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WOODY VEGETATION DIVERSITY AND REGENERATION IN AN ABANDONED SUGAR ESTATE IN SEMI-ARID ZIMBABWE

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ABSTRACT

This study assessed woody species diversity and regeneration, 30 years after cessation of sugar cane production in Chirundu Estate situated in the Zambezi river valley floor of Zimbabwe. Nineteen plots were studied to compare woody vegetation in the undisturbed and disturbed areas. The undisturbed area had 42 species and exhibited greater ($p<0.05$) woody vegetation species diversity than the disturbed area with 19 species. Cultivation converted a *Combretum mossambicensis* dominated thicket to a *Dichrostachys cinerea* thicket. Six vegetation subtypes were separated by the Hierarchical Cluster Analysis of species richness data whilst the Detrended Correspondence Analysis identified three groups. Cultivation was accountable for 50% variation in vegetation species composition. Vegetation regeneration in the undisturbed area as measured by the sapling-to-tree ratio (STR) was low (mean STR=0.444(0.309)) and medium (mean STR=0.630(0.517)) in the disturbed area but were not significantly ($p>0.05$) different. It was concluded that vegetation in the disturbed area was still in early stages of succession and the co-existence of early and late succession species indicated some degree of disequilibrium dynamics whilst high herbivory and arid conditions of the estate were attributable to the retarded rate of woody vegetation succession.

Key words: species richness, succession, disturbance, herbivory, disequilibrium.

INTRODUCTION

Forces that influence species composition, diversity, dynamics and stability of an ecosystem result in unique patterns of change. Vegetation is one component of ecosystems widely studied to explain changes in biodiversity (Muller-Dombois and Ellernberg, 1974). Models of vegetation change emphasize the influence of environmental variables during succession (Dublin *et al.* 1990). Some of the variables interact to influence the pattern and trends in vegetation change such as elephant browsing and wildfires in the Tsavo ecosystem in East Africa (van Wijngaarden, 1985). Several studies (O'Connor, 1992; Mapaure, 1997; Mapaure and Mcartney, 2001; Chidumayo, 2002) have confirmed the influence of these variables on succession.

Vegetation succession is often interrupted by herbivores, fires, humans, floods and droughts. Secondary succession occurs in areas where a disturbance affects a previously existing original plant community. Secondary succession leading to increase in woody biomass has been observed in the savanna ecosystems (Archer *et al*., 1988; Scholes and Archer, 1997; Skowno *et al*., 1999). In these ecosystems microphyllous (small leafed) plant species and fleshy-fruited species with short life cycles are the pioneers during secondary succession (Skowno *et al.,* 1999). These early invaders require a pool of uncontested resources while later dominant species tolerate small fluxes of resources. Macrophyllous (broad-leafed) species later establish under canopies of mature microphyllous species (Smith and Goodman, 1987).

In abandoned fields, old field succession starts with annual weeds, then perennials and grasses to short life cycle fast growing woody species (Tilman, 1986; Symonides, 1988). Species diversity increases with age of the abandoned field as more species invade with time (Johnson *et al*., 1991). Soil fertility, especially nitrogen level has been shown by Aweto (1981) and Tilman (1987) to influence plant species composition, abundance, dispersal and colonisation. Other environmental factors such as change in moisture regime, herbivore pressure, fire, light intensity also influence patterns and rates of vegetation change on old fields (Magadza, 2000; Mhlanga and Mapaure, 2000). Chidumayo (2002) reported significant effects of land tenure on rate of biomass accumulation in re-growth during secondary succession following clearing of mature miombo woodland.

Semi-arid environments, such as the Zambezi River Valley are known to take a long time to recover or may not recover from human disturbance through cultivation (O'Connor, 1992; Dalberg, 2000). Studies on vegetation disturbance in Southern Africa have been focusing on fire in savannas (Bond and Wilgen, 1996).

However, in the Zambezi River Valley floor (ZVF) fire is not a major factor due to low biomass productivity related to the aridity of the area. According to Chidumayo (2002) fire still plays a big role in regeneration of mature *miombo* woodlands where it is responsible for tree mortality with the highest impact reported in national parks. The few studies on human impacts on vegetation in the ZVF have only concentrated on flood plains like the Mana Pools and the Zambezi Delta in relation to changes in flooding cycles as a result of the construction of the Kariba dam (Magadza, 2000; Timberlake, 2000). The rate of vegetation recovery of disturbed areas has implications on biological diversity conservation in the Zambezi Valley. This study sought to assess woody vegetation species composition, richness, diversity, regeneration and role of soil and herbivory factors during old field succession after 30 years of abandonment of sugar plantations at Chirundu Estate.

MATERIALS AND METHODS

The study site: The former Chirundu Estate (2 700 ha) is located about 352 km North West of Harare in the Zambezi valley floor. The northern boundary of the Estate is the Zambezi River, whilst the Hurungwe Safari Area surrounds the greater part of the Estate (Fig. 1). Within the estate is an undisturbed portion of about one third of the whole estate (Figure 1). Chirundu Estate was cleared for irrigated sugar production between 1960 and 1971, but the sugar project was abandoned in 1971 due to viability challenges. A 100 ha portion was reopened in 1980 for banana production. The rest of the Estate has been a wildlife hunting concession since 1979.

The Estate experiences a semi-arid hot climate characterised by mean (30-years) annual rainfall of 628 mm and mean annual temperature of 25^{o}C with clear skies for most of the year (Thompson and Purves, 1978). These conditions favour high evaporation and prevent accumulation of moisture in the soils. The soils in the estate are predominantly fine to medium grained sands and loamy sands derived from Triassic sandstones (Thompson and Purves, 1978). The soils are also pervious and loose on raised ground and localised variants occur within the estate in response to deposition and erosion processes.

Floristically, the Zambezi River Valley falls within the Zambezian phytocorion dominated by the Southern African thicket-biome and with characteristic species present (White, 1983; Cowling *et al*., 2005). The thicket vegetation of this phytocorion structurally has a dense stratum of shrubs and low trees, a paucity of grass biomass and consequently fire intolerant (Cowling *et al*., 2005). The dominant woody species include *Dichrostachys cinerea*, *Combretum mossambicensis*, *Senna singueana*, *Acacia tortillis*, *Colophospermum mopane*, *Combretum singueana*, *Karomia tettensis* and *Combretum elaeagnoides*. The thickets were reported by Cowling *et al*.(2005) to generally support a diverse wild mammal fauna comprising 48 large and medium-sized species (>2kg) and of these, 28 are herbivores that include antelopes and large-bodied like the elephant (*Loxodonta africana*).

Vegetation assessments: The experiment had two treatments: (i) ‘Disturbed’ formerly cultivated area (ii) ’Undisturbed’- area not opened up for cultivation and assumed to have the same vegetation community as the original vegetation. A completely randomized design was adopted for vegetation assessment and the treatments constituted the sampling strata on which 25 m x 25 m plots were randomly located. The 25x25m sample plots captured at least 75% of the dominant species in the area (Muller-Dombois and Ellenberg, 1974). There were 12 replicate plots in the disturbed area (denoted D1 to D12) and seven in the undisturbed area (denoted N1 to N7) giving a total of 19 for the two areas. The sampling plots were located using a grid system. Woody species within the plots were identified and enumerated in March/April 2002. A distinction was made between ‘trees’ (d.b.h. > 2 cm), ‘saplings’ (d.b.h. ≤ 2 cm), and ‘seedlings’(<50 cm tall) for dicotyledonous tree species (Fleischmann *et al*., 2005;Dhaulkhandi *et al*., 2008).The status (live or dead) of the woody vegetation was also recorded. Regeneration status was based on the sapling-to-tree ratio (STR) calculated for all woody species in each plot. The regeneration levels were then classified on the basis of STRs according to Gilligan and Muir (2011) as: very low, STR≤0.1; low, 0.1 < STR < 0.5; medium, 0.5≤ STR <1; high, STR≥ 1. Species that could not be identified in the field were sent to the Zimbabwe National Herbarium, Harare for further identification. The ICBN (2005) Vienna Code was adopted for botanical classification.

Measurement of explanatory variables: Within each vegetation sampling plot, soil sampling points were randomly located. Intact soil cores of 7.0 cm-diameter and 5.2 cm height (200 cm^{3}) were collected from the soil surface for bulk density determination. The soil cores were oven-dried at 105 ^{o}C for 24 hours. Bulk density was then calculated from the volume of soil cores and oven dry mass.

Soil texture was determined by the feel method. Composite soil samples (about 2kg) were prepared from 10 subsamples collected from the top 10 cm for organic carbon determination and pH measurement in the laboratory. The pH of the soil was determined in 0.01M$CaCl_2$ with a glass electrode (model 704 Mefrohm) (soil: $CaCl_2$ ratio 1:2) after calibration in pH buffers of 4 and 7 (Okalebo *et al*., 2002);the organic carbon content by the Modified Walkley Black method using acidified aqueous potassium dichromate (Anderson and Ingram,1993).

Herbivore damage was defined as the visible vegetation utilisation and scored on a modified Braun-Blanquet scale of 1 to 3 for each plot (O'connor, 1992; Mhlanga and Mapaure, 2000) where:

1 = no visible damage to slight browsing indicated by removed young stems and chewed leaves;

2 = branches broken or debarking and scarred stems; and

3 = removed branches, fallen trees and dead trees.

The ratings were based on overall assessment of all the plants in each plot.

Data analyses :Data were subjected to the Mann-Whitney U-test (at 5%) according to Hendry (2008) to compare the weighted species presence, diversity index, STR, soil bulk density, organic carbon, and herbivore damage between the disturbed and undisturbed areas in the estate. The statistical package for social sciences (SPSS) version 15 (2006) was used for data analysis. The Shanon-Weiner diversity Index (H') was calculated according to Equation 1 (Krebs, 1989):

$H' = -\Sigma(p_i)(\ln p_i)$ …(1)

where p_i is the proportion of all individuals in the sample belonging to the i^{th} species.

Species richness was derived from the number of individuals of a species in the plots on a weighted basis. The species richness data was used to classify sampling plots using the agglomerative method of Hierarchical Cluster Analysis (HCA) in MINITAB. The distance measure in HCA was single linkage while the constant height cut-off method defined the clusters on the dendrogram (Langfelder *et al*., 2008).

The CANOCO version 4 for windows software package (Ter Braak and Smilauer, 1998) arranged sampling plots in ordination space from the weighted species richness matrix using the Detrended Correspondence Analysis (DCA) approach.

Factors hypothesized to influence vegetation change were captured in a spreadsheet as environmental variables. Qualitative data on soil texture and treatment level were allocated numerical codes. Sandy soil was coded 1, while loam soil was coded 2. Similarly undisturbed area was coded 1 and disturbed area 2. Species richness data were then integrated with environmental variables for direct gradient analysis, using Canonical Correspondence Analysis (CCA). The method focused on biplot scaling of species and environmental data on inter-sample ordination distance. The influence of environmental variables on species composition was then interpreted from the resultant ordination diagram showing the influence of each variable on the arrangement of sites in ordination space.

RESULTS

Woody species composition, abundance and diversity: A total of 61 woody species were identified in the entire Estate thickets and the undisturbed area had 42 species compared to 19 in the disturbed area. The most frequently observed species in the disturbed area were: *Dichrostachys cinerea>> Combretum mossambicensis> Senna singueana> Acacia tortillis*. In the undisturbed area the most frequently encountered species were *C. mossambicensis>D.cinerea>>Colophospermum mopane> S. singueana>Karomia tettensis>Combretum elaeagnoides* (Fig 2). Cultivation therefore converted a *Combretum mossambicensis* dominated thicket into a *Dichrostachys cinerea* thicket. Vegetation diversity was higher ($p<0.05$) for the undisturbed area plots than for disturbed area plots whose respective mean H' values were 1.79 (0.427) and 0.91 (0.46). However, the species richness was significantly ($p<0.05$) correlated ($r=0.84$) to the diversity index in the undisturbed area (Table 1). Vegetation regeneration in the estate was evaluated by the sapling-to-tree ratio (STR). The mean STR value for the undisturbed area was 0.444 (0.309) implying low regeneration whilst the mean STR for the disturbed area was 0.630 (0.517) in the medium category (Table 1). However, there were no significant ($p>0.05$) differences in mean STR values between the areas but high variability was exhibited (Table 1).

Vegetation dominance cluster analyses: Hierarchical Cluster analysis (HCA) of weighted species presence data grouped plots into six floristic clusters basing on similarity of dominant species in the estate which ranged from 100% to 53% (Figure 3).The clusters largely represented the thicket subtypes. Nine plots out of twelve from the disturbed area with more than 80% similarity were grouped into cluster 1, with a dominance of D. *cinerea*. Cluster 2 had two plots each from disturbed (D7 and D10) and undisturbed (N1 and N2) areas with a similarity of more than 90% and were dominated by *D. cinerea* and *S. singueana* (Fig.2). Cluster 3, with only plot D4 (Fig. 2) was dominated by *A. tortillis* whilst cluster 4, dominated by *C. mossambicensis* had two plots (N3 and N4) in the undisturbed area with a similarity of about 95% (Fig 2, Fig 3). The fifth cluster had plot N5, from the undisturbed area and was dominated by *C. mopane.* Plots N6 and N7 from the undisturbed area comprised cluster 6 and were characterized by a combined dominance of *A. ataxacantha* and *K. tettensis.* Fig.3 also shows that similarity between clusters was lower than within the clusters. The between cluster similarity ranged from 75% (Clusters 1&2) in the disturbed area to 55% (clusters 3&4) in the undisturbed area.

The detrended correspondence analysis (DCA) of weighted species richness data arranged sampling plots in ordination space and three recognizable groups (I-III) of species that overlapped extensively in the ordination were identified (Fig.4). Larger separation was along the first than the second DCA axis. The first axis represented the disturbance gradient while the second was for other gradients like edaphic factors. Seven plots from the disturbed area formed a cluster close to the origin (Group I) which was dominated by *D. cinerea*. Group II comprised a mixture of plots from disturbed and undisturbed areas (Fig.4). The woody vegetation in this group consisted of mostly *D. cinerea*, *S. singueana* and *C. mossambicensis*. A third (Group III) vegetation category comprised plots from mostly (71%) the undisturbed area, made up of original species composition prior to disturbance.

Environmental factors affecting species distribution: Results of soil analyses and herbivore damage scores are shown in Table 3. There was no significant ($p>0.05$) difference between the disturbed and undisturbed areas with respect to soil organic C and bulk density. However, the soil pH on the undisturbed area was higher ($p<0.05$) than on disturbed area. Table 3 also show no significant differences ($p>0.05$) in herbivore damage on mature trees between the disturbed area and the undisturbed area.

Species-environmental relationships (direct gradient analysis): Results of the effects of individual environmental factors on species composition are presented in Table 4. The first CCA ordination axis explained 55.5% of variation in species composition while the second axis explained 25.1% of the variation (Figure 5). The influence of environmental variables was significant ($p<0.05$) for all canonical axes.

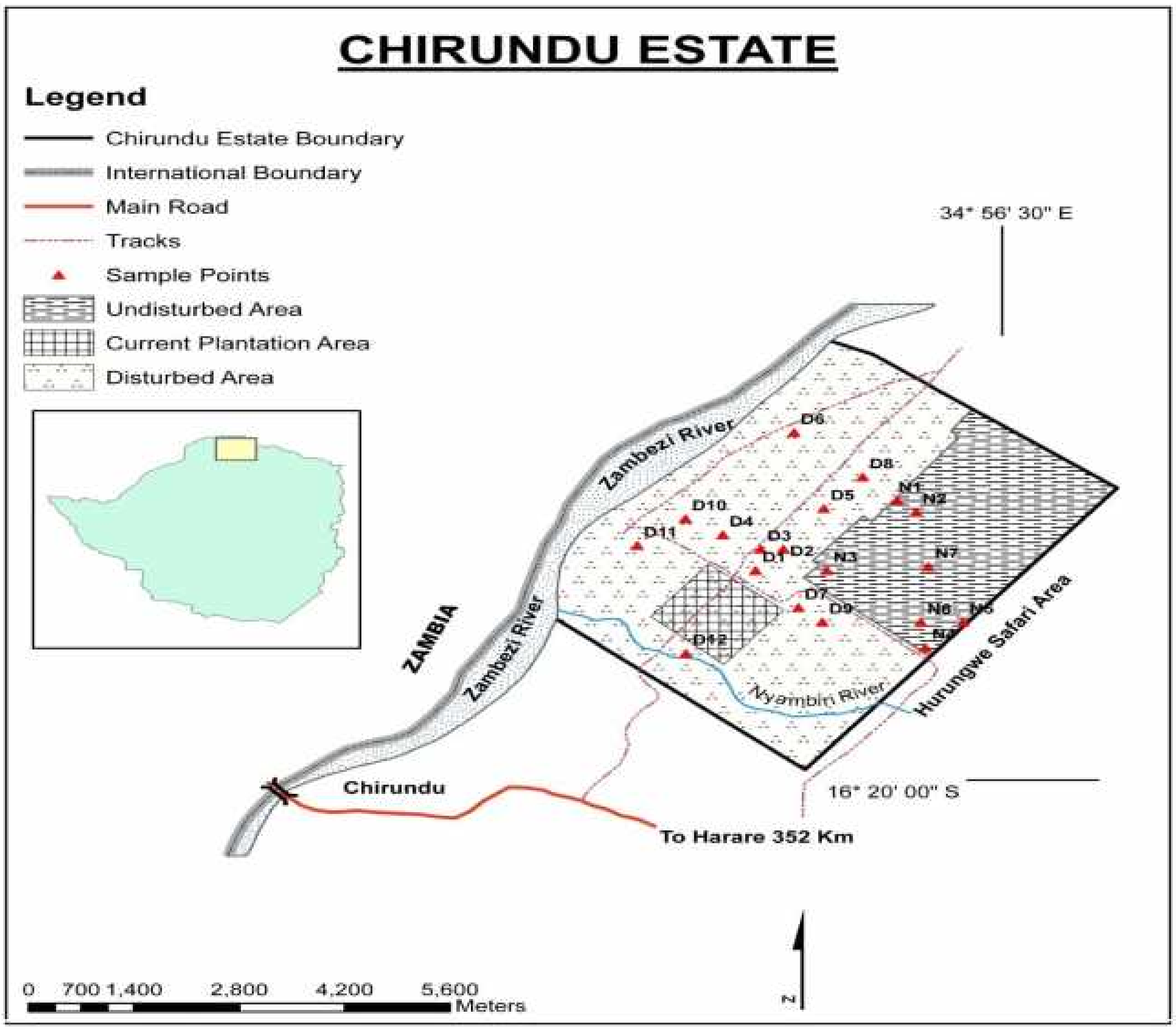

Figure 1: Layout of Chirundu sugar Estate, Northern Zimbabwe

Table 1:Mean (standard deviation) of species richness, sapling-to-tree ratio and diversity index of the sampling plots at Chirundu Estate

Treatment	R	STR		H'	Species number
		Value	regeneration		
Disturbed area	7.75 (3.24)	0.630(0.517)	medium	0.91(0.46)	19
Undisturbed area	20.57(5.78)	0.444(0.309)	low	1.79(0.427)	42
Sig.	*	ns	-	*	

NB: Total plants counted were 3306 in disturbed area and 3011 in undisturbed area; R=richness; STR=Sapling to tree ratio; H' = Shanon-Weiner Diversity index; Statistical significance at probability p<0.05 (*), ns not significant (p>0.05)

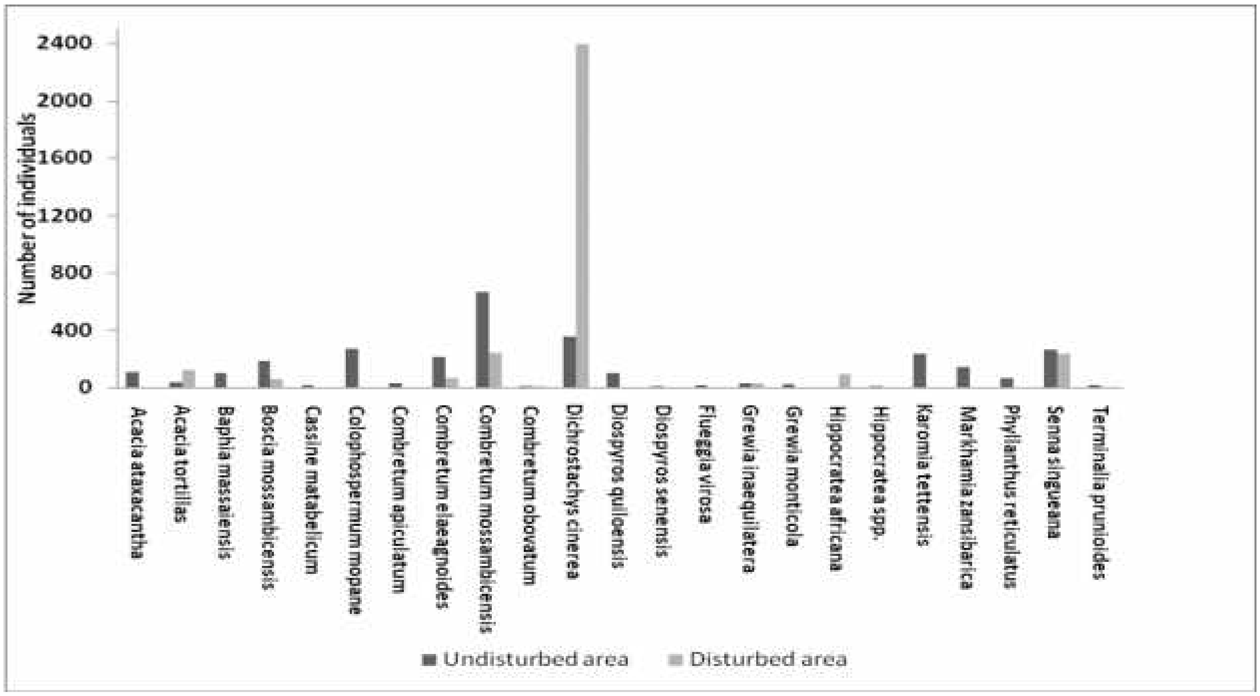

Figure 2: Dominant (>10) woody species presence in the disturbed and undisturbed areas of Chirundu Estate

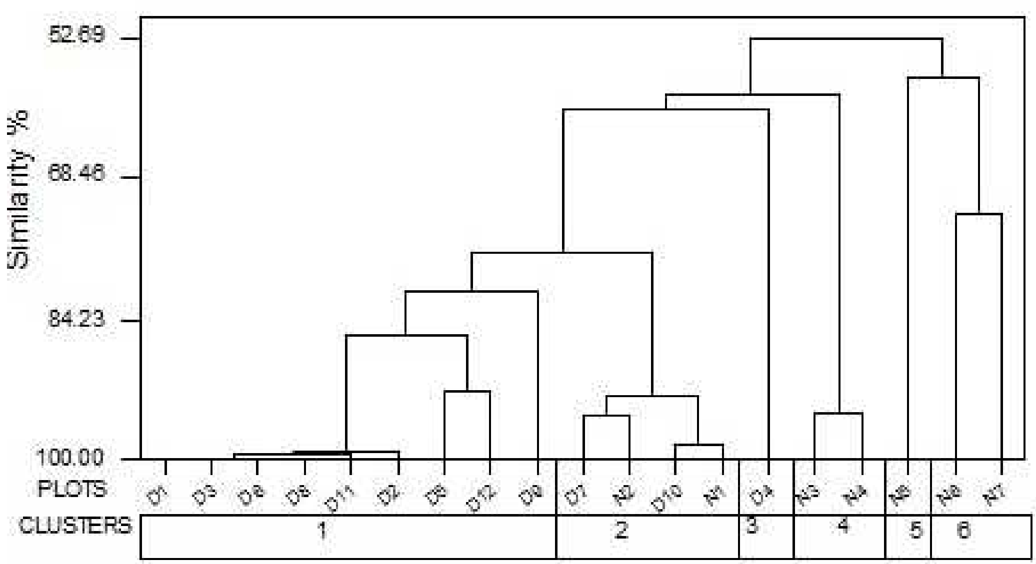

Figure 3. Hierarchical Cluster Analysis dendogram showing classification of vegetation plots based on weighted species presence

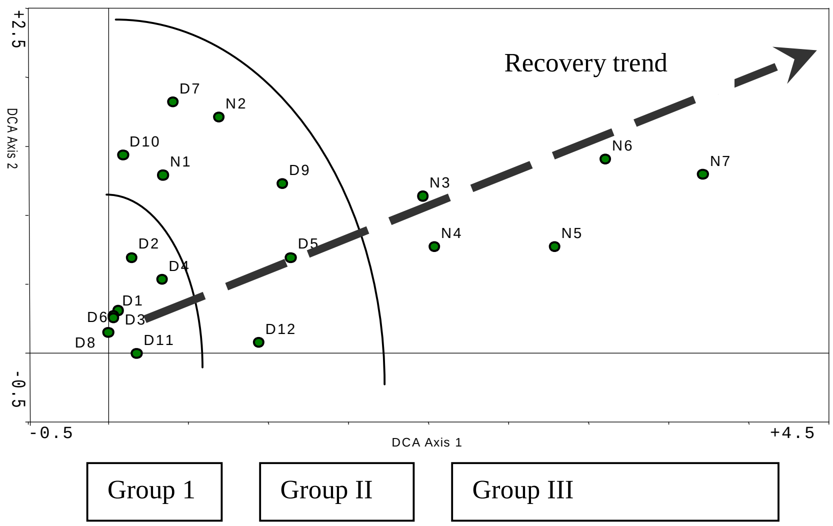

Figure 4. DCA ordination diagram showing separation of woody vegetation plots into three groups relating to disturbance (axis 1) and other gradients (axis 2) (data labels indicate plot numbers)

Table 2. Linear correlation of species richness (R), species diversity (H') and sapling-to-tree ratio (STR) at the disturbed and undisturbed areas of Chirundu Estate.

Area	Linear equation, $Y=a + bx_i$	Correlation coefficient, r
Disturbed area		
	H'=0.10R+0.72	0.19
	STR=0.05R+0.52	0.36
	H'=-0.15STR+1.14	0.56
Undisturbed area		
	H'=0.06R+0.51	0.84*
	STR=0.27R-3.39	0.50
	H'=0.05R+1.68	0.37

* Significant at 5% level

Table 3. Environmental factors hypothesized to influence vegetation succession in Chirundu Estate.

Plot	Bulk density (gm/cm^3)	pH (1:2 $CaCl_2$)	Soil Organic carbon (%)	Soil texture	Herbivore damage score
D1	1.582	4.7	0.46	Loam	3
D2	1.505	4.3	0.41	Sandy	2
D3	1.57	5.1	0	Loam	3
D4	1.497	4.7	0.66	Sandy	2
D5	1.482	4.7	0.56	Loam	2
D6	1.597	4.9	0.86	Loam	2
D7	1.577	3.8	0.4	Sandy	2
D8	1.521	5.2	0.69	Loam	3
D9	1.598	4.3	0.95	Sandy	1
D10	1.597	4.3	0.51	Sandy	2
D11	1.606	4.5	0.38	Sandy	3
D12	1.405	6.4	0.53	Loam	2
N1	1.643	6.5	0.6	Loam	2
N2	1.55	5.8	0.52	Loam	2
N3	1.528	4.7	0.32	Sandy	2
N4	1.674	5.5	0.62	Loam	3
N5	1.584	5.3	0.5	Loam	3
N6	1.403	5.3	0.86	Sandy	2
N7	1.341	5.0	0.66	Sandy	2
Mean disturbed	1.544±0.063	4.742	0.534± 0.246		2.25
Mean Undisturbed	1.532±0.121	5.443	0.583±0.166		2.29
Sig	ns	*	ns	-	ns

Table 4. Variation explained by environmental factors and significance levels.

Factor	Cumulative explained variance (%)	F ratio	P value
Cultivation	50	3.31	0.000
Soil texture	70	1.33	0.1816
Soil pH	89	1.02	0.4291
Organic Carbon	102	1.30	0.2216

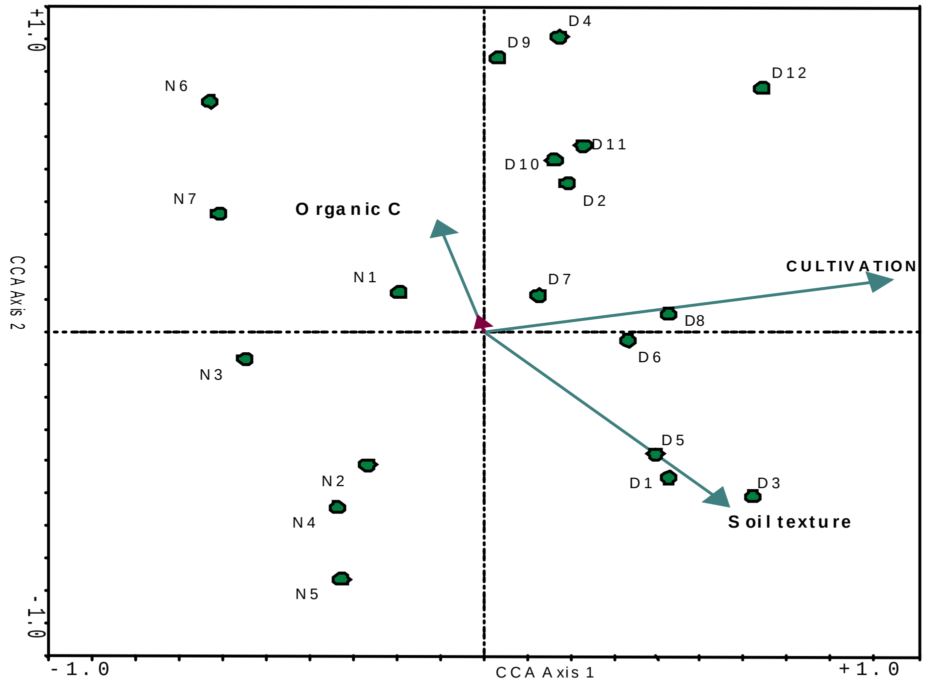

Figure 5. CCA ordination scatter plot indicating the influence of cultivation, soil organic carbon and soil texture on species composition in Chirundu Estate.

DISCUSSION

Species composition dynamics and succession: Individual plants and plant associations interact in various ways during the course of vegetation change. Competition for resources such as light, nutrients, space is one of the major processes taking place during succession (Kellman and Kading, 1992). Plants that succeed to establish in early stages of succession (pioneer species), such as *D. cinerea* evolved characteristics for colonising unoccupied areas. The pioneer species would create conditions for the establishment of later species (facilitation). Facilitation was achieved by creation of microclimate suitable for establishment and providing shade to seedlings of later species and short life cycles to create space for the later species (Kellman and Kading, 1992).

The lower species richness in disturbed area suggested that the vegetation change was not yet complete. The absence of some species in the disturbed area such as K. *tettensis* and *C. mopane* implies that, the succession process is in early stages. The presence and dominance of *D. cinerea*, a micro-phyllus pioneer species in the disturbed area was also indicative of the early stages of succession (Smith and Goodman, 1987) .*D. cinerea* indicated high recruitment and possible persistence. Presence of juicy fruited species such as *B. mossamicensis* in large numbers in the disturbed area also conforms with the findings of Skwono (1999) in their research on pioneer species in early succession of savanna ecosystems. The juicy fruit berries of *B. mossambicensis w*ere consumed and propagated by birds whilst the fleshy and scented pods of *A. nilotica* were consumed and spread by browsing antelopes such as eland and impala.

Species diversity: Diversity theory predicts that species numbers should be highest at intermediate levels of both disturbance and environmental stress. The disturbed area has not fully recovered and the species richness and diversity indices were significantly ($p<0.05$) different from those of the undisturbed area. Species richness and diversity confirm that succession is progressing well.

The trends shown by the DCA towards recovery of vegetation in the disturbed and undisturbed areas agrees with findings of Brosofske *et al*. (1994), reflecting the relatively homogeneous nature of disturbance since a sole company was involved in commercial sugar production. Although more than half of plots from the disturbed area were clustered together, the few mixed clusters suggest that some plant communities were in transition between disturbed vegetation and undisturbed vegetation (Group II, Fig. 3). Group I and Group III vegetation types (Fig.3) seem to be maintained by herbivores as herbivore numbers were reported to be higher than normal according to observations by management and aerial survey counts (Mackie, 2002).

Some patches of vegetation in the disturbed area were at a later stage of succession towards original state with a mixture of pioneer and climax species. This co-existence of early and late succession species indicate some degree of disequilibrium dynamics according to Davis *et al*. (1984). After 30 years of abandoning cultivation, the vegetation community in disturbed area was still in early stages of succession as shown by large numbers of *D. cinerea*, a pioneer species (Fig. 2). The slow succession could also be attributed to low rainfall unlike in tropical rainforest, where some plant communities have been observed to re-establish within three years of disturbance (Aweto, 1981).

The lower composition and diversity on disturbed areas seem to suggest that some species have not yet returned or may not return. The absence of species like *A. ataxacantha, K. tettensis* and *C. mopane* could be attributed to out competition with pioneer species, differential longevity, selective herbivory on seedlings and poor conditions for establishment. Some species such as *Faidherbia albida* and *Adansonia digitata* require a rare combination of factors to germinate and invade new areas (Dunham, 1992). This combination of factors associated with rare events may explain the absence of some species within the disturbed area.

Good and Good (1972) cited in Dhaulkhandi *et al*. (2008) reported that successful regeneration of tree species lies in the ability to initiate new seedlings, ability of seedlings and saplings to survive and grow. The STR gave a measure of regeneration potential in Chirundu estate during succession. The low STR values ($0.1 < STR < 0.5$) observed in the disturbed area of the estate indicated low recruitment of saplings and implying lower regeneration potential and similar findings were reported by Gilligan and Muir (2011) in their study of white oak woodlands regeneration, though in different geographic settings. The high presence of herbivores could be having an overriding effect on the recovery of vegetation. Selective herbivory and differential tolerance to herbivore damage could be contributing towards the observed transitional vegetation and suppression of further development of pioneer communities. Control of herbivore populations in the area could increase the rate of vegetation recovery.

Conclusion: Vegetation succession and regeneration patterns at the abandoned sugar were still in the early stages of succession as shown by dominance of pioneer species in the disturbed area. High herbivory and arid conditions of the estate are hypothesized to retard rate of vegetation recovery.

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