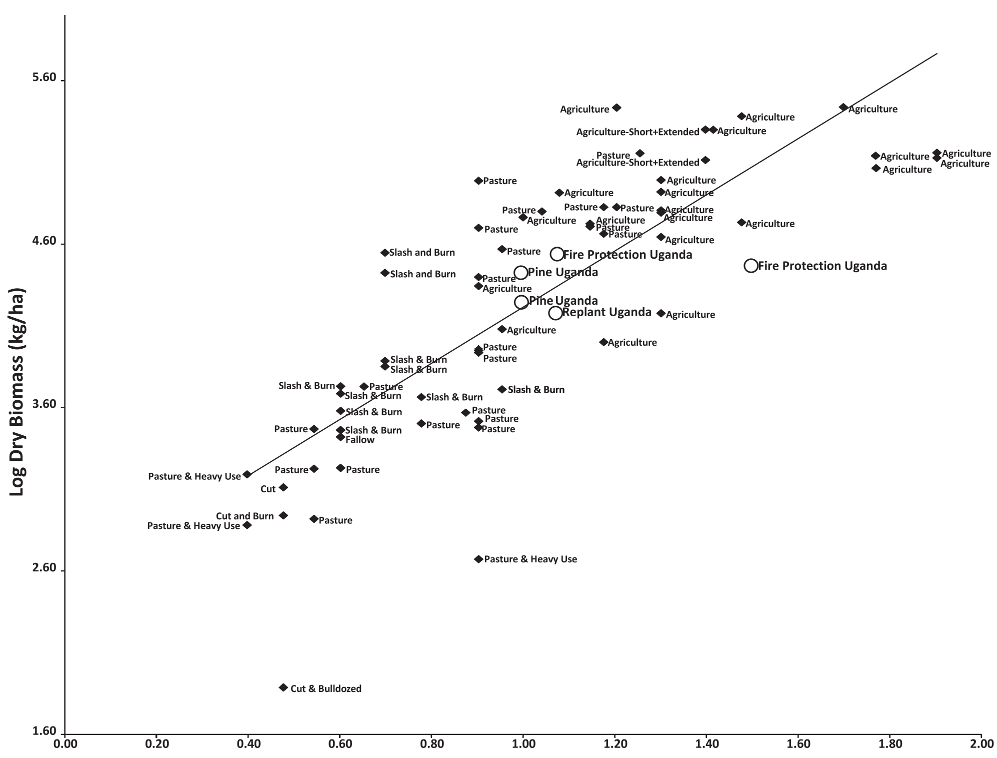

Fig. 1. A log/log plot of dry biomass (kg/ha) and years since disturbance for tropical forest sites. The Ugandan sites are indicated by open circles and the other sites by diamonds. We indicate the type of land use described in the original study by each point.

cial aspects as they are equally important in ensuring the success of any forest restoration project (Shono et al., 2007). The harvesting of the pines had a number of negative social ramifications. Since the crews that harvested the pines were typically not from the local area, there was considerable conflict between the imported labor and the local community. In addition, the hauling out of the pines significantly degraded the roads, which had to be repaired by the local community. Finally, a large number of snares were found near the harvester's within-park camps, suggesting they were collecting a great deal of bushmeat. However, with careful planning all of these problems could be avoided.

The intensive reforestation program that involved the FACE/UWA project planting native trees into the degraded grasslands was accumulating biomass at a rate of 1306 kg/ha/year at the time of sampling. This is a very reasonable rate of regeneration to meet the goals of many restoration efforts; however, it was not as high as simply initially protecting the area from fire. This project should also be evaluated in terms of cost effectiveness and it impact on social life of the neighboring communities. The intensive reforestation program cost US\$ 120,000 per km^2. There are cases where restoration efforts are more expensive than this. For example it costs US\$ 150,000 per km^2 to restore degraded lands in Malaysia (Pinso and Moura-Costa, 1993) and US\$ 250,000 per km^2 to restore bauxite mined land in Amazon (Parrotta and Knowles, 1999). Thus, this approach is costly and most tropical countries do not have such finances. However, this project had a number of social benefits. There are approximately 125 regular workers employed by the FACE/UWA project and during active planting periods the work force grew to approximately 500 people, with the vast majority being local. Also, planting progressed from the south-eastern side of the park to the south-western side, so two communities on either side of the park benefited. Even after the planting has been concluded, the local people are still employed in the maintenance of the established fire lanes so that the seedlings are not destroyed by wildfires. In addition, these communities have access to free seedling to plant in their gardens and the communities readily took advantage of this program.

Given the rate of biomass accumulation and since it is not expensive to hire teams from the local community to cut and maintain fire lanes and fight fire, at US\$ 500/km^2/year, simple fire protection of areas close to the forest may be the most cost efficient way to promote regeneration of a species rich forest. It should be noted that caution must be taken when comparing rates of biomass accumulation of sites that are of different ages, since direct comparisons are making the assumption that there is a linear relationships between biomass accumulation and time – this relationship is more likely to follow a logarithmic distribution as indicated by Fig. 1 and they may exhibit reversals in biomass accumulation as indicated by death of the early successional species in the fire protected sites in Kibale.

4.2. Large scale above ground biomass in the tropics

The pattern seen globally (Fig. 1) is very positive. When considering the entire data set, 66% of the variation in biomass accumulation was explained by the time since abandonment. This is a relatively good predictor of biomass accumulation considering that these areas received different land-use treatments, had different climates, and were found in regions of the world. Unfortunately, the majority of the literature generally does not provide sufficient detail to evaluate how past land-use practices influences biomass accumulation. Often only simple descriptions of the prior land-use practice is provided (e.g., agriculture) and no information is presented about important variables, such as the distance to seed sources, the length of time the human activities were conducted on the land, etc. In addition, the biomass values reported by difference studies evaluate different types or regrowth. The present study considered only the woody tree species, while some other studies also considered biomass of shrub and grasses. The use of different methods for calculating above ground biomass is also an important source of variance when comparing above ground biomass between studies (Chave, 2004, 2005). What this calls for is well designed experiments in the same regions using identical methods, so as to control for as many factors as possible, while varying land-use practices.

Consistent with other tropical studies (Brown and Lugo, 1990; Guariguata and Ostertag, 2001), our results showed slow initial biomass accumulation (rates of 59–1100 kg/ha/year), a high rates (2700–8000 kg/ha/year) in intermediate stages (10–25 years), followed by a decrease in biomass accumulation (1700–2200 kg/ha/year; Table 1). The slow initial start possibly occurred because of the effect of seasonal water limitation on young vegetation (Ewel, 1986; Murphy and Lugo, 1986) or the absence of a seed bank due to a long and extensive land use history (Zimmerman and Aide, 2000), as well as repeated fires after pasture abandonment. In addition, isolation from currently available seed sources due to large scale deforestation (Arroyo-Mora, 2005), absence of remnant vegetation (Guariguata and Ostertag, 2001), and increased seedling mortality due to low soil moisture may also restrict forest establishment. Despite the slow initial growth, it is possible that once a secondary forest becomes established, less competition for light between saplings or a reduction in competition with grasses, and access to deeper soil water may allow for high rates of biomass accumulation. Overall, the results from our field study in Uganda and comparative analysis suggests that, once established, secondary forests accumulate above-ground biomass at rates following similar patterns across a diversity of systems. Also, there is no evidence to suggest that the Kibale sites are in anyway atypical as they do not fall far from the overall predicted line.

In the end, basing the argument on the Society for Ecological Restoration (2004) Primer that provides a list of ecosystem attributes as a guideline for measuring forest restoration success and results from studies from other tropical regions, it is evident that all the three restoration treatments carried out in Kibale by UWA produce valuable restoration gains and the choice of the methods will depend on the management goals, financial costs, and consideration of the impact of the method on the local community.

5. Conclusions

We provide a quantification of above-ground biomass accumulation for areas in Kibale National Park, Uganda with different histories of disturbance and subsequent management. From the simplest to the more complex these include: fire prevention, using pines to encourage the formation of a suitable habitat for tree regeneration and including enrichment planting after the pines are harvested or not, and enrichment planting alongside of fire protection. Each restoration approach has different financial and social costs. Subsequently, a review of global patterns of biomass accumulations shows that the time since abandonment was a relatively good predictor of biomass accumulation despite the fact that the different areas received different land use treatments, had different climatic regimes, and were found in locations throughout the tropics. Our study demonstrates that once left to regenerate, secondary forests accumulate above ground biomass in a very positive manner; however, the speed of biomass accumulation can be facilitated by site-specific restoration strategies. Both the cost and efficiency of different restoration strategies vary dramatically and our research suggests that making larger financial investments does not necessarily result in more positive conservation gains.

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