

Communities of Trees Along a Tropical Forest Restoration Gradient¹

A. A. Owiny

Makerere University, PO Box 7062 Kampala, Uganda

e-mail: owinyiarthur@yahoo.com

Received April 27, 2015

Abstract—Increasing rates of deforestation in tropical forests have been linked to agriculturalists. A critical concern generating debate is how well communities of trees recover into a more species rich ecosystem after restoration planting. The aim of the study was to evaluate the pattern of recovery of communities of tree, assess the influence of *Acanthus pubescens*, *Lantana camara* and *Pennisetum purpureum*, on the recovery as well as how restoration planting facilitates recruitment of other native tree seedlings along a gradient of forest restoration in Kibale National Park, Uganda after evictions of illegal settlers. We studied six restoration forests ranging in age from 3 to 16 years, naturally regenerating and three primary forests. Our results showed that recovery with natural regeneration was more effective than restoration planting although the latter enhanced recruitment of other native tree seedling. Tree recovery was generally correlated with age so that species density and diversity increased although at different rates. A reverse pattern was found for dominance but no clear pattern was found for tree density (individual/ha). Communities of tree showed directional patterns of change however community composition were still distinct among the different forests. *A. pubescens*, *L. camara* and *P. purpureum* negatively correlated with species density, tree density and diversity but a positive correlation was found for dominance. Restoration planting can reestablish forests with high species density, tree density and diversity, but this is dependent on age and the extent of the herbs, grasses and shrubs cover in tropical forests.

Keywords: *A. pubescens*, Anthropogenic disturbance, Natural regeneration, *P. purpureum*, Restoration planting, Tree recovery, Uganda

DOI: 10.1134/S1067413616010094

1. INTRODUCTION

Tropical rain forests are decreasing at an approximate rate of 12.5 million hectares annually due to deforestation and agricultural encroachment (Kobayashi, 2007). These estimates might be higher because illegal activities often go unnoticed. As such, forest restoration through planting or deliberate seeding is an important management tool for rehabilitating and hastily restoring forest ecosystems which have lost vegetation cover (Ormerod, 2003; Abebe et al., 2006). But whether restoration planting enhances recruitment of other native trees more than natural regeneration alone remains less well understood.

Nonetheless, despite restoration approaches being operational (Kuper, 1996; Parrotta et al., 1997), the lack of adequate information on how to evaluate restoration success remains a challenge (Dunn, 2004; Bowen et al., 2007). Yet it is vital to determine the most efficient methods of enhancing natural colonization of tree species into regenerating forests in heavily degraded areas. Instead, there is debate about the prediction that future tropical deforestation rates will decrease (Wright and Muller-Landau, 2006), thus

increasing the area of regenerating forests. The current level of knowledge does not support this approach (Bowen et al., 2007). Moreover, survival of many forest species depends on the capacity of disturbed areas to replenish and support their populations (Putz et al., 2000).

In this study, the success of restoration efforts in recovery of tree communities was studied. After evictions of illegal settlers, tree planting was necessary because woody herbs, shrubs and grasses such as *Acanthus pubescens* (Acanthaceae), *Aframomum* spp. (Zingiberaceae), *Lantana camara* (Verbenaceae), *Mimulopsis* spp. (Acanthaceae) and *Pennisetum purpureum* (Poaceae) colonized forests, precluding tree regeneration (Struhsaker, 2003). As such a mixture of pioneer, intermediate and climax tree species were planted to restore forest cover (see UWA-FACE Project management plan, 2006). The Uganda Wildlife Authority (UWA) and FACE the Future (previously Forests Absorbing Carbon Emissions (FACE) Foundation), are jointly managing restoration of approximately 10000 of the 15000 ha degraded area (Chapman and Lambert, 2000; Struhsaker, 2003; Omeja et al., 2011). Given the extent of restoration efforts, it is imperative to under-

¹ The article is published in the original.

stand the success of plantations compared to natural regeneration.

In addition understanding the influence of understorey vegetation on restoration can provide management with necessary information for monitoring forest restoration. Long term tree community dynamics and responses to thick understorey vegetation; the major cause of “arrested succession” are poorly understood. Invasion by e.g., *A. pubescens*, *P. purpureum* and *L. camara*, some of which are exotic, constitutes the second largest threat to biodiversity; leading to declines, extinction of native trees and alteration of species richness (Sharma and Raghubanshi, 2011). We predicted that *A. pubescens*, *P. purpureum* and *L. camara* negatively affects species density, tree density, diversity and dominance (Chapman and Chapman, 2004).

We evaluated the pattern of recovery of communities of trees and the role of restoration planting in facilitating natural recruitment of other native tree species in the differently aged restoration areas. Our objectives were to; 1—Compare changes of species density, tree density, diversity and dominance, in the differently aged restoration, naturally regenerating and primary forests. 2—Compare the recruitment of nonplanted tree seedlings in the differently aged restoration, and naturally regenerating forests. 3—Assess the influence of *A. pubescens*, *P. purpureum* and *L. camara* on the recovery of trees.

2. MATERIALS AND METHODS

2.1. Study Area

This study was conducted at Mainaro area, in the southern section of Kibale National Park (KNP), Western Uganda (0°13′–0°41′ N and 30°19′–30°32′ E) between February and April 2013. KNP is located near the foothills of the Ruwenzori Mountains, and covers about 795 km² (Wasserman and Chapman, 2003). It is a mid-altitude, moist-evergreen forest receiving an average rainfall of 1697mm annually. Rainfall peaks are in March–May and in September–November. The temperatures range between 14.9 to 20.2°C (Nyafwono et al., 2015).

Between 1960s and 70s, the southern section of KNP was encroached by agriculturalists and settlers while still a forest reserve (Chapman and Lambert, 2000), resulting in human-modified landscapes, composed of a mosaic of primary forests (MIF’s), adjacent to degraded forest (AC’s), and regenerating forest (NREG’s) fragments. In 1994, after eviction, UWA and FACE commenced restoration activities. Thirty seven species were planted but only 30% survival rate was achieved due to lack of proper baseline information. In 1996, site matching was done, and tree species were reduced from 37 to 22, later to 16 in the subsequent years, and finally 10 fast growing species were maintained from 2004 to date; (i.e., *Bridelia micran-*

thus, *Cordia africana*, *Cordia millenii*, *Croton macrocarpus*, *Croton macrostachyus*, *Mimusopsis bagshaweii*, *Prunus africana*, *Sapium ellipticum*, *Spathodea campanulata*, and *Warburgia ugandensis*). Between 1997–1998 there was no planting due to evaluations, and in 2009 because of lack of funds. The tendering, propagating, transplanting and all seedling management procedures are described by Omeja et al. (2011).

2.2. Study Design

The Mainaro area was classified and mapped a priori into six restoration areas following planting history, (3, 5, 8, 11, 14, and 16 years, hereby classified as Age Classes AC 3, AC 5, AC 8, AC 11, AC 14 and AC16), naturally regenerating forest (NREG) and three primary forests areas MIF 1, MIF 2 and MIF 3 (Table 1). Plot locations were randomized using a grid system laid on top of the study areas which land use history was determined prior to the study, based on historical records. Initially, we had 20 plots to each study area. But later the inspection of Landsat images enabled us to determine the exact logging year at each area. This led to re-classification of some areas and production of uneven number of plots in those areas. If a plot was located into foot trails or inaccessible points then it was re-oriented perpendicular from that direction.

2.3. Tree Measurements

For each plot, we counted trees and measured diameter at 1.3 m (diameter at breast height, dbh). Four nested plots were established to measure; mature trees (dbh > 20 cm), poles (dbh 10–20 cm), saplings (dbh 5–10 cm) and seedlings (diameter < 5 cm). Mature trees, poles, saplings and seedlings were measured in sub plot sizes of 40 × 20 m, 20 × 20 m, 20 × 10 m and 10 × 10 m respectively (modified from Tabuti, 2007).

For each plot, tree density (Individuals/ha) were calculated in each sub-plot and then values of all sub-plots were summed together. Tree species encountered were primarily identified in the field but in a few cases samples were collected and identified at the Makerere University Herbarium. Majority of the species were identified to species level. At each plot, the cover of *A. pubescens*, *L. camara* and *P. purpureum* were independently and visually estimated in percentages: 0, <1% ≤ 0.5, <10% ≤ 1, <20% ≤ 2, <30% ≤ 3, <40% ≤ 4...100% (see Nyafwono et al., 2015). To minimize the risk of subjective error, visual estimation was conducted within one season (Korhonen et al., 2006; Nyafwono et al., 2015).

2.4. Data Analysis

Species accumulation curves (showing observed species counts) were generated for each of the differently aged restoration, naturally regenerating and pri-

Table 1. Description of the differently aged restoration, naturally regenerating and the primary forests of Kibale National Park, Uganda. Planting history, (3, 5, 8, 11, 14, and 16 years, hereby classified as Age Class; AC 3, AC 5, AC 8, AC 11, AC 14 and AC 16), naturally regenerating forest (NREG) and three primary forests areas MIF 1, MIF 2 and MIF 3

Restoration, regenerating and primary forests	Mean years since restoration	Years of replanting	Order of recovery	Number of plots
AC 3	3	2010–2011	1	20
AC 5	5	2006–2008	2	20
AC 8	8	2003–2005	3	20
AC 11	11	2000–2002	4	21
AC 14	14	1999	5	22
AC 16	16	1994–1996	6	21
NREG	N/A	Regenerating	7	41
MIF 1	N/A	Primary forest	8	20
MIF 2	N/A	Primary forest	8	23
MIF 3	N/A	Primary forest	8	20

Data for: Age Class (ACs) and Naturally Regenerating (NREG) obtained from the replanted area compartments of different years (UWA-FACE Project management plan, 2006). Age data for ACs are mean of years of restoration planting. Mainaro Intact Forest (MIFs) obtained from Landsat images (<http://earthexplorer.usgs.gov/>), processed by Erdas Imagine 2011 (Version 11.0.2) covering years between 1994 and 2011.

primary forest with program Primer-E, v6 (Clarke and Gorley, 2006). True numbers of tree species were obtained with Chao 2 species richness estimator (Colwell and Coddington, 1994).

For each study plot, we evaluated overall tree community and tree seedling data for, (1) Species density, (2) Tree density (individuals / ha), (3) Simpson diversity index (Simpson's $D = 1 - \sum((N_i(N_i - 1))/(N(N - 1)))$); where N_i = number of individuals in species i and N = total number of individuals) and (4) Berger-Parker dominance index (proportion of all individuals represented by the most abundant species, P_{\max} ; Magurran and McGill, 2011). We tested each of the variables separately with one-way ANOVA, including pair-wise post-hoc tests (Tukey). Prior to the overall tree data analysis, species density and tree density (individual/ha) were square root transformed to improve normality. But for Simpson's D and P_{\max} whose distributions were skewed and could not be normalized; non-parametric Kruskal-wallis rank sum tests were used. For seedling analysis, species density and seedling density (individuals/ha) were square root transformed, while dominance was fourth root transformed to improve normality. Non-parametric Kruskal-wallis tests were performed for Simpson's D . To test for difference and how "age" contributes to recovery of univariate variables, spearman correlations were calculated between the average values of overall variables and the "order" of recovery (Table 1). Analyses were conducted with IBM SPSS Version 19.

To assess for variations in tree community structure among the ten forests areas, Non-metric multi-dimensional scaling (NMDS; conducted with pro-

gram Primer-E, with 50 restarts) was used. Prior to this analysis, we conducted pre-treatments for the abundance data with square root transformations to down-weight the influence of most abundant species. We calculated a zero adjusted Bray-Curtis similarity matrix between samples, after adding a dummy variable 1 to the resemblance measure. For clarity, a graph representing distances among centroids was generated (Anderson et al., 2008).

The Permanova+routine of Primer-E (Anderson et al., 2008) was used to test if, and to what degree, restoration, naturally regenerating and primary forest (fixed factor) explained the variations in overall tree communities, on the basis of the Bray-Curtis similarity matrix. We conducted 999 random permutations using method "unrestricted permutation of raw data" and type III sums of squares. To test for a directional change in the tree communities along the restoration gradient, a distance-based linear model (DISTLM, conducted with program Primer-E), was fitted, where the Bray-Curtis similarity matrix was modeled with the "order" of recovery as the explanatory variable (values between 1 and 8; Table 1).

To test for the influence of *A. pubescens*, *P. purpureum* and *L. camara* cover on species density, tree density, diversity, and dominance, Spearman Rank order correlation and regression analysis were fitted, so that cover of any of the herbs, shrubs and grasses were the explanatory factor. The distributions of *A. pubescens*, *P. purpureum* and *L. camara* covers were highly skewed, and therefore differences among the restoration, naturally regenerating and primary forests were compared with non-parametric Kruskal-wallis rank sum test.

3. RESULTS

An overall total of 19517 trees representing 118 taxa were sampled from 228 study plots across the differently aged restoration, naturally regenerating and primary forests. All except nine taxa were identified at species level (seven were identified at genus level, and two remained unidentified). The naturally regenerating had more tree species compared to the differently aged restoration forests. The highest number of species recorded in restoration forests were in AC 16 (49) and the least in AC 3 (19) (Table 2). Species-accumulation curves for the different forests did not reach asymptotes (Fig. 1).

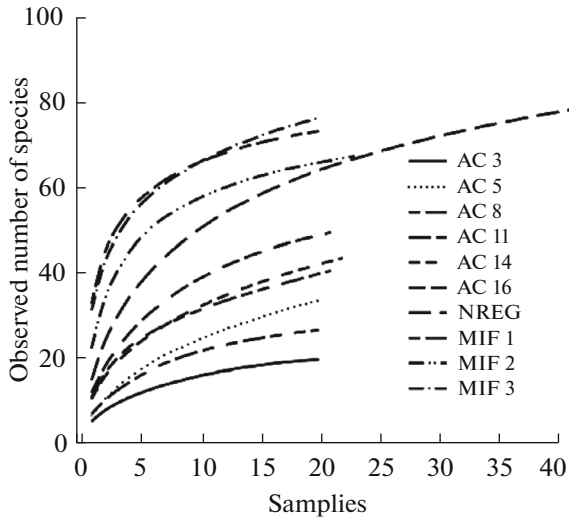


Fig. 1. Species-accumulation curves of trees in the differently aged restoration, naturally regenerating and three primary forests in Kibale National Park, Uganda. In this graph, the increasing total number of species is plotted, while samples (species count in each plot) are successively pooled, the order of samples permuted 999 times.

3.1. Species Density, Tree Density, Diversity and Dominance Patterns

We found significant differences in species density and Simpson's D values between the six restoration forests, naturally regenerating and primary forests (Species density, ANOVA, $F_{9,218} = 122.64$, $P < 0.001$; Fig. 2a, Simpson's D values, Kruskal-Wallis test, $\chi^2 = 128.79$, $df = 9$, $P < 0.001$; Fig. 2c). The naturally

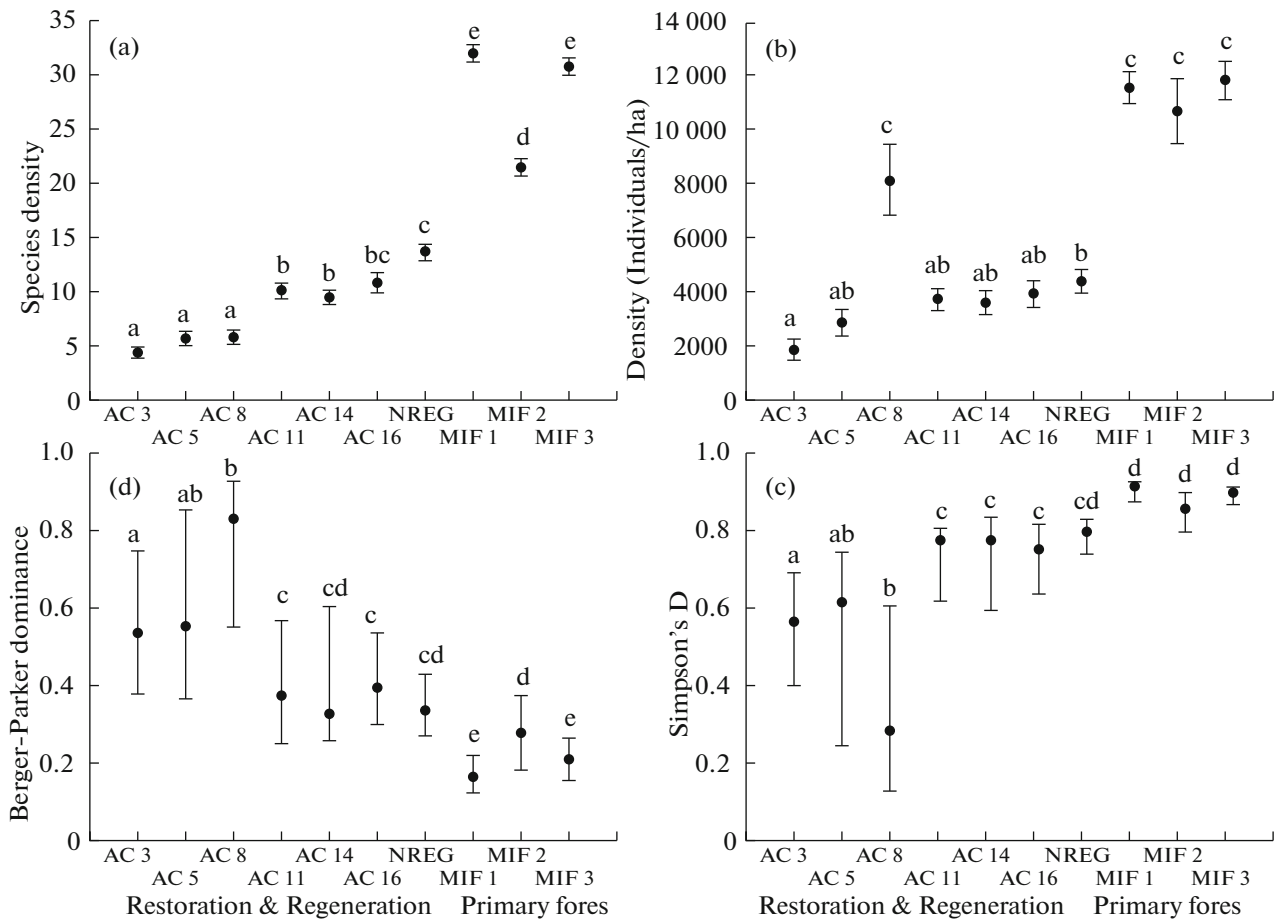


Fig. 2. Tree community averages (\pm SE) of (a) Species density, (b) Tree density (individuals ha^{-1}), (c) Simpson's diversity and (d) Berger-Parker dominance in the restoration, naturally regenerating and primary forest in KNP, Uganda. Species density and Tree density values represent backtransformed values. Bars are SE and different letters represent significant differences (Tukey's HSD, $P < 0.05$).

regenerating had substantially higher species density and diversity compared to the restoration forests.

There were significant differences in overall tree density (individuals/ha), among the restoration, naturally regenerating and primary forests ($F_{9,218} = 28.13$, $P < 0.001$). Primary forests (MIF 1-3) had substantially higher tree density compared to the naturally regenerating and restoration forests (Fig. 2b). Tree density increased with age from the recently planted (AC 3–8), to the oldest restoration areas (AC 11–16).

Berger-Parker dominance index values significantly differed among the restoration, naturally regenerating and primary forests (Kruskal-Wallis test, $\chi^2 = 104.14$, $df = 9$, $P < 0.001$). Dominance declined along the restoration gradient, so that the recently planted areas (AC 3–8) had significantly higher dominance than older restoration areas AC 11–16 (Fig. 2d).

Increase in univariate variables were correlated with “age” of planting; the order of recovery correlated positively with average species density (Spearman’s $\rho = 0.89$; $P < 0.001$), and negatively with average Berger-Parker dominance index ($\rho = -0.17$; $P = 0.009$). But no clear correlation pattern was found between “age” and recovery of tree density (individuals ha^{-1}) ($\rho = 0.61$; $P < 0.001$), and Simpson’s D ($\rho = 0.26$; $P < 0.001$).

3.2. Composition of Tree Communities and Convergence Towards Primary Forests

There was a significant directional pattern in communities of trees along the restoration gradient, from the most recently to the oldest plantations, naturally regenerating and primary forests (DISTLM; $P = 0.001$, $R^2 = 0.24$) as illustrated by the NMDS ordination of centroids (2D stress = 0.01, Fig. 3). Tree community composition of the forests significantly differed from each other (PERMANOVA, Pseudo- $F_{9,218} = 20.9$; $P = 0.001$). The restoration, naturally regenerating and primary forests explained $R^2 = 0.516$ of the variation in overall tree assemblage.

The average similarity between the oldest restoration forest (AC 16) and primary forests were MIF 1 (12.77%), MIF 2 (11.1%) and MIF 3 (11.63%), which was lower compared to the average similarity between the naturally regenerating forest and primary forests MIF 1 (18.31%), MIF 2 (16.37%) and MIF 3 (18.10%) respectively. But, they were both less than the average similarity between the three primary forests MIF 1 and 2 (38.59%), MIF 1 and 3 (50.34%), and MIF 2 and 3 (37.05%). The recent plantations (AC 3, AC 5 and AC 8) had the least similarity to the primary forests. Average similarity within primary forest plots MIF 1 (56.30%) and MIF 3 (56.95%) were approximately the same, except for MIF 2 (40.79%).

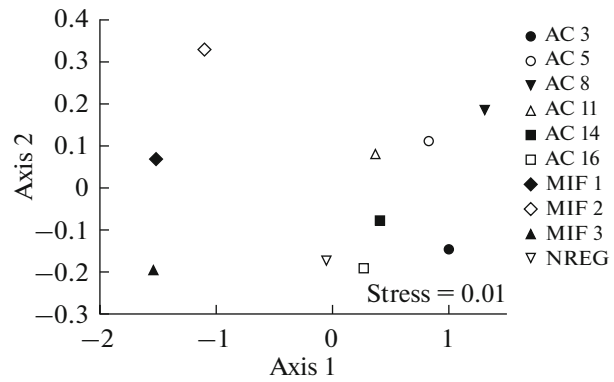


Fig. 3. MDS ordination graph of tree communities showing the centroids of the six restoration, naturally regenerating and three primary forests.

3.3. Tree Seedling Communities

We recorded a total of 13 335 nonplanted tree seedlings in the study. In the restoration forests, the highest were in AC 8 and the least were in AC 3. We also found that 60 tree species recruited in the naturally regenerating compared to 59 in the restoration forests. The highest were 40 species in AC 16, 38 species in AC 14, 33 species in AC 11, 21 species in AC 8, 29 species in AC 5 and the least were 16 species in AC 3.

There were significant differences in seedling species density (ANOVA, $F_{9,218} = 94.19$, $P < 0.001$; Fig. 4a) among the restoration, naturally regenerating and primary forests. Seedling density (individuals/ha) significantly differed among the different forests ($F_{9,218} = 23.60$, $P < 0.001$; Fig. 4b). Also Simpson’s D values of tree seedlings significantly differed (Kruskal-Wallis test, $\chi^2 = 123.75$, $df = 9$, $P < 0.001$; Fig. 4c) among the forests. Berger-Parker dominance index values also differed among seedling communities in the different forests ($F_{9,218} = 20.15$, $P < 0.001$; Fig. 4d).

3.4. Influence of *A. pubescens*, *P. purpureum* and *L. camara* on Communities of Trees

The percentage cover of *A. pubescens* (Kruskal-Wallis test, $\chi^2 = 83.22$, $df = 9$, $P < 0.001$), *P. purpureum* ($\chi^2 = 165.11$, $df = 9$, $P < 0.001$) and *L. camara* ($\chi^2 = 102.16$, $df = 9$, $P < 0.001$) significantly differed among the restoration, naturally regenerating and primary forest. The average cover of *P. purpureum* decreased along the restoration gradient so that the recently planted AC 03 had the highest (80–90%), lowest in AC 14 (<10%) and none in the oldest restoration forest AC 16 (Table 2). At plot level, *A. pubescens*, *P. purpureum* and *L. camara* cover correlated negatively with species density, tree density and Simpson’s D, but a positive correlation was found for dominance (Fig. 5; Table 3). When considered separately, *P. purpureum*

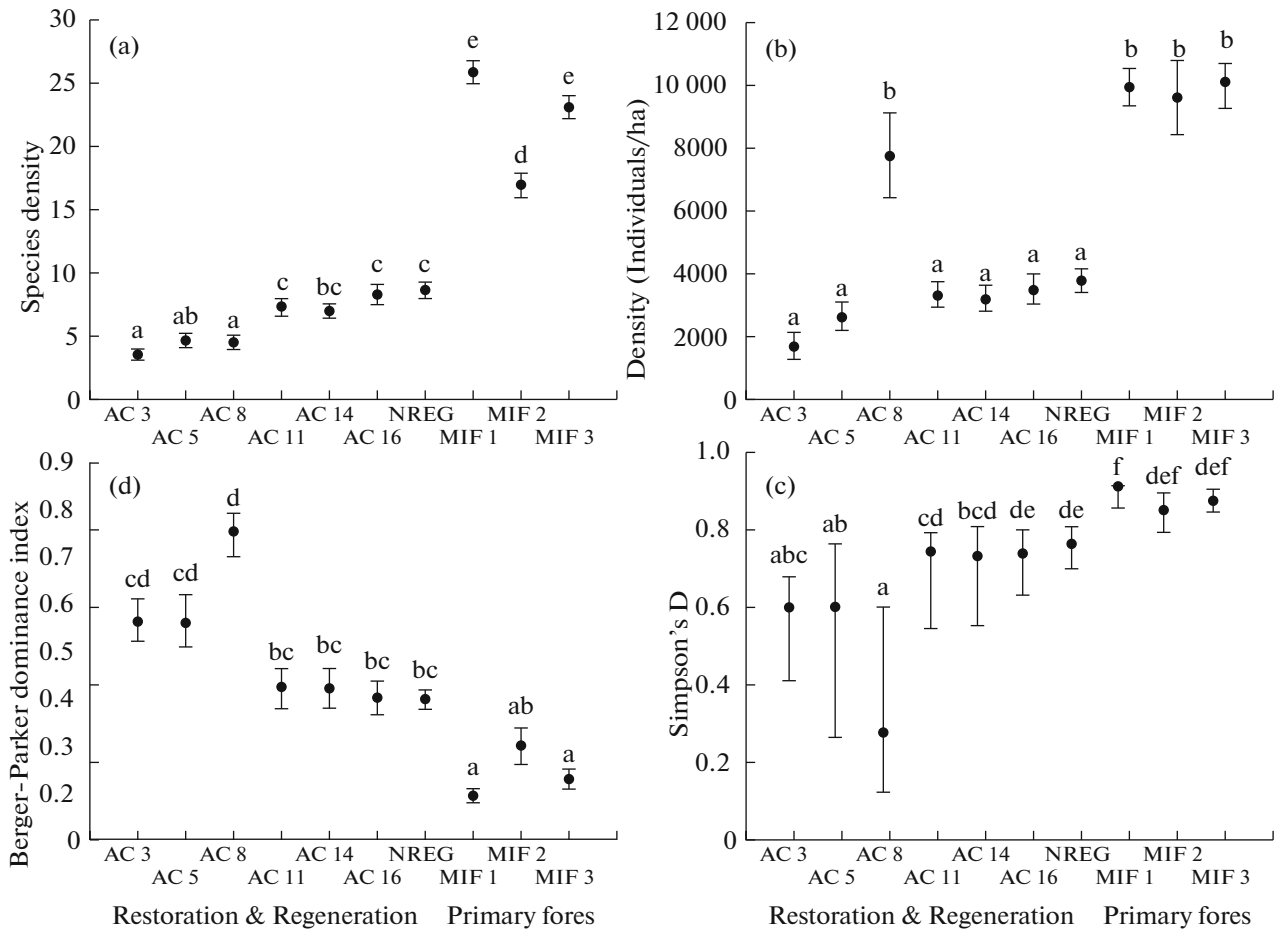


Fig. 4. Averages of tree seedlings (\pm SE) of (a) Species density, (b) density (individuals ha^{-1}), (c) Simpson's D and (d) Berger-Parker dominance in the restoration, naturally regenerating and primary forest in KNP, Uganda. Species density, density (individuals/ha) and dominance values represent back transformed values. Bars are SE and different letters represent significant differences (Tukey's HSD, $P < 0.05$).

had the strongest influence on the recovery compared to *A. pubescens* and *L. camara*. But *P. purpureum* influenced tree dominance ($R^2 = 0.58$) more compared to

A. pubescens ($R^2 = 0.23$), and *L. camara* cover ($R^2 = 0.06$; Table 3). *L. camara* had the least negative influence on the recovery of trees.

Table 2. Species density, estimated species (Chao 2 \pm SD) of tree communities, total of nonplanted regenerating tree seedlings and average percentage cover of *A. pubescens*, *L. camara* and *P. purpureum* in forests of Kibale National Park. Values of percentage cover were; 0, <1% \leq 0.5, <10% \leq 1, <20% \leq 2, <30% \leq 3, <40% \leq 4 ... 100

Restoration, regenerating and primary forests	Estimated species density	Nonplanted seedlings	<i>A. pubescens</i>	<i>P. purpureum</i>	<i>L. camara</i>
AC 3	20.1 \pm 1.6	19	1.48	8.85	0
AC 5	58.6 \pm 17.9	33	0.65	7.3	0.25
AC 8	30.9 \pm 4.8	26	1.45	6.33	0.15
AC 11	68.1 \pm 20.9	40	1.5	2.9	0.31
AC 14	61.3 \pm 12.2	43	1.91	1.75	1.05
AC 16	56.7 \pm 5.6	49	2.1	0	3.67
NREG	105.6 \pm 16.4	78	2.21	0.8	0.17
MIF 1	81.3 \pm 6.9	73	0	0	0
MIF 2	75.6 \pm 6.8	67	0.04	0	0
MIF 3	87.3 \pm 7.6	76	0	0	0

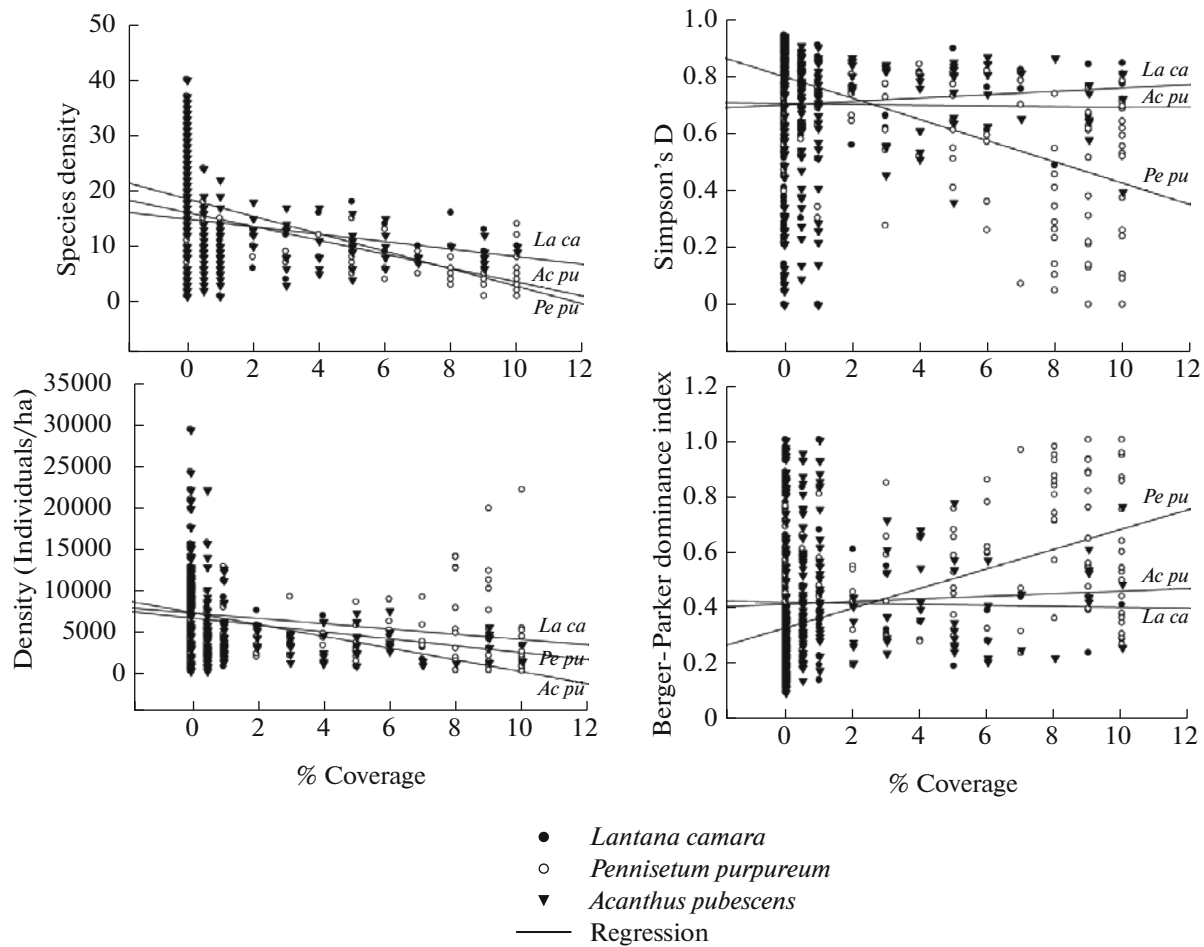


Fig. 5. Scatterplots of tree communities in 228 study plots, showing influence of *A. pubescens* (*Ac pu*), *P. purpureum* (*Pe pu*) and *L. camara* (*La ca*) cover on Species density, Tree density (individuals/ha⁻¹), Simpson's D, and Dominance using Regression and Spearman Rank order correlation (R^2). Plots represent the six restoration, a naturally regenerating and three primary forests.

4. DISCUSSION

Restoration planting can ignite successional changes in tree communities (Nyafwono et al., 2015), reestablishing forests with high species density, tree density and diversity, however these are dependent on the age of restoration and the extent of cover of understorey vegetation e.g., herbs, grasses and shrubs cover.

According to the patterns observed, tree community recovery generally correlated with "age" along the restoration gradient. Species density gradually increased, while dominance declined. However, no clear pattern was found for tree density (individuals/ha) and diversity. The increase in tree density and the corresponding decrease in diversity with the same approximate age (AC 8) can be linked to the fruiting cycles of planted trees, marked by high establishment of seedlings beneath canopies of the bearing trees. The results show that floristic re-assembly of tree species composition involves the process of replacement of species and not just the mere addition of new ones. This pattern is similar to (Kritzing and van Aarde, 1998;

Davis et al., 2003) where the increase in species richness and diversity over a period of time were accompanied by a clear turnover of species.

Tree community composition had not converged to the composition typical of primary forests. However they approached, providing an optimistic assessment that tree community recovery in the restoration forests were at an early phase of recovery. Increase in average Bray-curtis similarity index along the restoration gradient is evidence for possible convergence within a reasonable period; a shift in composition of trees towards the primary forest (Wassenaar et al., 2005).

Restoration planting facilitated the recruitment of other native tree seedlings in the forest. Seedling recruitment was supported by gradual increases in species density, tree density (individuals/ha), diversity, and a decrease in dominance of other native tree seedlings. Our findings concur with Omeja et al., (2011), that many tree species naturally established under planted trees of KNP. This was possibly because, restoration planting provided artificial perching struc-

Table 3. Spearman's rank correlation and Regression tests for the influence of *A. pubescens*, *P. purpureum* and *L. camara* on trees in the different restoration, naturally regenerating and primary forests of Kibale National Park

Herbs, shrubs and grasses	Spp Density	Density (individuals/ha)	Simpson's D	Berger–Parker dominance
<i>A. pubescens</i>	$R^2 = -0.44$, $P < 0.001$	$R^2 = -0.49$, $P < 0.001$	$R^2 = -0.28$, $P < 0.001$	$R^2 = 0.23$, $P < 0.001$
<i>P. purpureum</i>	$R^2 = -0.74$, $P < 0.001$	$R^2 = -0.33$, $P < 0.001$	$R^2 = -0.66$, $P < 0.001$	$R^2 = 0.58$, $P < 0.001$
<i>L. camara</i>	$R^2 = -0.14$, $P = 0.032$	$R^2 = -0.18$, $P = 0.006$	$R^2 = -0.08$, $P = 0.24$	$R^2 = 0.06$, $P = 0.38$

tures, food resources for seed dispersing birds and mammals, and acted as pathways or stopovers for migration of animal species subsequently accelerating seed deposition (Guariguata and Ostertag, 2001). Omeja et al., (2011) recorded 39 new tree species, however we found 59 tree species, suggesting that 20 new tree species established in the restoration area in seven years. Like (Parrotta et al., 1997; Duncan and Chapman, 2003; Farwig et al., 2009), I found that restoration planting can enhance forest recovery by influencing conditions that support natural recruitment of new trees species.

The decrease in species density, tree density and diversity showed that increase in cover of the understorey vegetation negatively influences tree growths. The dense growths of *A. pubescens*, *L. camara* and *P. purpureum* stratum suppressed tree development, possibly slowing the process of reconstructing the degraded area into a species rich ecosystem. These findings accords well with (Slocum et al., 2004; Lawes and Chapman, 2006; Duclos et al., 2013) that sub canopy herbs, shrubs, and grasses inhibits tree recruitment.

Pennisetum purpureum had the strongest effect of suppressing tree recovery. This might be attributed to the dispersal and space limitation which arise when *P. purpureum* colonizes forests. Our finding accords well with, (Francis, 2004, p. 542) who suggested that *P. purpureum* suppresses trees, herbs and other grasses. Also, *L. camara* had a negative influence on species density, tree density and diversity, consistent with Omeja et al., (2011). We attributed this pattern to the growth architecture of lantana, where light infiltration to the ground is restricted resulting in a decline of tree seedlings and changes in species composition and soil properties (Sharma and Raghubanshi, 2011). *Acanthus pubescens* cover also negatively affected trees recovery. This is possibly due to the recruitment limitation associated with the wood herb causing “arrested succession” (Chapman and Chapman, 2004; Paul et al., 2004; Lawes and Chapman, 2006).

5. CONCLUSIONS

This study has shown that forest recovery is more effective with natural regeneration compared to restoration planting, especially if regenerating forests were not degraded to a threshold below which they cannot recover unaided. Restoration planting also enhanced recruitment of nonplanted tree seedlings. Dense cover of *P. purpureum*, *A. pubescens* and *L. camara* negatively affected tree recovery.

ACKNOWLEDGMENTS

Permission to conduct this study was granted by the Uganda Wildlife Authority and the Uganda National Council of Science and Technology. I thank Sabiiti Richard, Erimosi Agaba, for helping during fieldwork, and staff at Makerere University Biological Field Station for assistance with inventory and field work.

REFERENCES

- Abebe, M.H., Oba, G., Angassa, A., and Weladji, R.B., The role of area enclosures and fallow age in the restoration of plant diversity in northern Ethiopia, *Afr. J. Ecol.*, 2006, vol. 44, pp. 507–514.
- Anderson, M.J., Gorley, N.R., and Clarke, R.K., *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*, Plymouth, UK: PRIMER-E Ltd., 2008.
- Bowen, M.E., McAlpine, C.A., House, A.P.N., and Smith, G.C., Regrowth forests on abandoned agricultural land: A review of their habitat values for recovering forest fauna, *Biol. Conserv.*, 2007, vol. 140, pp. 273–296.
- Chapman, C.A. and Chapman, L.J., Unfavorable successional pathways and the conservation value of logged tropical forest, *Biodivers. Conserv.*, 2004, vol. 13, pp. 2089–2105.
- Chapman, C.A. and Lambert, J.E., Habitat alteration and the conservation of African primates: Case study of Kibale National Park, Uganda, *Am. J. Primatol.*, 2000, vol. 50, pp. 169–185.
- Clarke, K.R. and Gorley, R.N., *PRIMER v6: User Manual/Tutorial*, Plymouth, UK: PRIMER-E Ltd., 2006.
- Colwell, R.K. and Coddington, J.A., Estimating the extent of terrestrial biodiversity through extrapolation, *Phil. Trans. Roy. Soc. London B*, 1994, vol. 345, pp. 101–118. doi 10.1098/rstb.1994.0091

- Davis, A.L.V., van Aarde R.J., Scholtz, C.H., and Delpont, J.H., Convergence between dung beetle assemblages of a post-mining vegetational chronosequence and unmined dune forest, *Restor. Ecol.*, 2003, vol. 11, pp. 29–42.
- Duclos, V., Boudreau, S., and Chapman, C.A., Shrub cover influence on seedling growth and survival following logging of a tropical forest, *Biotropica*, 2013, vol. 45, pp. 419–426.
- Duncan, R.S. and Chapman, C.A., Consequences of plantation harvest during tropical forest restoration in Uganda, *For. Ecol. Manag.*, 2003, vol. 173, pp. 235–250.
- Dunn, R.R., Recovery of faunal communities during tropical forest regeneration, *Conserv. Biol.*, 2004, vol. 18, pp. 302–309.
- Farwig, N., Sajita, N., and Böhning-Gaese, K., High seedling recruitment of indigenous tree species in forest plantations in Kakamega Forest, western Kenya, *For. Ecol. Manag.*, 2009, vol. 257, pp. 143–150.
- Francis, J.K. (Ed.), *Wildland Shrubs of the United States and its Territories: Thamnisc Descriptions*, vol. 1, Gen. Tech. Rep. IITF-GTR-26, San Juan, PR: U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry; Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 2004.
- Guariguata, M.R. and Ostertag, R., Neotropical secondary forest succession: Changes in structural and functional characteristics, *For. Ecol. Manag.*, 2001, vol. 148, pp. 185–206.
- Kobayashi, S., An overview of techniques for the rehabilitation of degraded tropical forests and biodiversity conservation, *Curr. Sci.*, 2007, vol. 93, p. 11.
- Korhonen, L., Korhonen, K.T., Rautiainen, M., and Stenberg, P., Estimation of forest canopy cover: A comparison of field measurement techniques, *Silva Fenn.*, 2006, vol. 40, pp. 577–588.
- Kritzinger, J.J. and van Aarde R.J., The bird communities of rehabilitating coastal dunes at Richards Bay, KwaZulu-Natal, *S. Afr. J. Sci.*, 1998, vol. 94, pp. 71–78.
- Kuper, J.H., *Report on UNP-FACE Project 1996: Uganda National Parks*, FACE Foundation, 1996.
- Lawes, M.J. and Chapman, C.A., Does the herb *Acanthus pubescens* and/ or elephants suppress tree regeneration in disturbed Afrotropical forest?, *For. Ecol. Manag.*, 2006, vol. 221, pp. 278–284.
- Magurran, A.E. and McGill, B.J. (Eds.), *Biological Diversity: Frontiers in Measurement and Assessment*, Oxford, UK: Oxford Univ. Press, 2011.
- Nyafwono, M., Valtonen, A., Nyeko, P., Owiny, A.A., and Roininen, H., Tree community composition and vegetation structure predict butterfly community recovery in a restored Afrotropical rain forest, *Biodivers. Conserv.*, 2015, vol. 24, pp. 1473–1485. doi 10.1007/s10531-015-0870-3
- Omeja, P.A., Chapman, C.A., Obua, J., Lwanga, J.S., Jacob A.L., Wanyama, F., and Mugenyi, R., Intensive tree planting facilitates tropical forest biodiversity and biomass accumulation in Kibale National Park, Uganda, *For. Ecol. Manag.*, 2011, vol. 261, pp. 703–709.
- Ormerod, S.J., Restoration in applied ecology: Editor's introduction, *J. Appl. Ecol.*, 2003, vol. 40, pp. 44–50.
- Parrotta, J.A., Turnbull, J.W., and Jones, N., Catalyzing native forest regeneration on degraded tropical lands, *For. Ecol. Manag.*, 2003, vol. 99, pp. 1–7.
- Paul, J.R., Randle, A.M., Chapman, C.A., and Chapman, L.J., Arrested succession in logging gaps: Is tree seedling growth and survival limiting?, *Afr. J. Ecol.*, 2004, vol. 42, pp. 245–251.
- Putz, F.E., Dykstra, D.P., and Heinrich, R., Why poor logging practices persist in the tropics, *Conserv. Biol.*, 2000, vol. 14, pp. 505–508.
- Sharma, G.P. and Raghubanshi, A.S., *Lantana camara* L. invasion and impact on herb layer diversity and soil properties in a dry deciduous forest of India, *Appl. Ecol. Environ. Res.*, 2011, vol. 9, no. 3, pp. 253–264.
- Slocum, M.G., Aide, T.M., Zimmerman, J.K., and Navarro, L., Natural regeneration of subtropical montane forest after clearing fern thickets in the Dominican Republic, *J. Trop. Ecol.*, 2004, vol. 20, pp. 483–486.
- Struhsaker, T.T., *Evaluation of the UWA-FACE Natural High Forest Rehabilitation Project in Kibale National Park, Uganda. A Report Prepared for the Centre for Applied Biodiversity Science of Conservation International and for the FACE Foundation—Conservation International*, Washington, DC, 2003.
- Tabuti, J.R.S., The uses, local perceptions and ecological status of 16 woody species of Gadumire Sub-county, Uganda, *Biodivers. Conserv.*, 2007, vol. 16, pp. 1901–1915.
- UWA-Face, *Project Plan of Operation Report—January to December 2006*, Kampala, Uganda: Uganda Wildlife Authority, 2006.
- Wassenaar, T.D., van Aarde, R.J., Pimm, S.L., and Ferreira, S.M., Community convergence in disturbed subtropical dune forests, *Ecology*, 2005, vol. 86, pp. 655–666.
- Wasserman, M.D. and Chapman, C.A., Determinants of colobine monkey abundance: The importance of food energy, protein and fibre content, *J. Anim. Ecol.*, 2003, vol. 72, pp. 650–659.
- Wright, S.J. and Muller-Landau, H.C., The future of tropical forest species, *Biotropica*, 2006, vol. 38, pp. 287–301.