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Species composition and functional structure of herbaceous vegetation in a tropical wetland system

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Abstract Understanding driving factors of spatial heterogeneity in plant species composition and functional structure is a key step towards wetland ecosystems restoration and biodiversity conservation. We surveyed 60 randomly selected plots of 20 × 50 m each and collected 12 explanatory variables to understand potential impacts of natural environmental conditions, human disturbance and spatial position of plots variables on plant functional groups (PFGs) and species composition within grasslands of the Kilombero Valley Floodplain wetland, Tanzania. Ordination analyses were used to identify important vegetation gradients and establish significant natural environmental conditions, human disturbance and spatial position of plots correlates. Partial redundancy analysis (RDA) and partial canonical correspondence analysis (CCA) were used to determine the individual and shared effects of these three sets of explanatory variables on the PFGs and species composition, respectively. In total, 115 plant species, including 22 weed and 3 invasive species, and five PFGs were registered. Annual graminoid was the most abundant, whereas perennial forb the least abundant PFG with 50 and 1 % relative covers, respectively. Overall, spatial position, altitude, total organic carbon, cow dung, distance to the river and distance to kraal (cattle enclosure near human settlement commonly made of wood materials for animal protection) were important descriptors of both PFGs and overall species composition. Separate CCA of only weed and invasive plant species showed that some species, particularly the invasive *Polygala paniculata* were strongly associated with cow dung, indicating that present increase in cattle numbers may result in future problems associated with this species. Intensification of human activities and alteration of natural environmental conditions associated with these factors should be discouraged to maintain plant species composition and functional structure for wetland restoration and sustainable biodiversity conservation.

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Introduction

The understanding of drivers of spatial variation in plant species composition and functional structure is crucial for wetland ecosystems restoration and biodiversity conservation. Such drivers includes both natural and anthropogenic factors (Briske et al. 2003; Moran et al. 2008) and propagule dispersal (Dai 2000). Wetlands occupy about 6 % of the world land mass and 10 % of land surface area of Tanzania (Ministry of Natural Resources and Tourism 2004; Zedler and Kercher 2004). During the last two centuries the losses of wetlands and their natural resources have steadily increased (Millenium Ecosystem Assessment 2005; Keddy et al. 2009), calling for urgent measures to restore and conserve the remaining wetland systems. For example, wetlands in Europe and America have been degraded due to altered hydrology, heavy metal depositions and industrial agriculture (Schipper et al. 2011). This has necessitated the formulation of pro-conservation policies on the remaining wetlands and restoration of floodplains (Wassen et al. 2003). In Africa, the causes of degradation are mainly agriculture, settlement and excessive exploitation of wetland resources (Schuyt 2005), resulting in loss of biological diversity and changes in species compositions of wetland vegetation. Climate change and invasive plant species may further exacerbate wetland ecosystems degradation (Rea and Storrs 1999; Parry 2007), affecting provision of ecosystem goods and services while leaving economy and livelihoods of rural communities at jeopardy (Schuyt 2005).

Increased human disturbances and changes in hydrological regimes will have profound ecological impact on wetlands and associated floodplain plant biodiversity (Capon 2005; Tousignant et al. 2010). For example, it has been found that livestock grazing affects wetland plant communities as it changes significantly the species composition and functional structure (Reeves and Champion 2004; Moran et al. 2008). It has also been reported that altered hydrology constrains plant dispersal and ultimately changes the floodplain species composition and functional structure (Andersson et al. 2000; Merritt et al. 2010).

While there are a number of studies addressing human impact and natural factors on tropical wetland vegetations, few have considered multiple factors (spatial, natural and human disturbance) and their interactions effects on the composition of plant species and functional structure. Moreover, few studies have investigated the relationship between these multiple factors and species composition and functional structure of the inundated grasslands invaded by weedy and invasive plant species. Accordingly, there is limited knowledge on how to effectively restore and protect the integrity, stability and functions of these important ecosystems. We therefore aimed to understand the potential impact of natural environmental conditions, human disturbance and spatial position of plots factors on the plant functional groups (PFGs) and composition of plant species (all species together and weed and invasive species separately). The knowledge developed may contribute to successful restoration strategies and facilitate a sustainable management of wetlands. We used Kilombero Valley in Tanzania which is under considerable human pressure due to unsustainable utilization (Booth et al. 2008). The study focused on the following questions: (1) Which PFGs and plant species characterize the Kilombero wetland grassland community? (2) Which factors among the explanatory variables (environmental, spatial and human disturbance) explain the functional groups, overall species composition, and the distribution of weeds and invasive species and (3) based on our results; what are the management recommendations for the Kilombero Valley? Because the area is used extensively, such as for grazing (Bonnington et al. 2007), we expected that anthropogenic factors would have stronger influence than naturally varying environmental variables and spatial position of plots on the PFGs and overall plant species composition in the grasslands ecosystem. We also expected that spatial position of plots would not be important for invasive plants and weed species composition due to their good dispersal ability.

Materials and methods

Study area

The study was carried out in the Kilombero Valley located in the Morogoro region of southern central, Tanzania (Fig. 1). Kilombero Valley was designated a Ramsar site in 2002, 2 years after Tanzania ratified the Ramsar Convention. The Ramsar site covers an area of 7,967 km^2. Kilombero Valley contains a large floodplain that forms the largest low altitude inland freshwater wetland in East Africa (Ministry of Natural Resources and Tourism 2004). The Valley has a catchment area of approximately 40,000 km^2 forming important wetland areas for a diverse livelihood (Kangalawe and Liwenga 2005) and biodiversity of international significance (Ramsar 2011). The average annual rainfall varies between 1,200 and 1,400 mm per year. The area has a bimodal rainfall pattern with short rains between December and February and long rains between March and May (Bonnington et al. 2007). Flooding is common in the Valley during long rains when rainfall exceeds evapotranspiration and reaches peak in May. The Valley remains flooded for almost 3 months. Plots that were sampled are regularly inundated but no plot was flooded during the vegetation survey. During maximum flooding the depth of water is estimated to be around 30 cm. The floodplain is characterized by deep and well-draining fertile clay soils that crack open in the dry season and are inundated during the long rains. The mean annual temperature is 26 °C (Hetzel et al. 2008). There are around 350 plant species in the area (Starkey et al. 2002). Starkey et al. (2002) identified eight major plant communities following the hydrological gradient from the river channel to the valley margins; namely riverside, low lying valley grasslands, tall grasslands, marginal grasslands, marginal woodlands, combretaceous wooded grasslands, miombo woodland and papyrus swamps plant communities. In this study, we focused on the grassland ecosystem at the margins of the floodplain, where human activities are high (Starkey et al. 2002). Fire occurs annually between August and October and the grassland is used extensively for cattle grazing (Starkey et al. 2002; Bonnington et al. 2007). The floodplain accommodates 75 % of the world‘s remaining puku (*Kobus Vardonii*) population and more than 300 bird species. Elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), common zebra (*Equus quagga*), hippopotamus (*Hippopotamus amphibious*) and lion (*Panthera leo*) are among the common species on the floodplain (Starkey et al. 2002). Several ethnic groups live in the area and economic activities ranges from agriculture, fishing to livestock keeping. A large area of the wetland is cultivated with rice, sugarcane and vegetables. Cattle, goats and sheep form the largest portion of domestic livestock, with cattle population estimates of 300,000 and goat and sheep of 43,000 (Mombo et al. 2011). According to the official census of 1998, the human population was estimated to be about 200,000, but the population has almost doubled by 2005 (Booth et al. 2008).

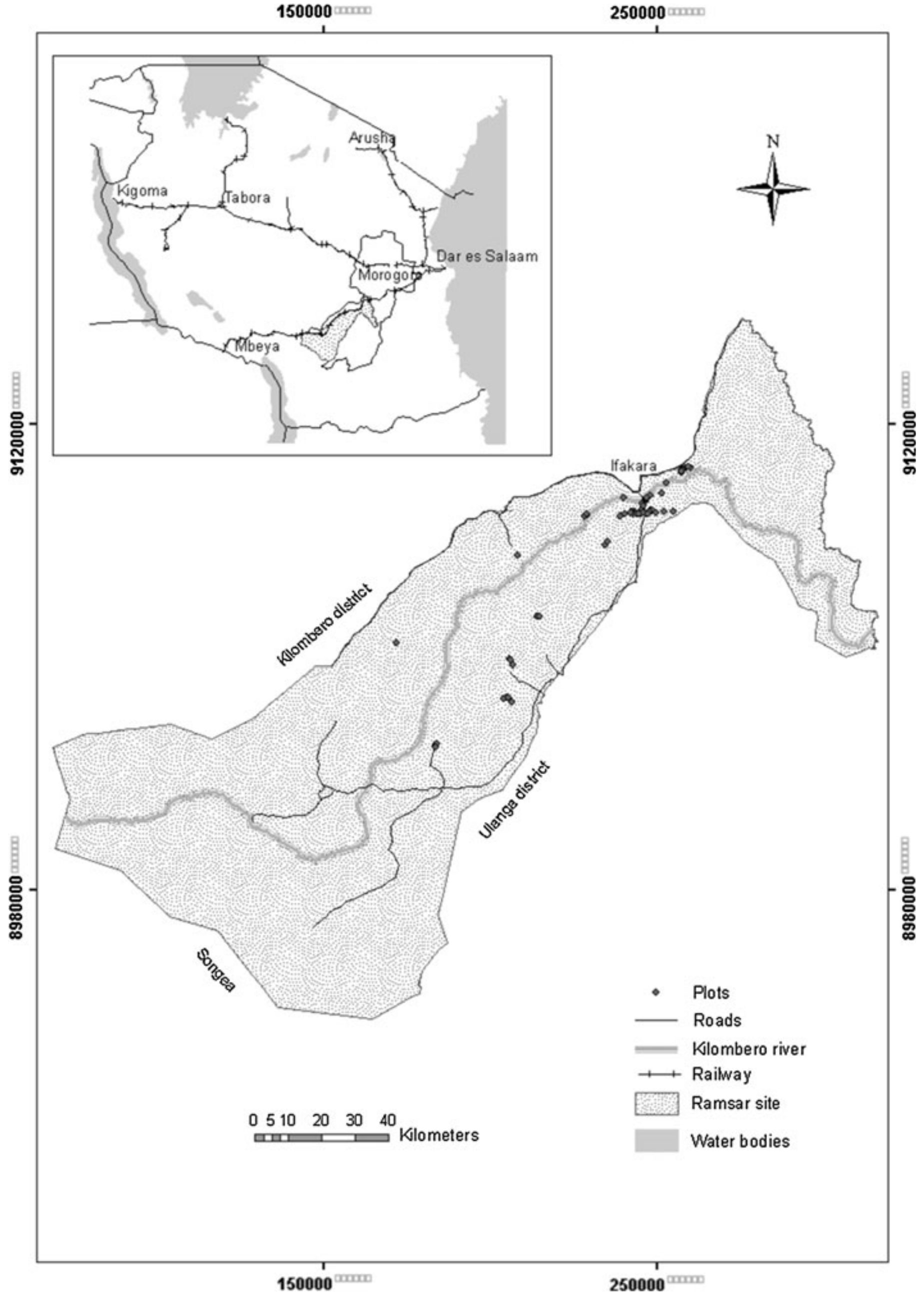

Fig. 1 Location map of Kilombero Valley, Morogoro, Tanzania

Vegetation sampling

Sixty plots were randomly selected and surveyed between February and March 2010 within a 6,265 km^2 area to assess plant community composition of the Kilombero Valley Floodplain wetland. The plots were positioned within the north-eastern side of the Valley where the Valley forms mostly a peneplain (Fig. 1). In this area, there are patches of rice farms which were avoided during the vegetation survey. Each plot (20 × 50 m) was geo-referenced using a standardized (UTM, WGS 84) hand held global positioning system (Garmin 76 Cx). In each plot, 20 quadrats of 0.5 × 0.5 m were randomly located using a table of random numbers and compass bearing (1–360°), resulting in a total of 1,200 surveyed quadrats. The shortest distance between plots was 450 m to minimize the dependence of data. The cover of species was estimated by using the point intercept method (Goodall 1952). The point intercept table was 50 × 50 cm with a total of 25 holes, each 10 cm apart. The table was 50 cm high. The table was placed above each quadrat and a pin (3 mm diameter and 80 cm long) was inserted vertically through all the sequentially located holes and all the contacts (frequency) to each plant species were recorded at every point. The number of contacts each species made with the pin was totalled in every quadrat. Then, the number of contacts for the same species from all the quadrats was aggregated per plot. Finally, the total number of contacts per species over all quadrats per plot was used in the analysis of species composition. Total number of contacts for each species from all the quadrats (1200) and all the plots (60) was determined and added together to obtain a grand total cover. The relative cover (%) of individual species was then calculated based on the grand total cover, ranked and the two most frequent species identified (Appendix). Species that could not be identified in the field were taken to the National Herbarium of Tanzania (NHT) in Arusha for identification and voucher specimens' deposition. Taxonomy of herbaceous plants follows: Haines and Lye (1983), Polhill (1988) and Beentje and Ghazanfar (2010). To quantify the PFGs, plants were classified into the following PFGs (using growth habit and life form): annual graminoids, perennial graminoids, annual forbs, perennial forbs, shrubs and vines. Then, cover of all species belonging to a particular functional group was totalled in its respective quadrat and plot. Finally, the cover per PFG over all quadrats per sampling plot was used in the functional group analysis. To obtain the most and least abundant functional groups, cover for each group from all the plots were totalled to obtain total cover of all groups within the surveyed area. The relative cover (%) of each functional group was calculated based on the total cover of all groups, percentages ranked and the most and least functional groups identified. To obtain relative cover for graminoids, forbs and shrubs, cover from all the quadrats and all the plots for the respective groups were totalled. The relative cover (%) of individual groups (graminoids, forbs and shrubs) was then presented as a proportion of total cover of all groups together. Since we only recorded a few individuals of vine we did not include this group in the functional group analysis. Four forbs and five graminoid species whose life forms could not be determined were excluded from all the analyses. A plant species was regarded as a weed if it has been reported to be unwanted and invasive if it is non-indigenous species causing environmental damage or economical loss (Simberloff and Rejmánek 2011).

Environment, disturbance and spatial position

We used altitude, soil moisture (SM), total organic carbon (TOC), number of cow dungs, number of grass tussocks (*Panicum coloratum*, *Panicum maximum*, *Panicum fluviicola*,

Table 1 The natural environmental conditions, spatial position of plots and human disturbance variables recorded in each plot within the grasslands of Kilombero Valley, Morogoro, Tanzania

Main variables	Unit	Mean	SD	Min	Max
Environmental					
Altitude	m	254.7	8.3	245	280
Tussocks	no.	7	13	0	56
Soil moisture	%	10.1	2.9	1.1	15.7
Total organic carbon	%	2.1	0.8	0.7	3.9
Distance between plot and river	m	5,219	3,873	430	14,358
Spatial position					
Spatial variable (x)	m	22,500	9,964	10,000	46,900
Spatial variable (y)	m	44,900	29,188	13,900	122,800
Human disturbance/anthropogenic factors					
Cow dung	no.	20	33	0	223
Grazed leaves	no.	50	68	0	369
Distance between plot and kraal	m	1,673	1,861	152	10,427
Distance between plot and farm	m	150	367	2.5	2,500
Distance between plot and house	m	1,725	2,081	15	7,500

Min minimum, *Max* maximum, *SD* standard deviation

Sporobolus pyramidalis, *Vetiveria nigratana*), grazing intensity and the distances between plots and house, farms, kraals and river, and the spatial position of plots (Table 1) as explanatory variables for the spatial variation in plant species and functional group composition across the grassland of the Kilombero Valley. In each quadrat surveyed we took one soil core and mixed 20 cores to make a composite soil sample for every plot. The soil samples were collected using a soil auger (0–20 cm depth, 5 cm diameter) and the soil samples were analysed at Sokoine University of Agriculture for TOC and SM content. The TOC was analysed using the wet digestion method (Walkley and Black 1934). The SM and TOC were determined by averaging two measurements per sample. To obtain SM, weights of fresh soil samples were recorded and the samples were oven dried at 105 °C to a constant weight and then reweighted. Moisture content of the soil was presented as a percentage of the dried soil weight. Prior to TOC analysis, the soil samples were air-dried, grounded in a mortar and sieved to <0.2 mm diameter after removing plant materials. It was always possible to see villages and farms from the sampling plots, but to physically visit the villages was often time consuming. Therefore linear distances between plots and the nearest houses and farms were visually estimated with the aid of three experienced field staff separately, and the mean distance was used in the analysis. Distances between plots and the three closest kraals (mean distance used in analysis) and the altitude of plots were estimated from standardized GPS readings. Because it was not possible to see the river banks from all the plots and the river is already geo-mapped, linear distances between plots and the river were estimated using ArcView GIS 3.3 (Environmental Systems Research Institute 2002). To estimate grazing intensity, we counted cow dung in a 4 × 4 m plot surrounding each quadrat. In addition, all pin contacts to leaves (frequency) were assessed and the number of grazed leaves scored. We summed all counted cow dung from all the quadrats to obtain a total number of cow dung in each plot. The grass tussocks were counted from each plot. Spatial position variables (x and y) were used to examine the potential effect of spatial position of plots on functional groups and species composition. The spatial variables were obtained with Google Earth (http://earth.google.com). First, all the plots coordinates were overlaid on the Google Earth map followed by construction of two lines; one perpendicular (x) and one parallel (y) to the main river. Second, respective distances between plots and the two lines were measured. On every occasion effort was made to ensure that a ruler was placed exactly perpendicular to x and parallel to y lines and a measurement was made from the line and ended at the centre of a plot every time. Finally, the two distances obtained were used as predictors of the spatial variation in PFGs and species composition, together with all other variables.

Statistical analyses

Multivariate analysis was used to explore how natural environmental conditions, human disturbance and spatial position of plots explain variation in overall species composition and PFGs, using CANOCO 4.5 and CanoDraw (ter Braak and Šmilauer 2002). Detrended correspondence analysis (DCA) was used to detect the type of multivariate analyses to be used (Hill and Gauch 1980). Relatively long gradient length, with 4.5 standard deviations, for the species data suggests a strong unimodal nature of the data. Therefore we used canonical correspondence analysis (CCA) for overall species composition (McCune and Grace 2002; ter Braak and Šmilauer 2002). We used redundancy analysis (RDA) to establish the relationship between PFGs and the predictor variables. The RDA assumes linear relationships between the response variables and the predictor variables and models mainly the absolute abundance and was therefore used to our data set (ter Braak and Šmilauer 2002). Multicollinearity was checked in preliminary CCA and RDA using variance inflation factors (VIFs), which were low for all variables (all VIFs < 8), indicating that the variables were relatively independent (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003). Species data were log $(1 + 2x)$ transformed to meet assumptions of multivariate normality and to moderate the influence of a few dominant species (ter Braak and Šmilauer 2002). Stepwise automatic forward selection was used to identify significant explanatory variables within each set of variables. Significance of variables, the CCA and RDA models, and of canonical axes were tested with Monte Carlo test using 499 unrestricted permutations (Legendre and Gallagher 2001). All variables that were significant at $P < 0.2$ were considered in the subsequent analyses. Partial ordination was carried out to determine independent and joint contributions of each subset of predictor variables (environmental, spatial and anthropogenic) to the explained variation for both PFGs and species composition, through the variation partitioning method (Anderson and Gribble 1998). Variance partitioning was performed only with the significant variables (Table 2). For PFGs, the partial ordination involved two sets of predictors (environmental and anthropogenic), and thus followed Borcard et al. (1992). Comparison of abundance between PFGs was achieved using one-way analysis of variance (ANOVA). Tukey's HSD post hoc test was used to separate groups that were significantly different at $P < 0.05$. Prior to ANOVA, cover data for annual and perennial forbs were square-root transformed and shrub data were log $(1 + x)$ transformed to improve normality and homogeneity of variances. In addition, a second data set involving only weed and invasive species together was constructed from the overall species data set. Then, a second CCA (3.1 SD), which followed the same procedures as the first CCA and variation partitioning were conducted.

Table 2 Forward selection of natural environmental conditions, spatial position of plots and anthropogenic factors on species composition (CCA) and plant functional groups (RDA) of grasslands in the Kilombero Valley, Morogoro, Tanzania

Variables	All species		Weed and invasive		Functional groups	
	F ratio	*P* value	*F* ratio	*P* value	*F* ratio	*P* value
Altitude	0.92	0.632	0.73	0.776	**1.93**	**0.100**
Cow dung	**2.06**	**0.036**	**3.68**	**0.004**	**3.54**	**0.030**
Soil moisture	0.98	0.488	1.11	0.298	1.22	0.264
Grazed leaves	0.94	0.460	0.94	0.416	0.32	0.858
Spatial variable (x)	**2.39**	**0.002**	**3.87**	**0.002**	0.21	0.936
Spatial variable (y)	0.95	0.478	0.81	0.604	0.15	0.968
Total organic carbon	**1.67**	**0.002**	**1.61**	**0.048**	1.12	0.308
Number of tussocks	**1.49**	**0.058**	**1.39**	**0.196**	0.69	0.572
Distance between plot and river	**1.28**	**0.042**	**1.37**	**0.112**	**4.41**	**0.002**
Distance between plot and kraal	**1.45**	**0.104**	**2.11**	**0.066**	**1.66**	**0.152**
Distance between plot and farm	1.12	0.312	1.32	0.214	0.49	0.742
Distance between plot and house	1.06	0.334	0.94	0.518	**1.55**	**0.164**

Only significant explanatory variables at $P < 0.2$ were included in the final models (in bold) for both species composition and PFGs. The CCA and RDA were used for constrained unimodal and the linear models, respectively

Results

Plant community and functional structure

A total of 115 plant species belonging to 22 plant families and 72 genera were recorded. Of all the species, 22 are reported as weeds and 3 as invasive. The three dominant families were Poaceae, Fabaceae and Cyperaceae with 41, 25 and 11 species, respectively (Appendix). The two most frequent species were *Echinochloa colona* and *Paspalum scrobiculatum* with 20 and 11 % relative covers, respectively. The five assessed PFGs differed significantly in their cover (one way ANOVA $F_{4,295} = 142.3$, $P < 0.001$). Annual graminoids (relative cover of 50 %) were most abundant while perennial forbs (1 %) were the least common. The annual and perennial graminoid differed (Tukey's HSD, $P < 0.05$) in their mean covers. The annual forb, perennial forb and shrub functional groups did not differ (Tukey's HSD, $P > 0.05$) in their mean covers. *E. colona*, *P. scrobiculatum*, *Hygrophila auriculata*, *Indigofera* spp. and *Crotalaria* spp. were the dominant species in annual graminoids, perennial graminoids, annual forbs, perennial forbs and shrubs, respectively. Overall, graminoids, forbs and shrubs had 93, 6 and 1 % relative covers, respectively.

Gradients in overall plant species composition

Spatial position of plots (x), cow dung, TOC and number of tussocks most significantly explained variation in the overall plant species composition (Table 2; Fig. 2). The first four CCA axes accounted for 78 % of the variation in the species-environment relationships. The eigenvalues of the first and second canonical axes were 0.3 and 0.26, respectively, and

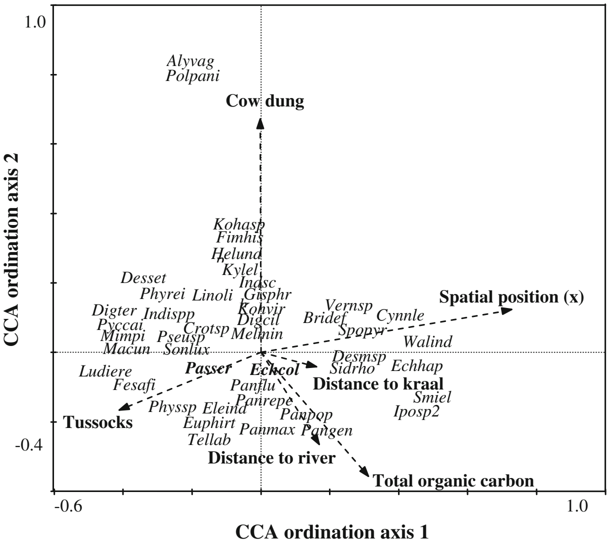

Fig. 2 CCA attribute plot for overall plant species composition constrained by natural environmental conditions, spatial position of plots and anthropogenic factors in the grasslands of Kilombero Valley, Morogoro, Tanzania. Eigenvalues of each canonical axis was 0.3, 0.26, 0.21 and 0.17 for the first four axes. Sum of all canonical eigenvalues is 1.193, whereas total inertia is 7.155. The first two axes account for 47 % of the variation in species–environment relationships. Only significant ($P < 0.2$) and independent factors are presented. Species shown are those with >3 % fit. Full species names and abbreviations are shown in Appendix

together the two axes accounted for 47 % of this variation and explained 8 % of the total inertia in the overall species data. Both the first canonical axis ($F = 2.30$, $P = 0.03$) and the overall model ($F = 1.77$, $P = 0.002$) were statistically significant. The first gradient separated overall species composition based on spatial position of plots (x) (interset correlation, $r = 0.84$) and number of tussocks ($r = -0.37$). The second gradient was caused by cow dung ($r = 0.8$) and TOC ($r = -0.32$). The two most abundant species (*E. colona* and *P. scrobiculatum*) were located at the centre of biplot, signifying them to be ubiquitous and independent of any of the explanatory variables (Fig. 2). *Panicum* species appear to associate with TOC (Fig. 2).

When the CCA ordination was constrained by significant natural environmental variables alone, spatial position of plots variable alone or anthropogenic variables alone, each subset significantly explained the variation in the overall species composition (Table 3). All three subsets of variables together explained 17 % of the variation in the overall species composition. The independent contributions from both natural environmental (7 %) and anthropogenic (6 %) variables were larger than the contribution from spatial position of plot variable (3.4 %). There were little overlaps in the variation explained by the three subsets of variables, as indicated by small variations shared by the different subsets (Table 3). The shared eigenvalue between natural environmental and human disturbance factors was negative, indicating that the two subsets did not have a common explained variation. Similarly, the shared eigenvalue for the three predictor subsets was also negative suggesting that the three subsets did not have a joint explained variation (Table 3).

Table 3 CCA variation partitioning to determine the relative influence of natural environmental conditions, spatial position of plots and anthropogenic variables on overall plant species composition of grasslands in the Kilombero Valley, Morogoro, Tanzania

Effect and main variables	Covariables	$\sum$ Canonical eigenvalues	Variation explained (%)	*F* ratio	*P* value
Total effect					
Environmental, anthropogenic, spatial		1.193	17.0	1.77	0.002
Partial effects					
Environmental	Anthropogenic, spatial	0.503	7.0	1.49	0.002
Anthropogenic, spatial		0.691	10.0	1.99	0.002
Anthropogenic, spatial	Environmental	0.659	9.0	1.95	0.002
Environmental		0.534	7.5	1.51	0.002
Spatial	Anthropogenic, environmental	0.246	3.4	2.19	0.002
Anthropogenic, environmental		0.947	13.0	1.65	0.004
Anthropogenic, environmental	Spatial	0.911	13.0	1.62	0.004
Spatial		0.283	4.0	2.39	0.002
Anthropogenic	Spatial, environmental	0.411	6.0	1.83	0.022
Spatial, environmental		0.782	10.9	1.69	0.002
Spatial, environmental	Anthropogenic	0.786	11.0	1.75	0.002
Anthropogenic		0.407	5.7	1.72	0.026
Joint effects					
Environmental and spatial		0.037			
Environmental and anthropogenic		−0.004			
Anthropogenic and spatial		0.001			
Environmental and anthropogenic and spatial		−0.002			

Percentage of variation explained by each canonical ordination is the sum of all constrained eigenvalues divided by the total inertia. Total inertia was 7.155 for plant species composition. *F* and *P* values were estimated by 499 unrestricted Monte Carlo permutation tests. Only significant variables were used in the variation partitioning and each subset of predictors is as indicated in Table 2

Gradients in PFG composition

Distance to the river, cow dung, altitude and distance to the kraal were most significant variables explaining variation in the PFGs (Table 2; Fig. 3). The first (eigenvalue, $\lambda = 0.13$) and the second ($\lambda = 0.1$) axes explained 18 % of the total variation in the PFG data. The first axis ($F = 8.01$, $P = 0.002$) and the overall model ($F = 2.73$, $P = 0.002$) were statistically significant. The first RDA axis was mainly a gradient of distance to the river ($r = 0.44$) and cow dung (interset correlation, $r = 0.36$) and separates annual and perennial graminoids (Fig. 3). The second axis represented mainly a gradient in altitude

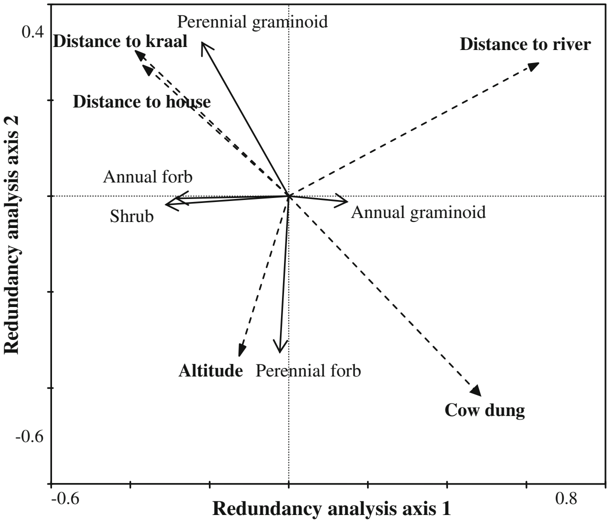

Fig. 3 RDA attribute plot for five plant functional groups with natural environmental conditions and anthropogenic factors in the grasslands of Kilombero Valley, Morogoro, Tanzania. The natural environmental conditions and anthropogenic predictor variables are shown as dashed arrows. Eigenvalues of each RDA axis was 0.13, 0.05, 0.02 and 0.01 for the first four axes. Sum of all RDA eigenvalues is 0.202. The first two axes account for 89 % of the variation in functional groups-environment relationships. Only significant ($P < 0.2$) and independent factors are presented

($r = -0.18$) and distance to kraal ($r = 0.17$) and separates annual from perennial forbs (Fig. 3). RDA using significant environmental and anthropogenic factors revealed that, the two sets together explained around 20 % variation in the PFGs. Both natural environmental (9 %) and anthropogenic (10 %) variables explained essentially the same amount of variation in the PFGs, with little overlap, as shown by the small shared eigenvalue (Table 4).

Gradients in composition of weed and invasive plant species

Spatial position of plots (x) and cow dung were most significant variables explaining variation in the composition of weed and invasive species (Table 2; Fig. 4). CCA showed that the first four axes accounted for 84 % of the variation in the species-environments relationships. Together the first (eigenvalue, $\lambda = 0.21$) and the second ($\lambda = 0.18$) axes accounted for the majority (57 %) of this variation and explained 12 % of the total inertia in the weed and invasive species data. The first axis ($F = 3.67$, $P = 0.008$) and the overall model ($F = 2.43$, $P = 0.002$) were statistically significant. The first dominant gradient is caused by plots spatial position variable (x) ($r = 0.76$). The second dominant gradient is caused by cow dung ($r = 0.86$) and the invasive species *Polygala paniculata* was associated with this gradient (Fig. 4). Altogether, the natural environmental, spatial position of plots (x) and anthropogenic variables explained 22 % of the total variation in the weed and invasive plant species composition. The anthropogenic variables explained more variation (9 %) in species composition than natural environmental (6.4 %) and plots spatial position (5.2 %) variable (Table 5). The shared eigenvalue for the three predictor subsets was negative suggesting that the three subsets did not have a common explained variation (Table 5).

Table 4 RDA variation partitioning to determine the relative influence of natural environmental conditions and anthropogenic variables on plant functional groups in the grasslands of the Kilombero Valley, Morogoro, Tanzania

Effect and main variables	Covariables	∑ canonical eigenvalues	Variation explained (%)	*F* ratio	*P* value
Total effect					
Environmental, anthropogenic		0.202	20.2	8.0	0.002
Partial effects					
Environmental	Anthropogenic	0.088	8.8	2.98	0.01
Anthropogenic	Environmental	0.103	10.3	2.32	0.01
Anthropogenic		0.114	11.4	2.4	0.01
Environmental		0.099	9.9	3.13	0.002
Joint effect					
Environmental and anthropogenic		0.011	1.1		

Percentage of variation explained by each canonical ordination is the sum of the canonical eigenvalues divided by the total inertia (1). *F* and *P* values were estimated by 499 unrestricted Monte Carlo permutation tests. Only significant variables were used in the variation partitioning and each subset of predictors is as indicated in Table 2

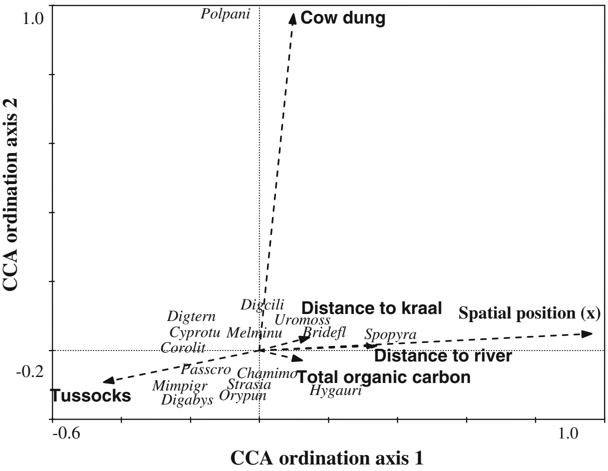

Fig. 4 CCA attribute plot for weed and invasive plant species composition constrained by natural environmental conditions, spatial position of plots and anthropogenic factors in the grasslands of Kilombero Valley, Morogoro, Tanzania. Eigenvalues of each canonical axis was 0.21, 0.18, 0.11 and 0.1 for the first four axes. Sum of all canonical eigenvalues is 0.684, whereas total inertia is 3.172, respectively. The first two axes account for 57 % of the variation in species-environment relationships. Only significant ($P < 0.2$) and independent factors are presented. Species shown are those with >1 % fit. Full species names and abbreviations are shown in Appendix

Discussion

Plant community, functional structure and dominant factors

Kilombero grassland is a dynamic landscape with species rich plant communities of conservation importance. Of the previously reported 350 plant species in the floodplain

Table 5 CCA variation partitioning to determine the relative influence of natural environmental conditions, spatial position of plots and anthropogenic variables on weed and invasive species composition of grasslands in the Kilombero Valley, Morogoro, Tanzania

Effect and main variables	Covariables	$\sum$ canonical eigenvalues	Variation explained (%)	*F* ratio	*P* value
Total effect					
Environmental, anthropogenic, spatial		0.684	22.0	2.43	0.002
Partial effects					
Environmental	Anthropogenic, spatial	0.204	6.4	1.45	0.032
Anthropogenic, spatial		0.480	15.1	3.33	0.002
Anthropogenic, spatial	Environmental	0.442	13.9	3.14	0.002
Environmental		0.241	7.6	1.54	0.014
Spatial	Anthropogenic, environmental	0.166	5.2	3.40	0.002
Anthropogenic, environmental		0.517	16.3	2.11	0.002
Anthropogenic, environmental	Spatial	0.485	15.3	2.07	0.002
Spatial		0.198	6.2	3.87	0.002
Anthropogenic	Spatial, environmental	0.278	8.8	2.96	0.002
Spatial, environmental		0.406	12.8	2.02	0.002
Spatial, environmental	Anthropogenic	0.404	12.7	2.15	0.002
Anthropogenic		0.279	8.8	2.75	0.002
Joint effects					
Environmental and spatial		0.035			
Environmental and anthropogenic		0.004			
Anthropogenic and spatial		−0.002			
Environmental and anthropogenic and spatial		−0.001			

Percentage of variation explained by each canonical ordination is the sum of the canonical eigenvalues divided by the total inertia. Total inertia was 3.172 for plant species composition. *F* and *P* values were estimated by 499 unrestricted Monte Carlo permutation tests. Only significant variables were used in the variation partitioning and each subset of predictors is as indicated in Table 2

(Starkey et al. 2002), 115 (33 %) species occur in the studied communities. Among the registered plants, some are typical floodplain species such as *Sida ovata* and *P. fluviicola.* Others are economically highly valued fodder species, such as *P. maximum* and *Digitaria macroblephara* (Hobbs 1996). The presence of weed species like *Oryza punctata* and *Digitaria abyssinica* (Holm 1997; Khan et al. 2000) and invasive species like *Mimosa pigra* and *P. paniculata* suggests that the ecosystem has been invaded and a further spread of *M. pigra* which could be a serious invader, should be prevented for Kilombero ecosystem to be restored. Annual graminoid was the dominant PFG in Kilombero. It is well established that regularly inundated floodplains are dominated by annuals and flood tolerant species (see Lenssen et al. 1999; Capon 2003). The dominance of this PFG could be due to flooding effects including herbaceous litter removal which could hinder germination of small-seeded species and increase understory light intensity, which promotes competitive ability of annuals and increase soil seed bank of the annuals following flooding (Vervuren et al. 2003; Bagstad et al. 2005; Keddy 2010).

Spatial position of plots (x), cow dung, TOC, altitude, distance to the river and distance to the kraal were generally the best predictors for overall species composition and functional group cover within the grasslands of Kilombero Valley. Cow dung, distances to the river and distance to kraal were predictors common to overall species composition and functional groups cover (Table 2). Variation partitioning indicated that natural environmental and anthropogenic factors explained the same amount of variation while the spatial position of plots variable (x) explained a relatively small amount of variation in the overall species composition. Moreover, the natural environmental and anthropogenic variables explained the same amount of variation in functional groups whereas the plots spatial position variable (x) was not important in the composition of PFGs. These results suggest that the spatial heterogeneity in the composition of overall species and functional groups is related to the natural environmental conditions and human disturbance within these grassland communities. However, these results should be interpreted with caution as the low percentage of variation explained by the spatial position of plots variable (x) does not necessarily indicate that spatial position of plots has less influence to the species composition. Borcard et al. (1992) recommends use of the same number of variables in each set of explanatory variables when carrying out partial ordination. In another study involving 33 environmental and 9 spatial variables, it was demonstrated that if forward selection is carried out before a constrained ordination, the number of variables in each set of variables does not matter, the inclusion of all or most of the important variables in each set was the most important to maximize the amount of variation explained (Økland and Eilertsen 1994). Therefore, differences in the variation explained by three sets of variables to our responses (overall species composition and functional groups cover) might have been influenced partly by the number of variables in the sets. Considering that the plots spatial position variable (x) was the main dominant factor (as a single predictor) associated with the most important ordination axis on the overall species composition (Fig. 2), it is possible that a relatively low variation expressed by the plots spatial position variable (x) (as a set) was partly a result of the low number of variables (in that set) during partial CCA and indeed does not necessarily signify that the spatial position of plots is less important to the species composition. On the other hand, the relatively low influence of plots spatial position variable (x) on overall species composition and the non significance of this variable to PFGs may suggest that, restricted seed dispersal of species do not contribute strongly to the spatial variation in composition of overall plant species and functional structure. One possible explanation is that seeds are dispersed through multiple vectors including water, wind and animals to most parts of the floodplain landscape (Dai 2000; Neff and Baldwin 2005). This suggests that other factors related to human disturbance (e.g. cow dung) and environmental conditions (e.g. altitude, distance to the river) may explain spatial heterogeneity is species composition and PFGs. Overall, these results only partially support our prediction that anthropogenic factors would have stronger influence than naturally varying environmental variables and spatial position of plots on the PFGs and overall plant species composition.

Altitude, distance to the river and TOC are associated with flooding conditions, which contributes considerably to biological productivity and development of plant communities (van der Valk 2006). Flood events are usually associated with litter depositions, changes in soil characteristics (e.g. organic content, chemistry, moisture) and nutrients availability (Moran et al. 2008). For Kilombero grasslands, it is likely that the flooding modifies physical and chemical environment which contributes to spatial heterogeneity in the overall species composition and functional groups. It is generally known that spatial differences in flooding pattern (which is related to altitude and distance to river) create a mosaic of habitats for wetland species and distinct plant communities (Lenssen et al. 1999; Lenssen and De Kroon 2005). Nonetheless, Figs. 2 and 3 suggests that distance to the river is not as important for overall plant species composition as for functional groups. Figure 2 also reveals a relatively small influence of distance to river on the overall species composition as opposed to other studies (e.g. Schipper et al. 2011) in wetlands where species segregate mainly along the hydrological gradient. One possible explanation for these observations could be that the current study focused on one major plant community (out of 8) along the hydrological gradient from the river channel to valley margins thus probably not allowing the distance to the river to be a pronounced factor in explaining species composition. Also, it may be that probably the distance to the river does not primarily reflect a hydrological gradient due to the influence of confounding factors like microtopography. It should be noted that Kilombero Valley is characterized by various physical features including peneplain and raised landforms which could mask the most important factors for spatial heterogeneity in plant species composition (Starkey et al. 2002).

Consistent with other studies (e.g. Howard 1992; Starkey et al. 2002) some forb and shrub species were associated with high altitudes within the Kilombero wetland system. A plausible explanation for this pattern is that most forbs and shrubs are less tolerant to inundation and therefore establish mainly at raised landforms. Moreover, Lenssen et al. (1999) demonstrated that shallow flooding restricted establishment of tall forbs (e.g. *Urtica dioica*) in a field experiment in the Netherlands, indicating that micro-topographic variation provides additional habitats, which widens plant species composition and functional structure (Swanson et al. 1988; Moser et al. 2007).

Large herbivores influence grasslands species composition and functional structure by removing herbage, trampling and dung and urine depositions (Hobbs 1996; Malo et al. 2000; Kohler et al. 2004). Herbage removal (measured as number of grazed leaves) was not an important factor for species composition and functional groups in our system. This is contrary to Kohler et al. (2004) who found herbage removal to be an important component in structuring species composition of pastures in a simulated cattle grazing experiment, suggesting that in our system other factors (e.g. spatial position of plots, dung deposition) are important to explain the spatial heterogeneity in species composition and functional groups cover. In Kilombero, cow dung and distance to kraals were important for PFGs and overall species composition. The kraal-distance variable represent a gradient in grazing pressure (Milchunas and Lauenroth 1993). We found that perennial graminoids increases with distance to the kraal (Fig. 2), suggesting that a decrease in grazing pressure promotes perennial graminoids; as found in other studies (e.g. McIntyre and Lavorel 2001). Dung deposition modifies site conditions by supplying nutrients and facilitates seed dispersal (Kohler et al. 2004). In particular, addition of nitrogen and phosphorus especially to low fertility soils leads to invasion of non native species which changes species composition and functional structure of the grassland vegetation. It is therefore possible that in our ecosystem, cow dung changes the site conditions through fertilization effects which together with seed distribution by dunging influence the species composition and PFGs. In this work, trampling was not investigated and therefore difficult to conclude on its effects to the studied grassland ecosystem. However, trampling disturbs the soil and creates gaps which promote growth of opportunistic plant species that ultimately changes the species composition (Bullock et al. 1995; Zedler and Kercher 2004) and possibly functional structure.

For weed and invasive plant species together, anthropogenic factors contributed more to the explained variation in species composition of these species (Table 5). The natural environmental and spatial position of plots (x) variables explained relatively low and essentially the same amount of variation in the composition of weed and invasive species thus our expectation that the spatial position of plots is not important for composition of these species due to their good dispersal ability is partially supported. These results are not surprising since human related disturbances are well known to facilitate successful establishment of non-native (including invasive species) and weedy plant species in many ecosystems (Hobbs 1991; Hobbs and Huenneke 1992). It is therefore possible that a change in grazing regime, due to increase in number of cattle, in the Kilombero Valley has contributed to the current spatial heterogeneity in species composition of weed and invasive plant species. Most of the invasive and weedy plant species take advantage of the changes in site conditions, especially increase in light and nutrients following a significant disturbance (Milbau and Andi 2004). Species *P. paniculata*, which appear to prefer disturbed areas, had strong affinity to cow dung, suggesting that its seeds are dispersed by cattle or that cattle dung facilitates its establishment by increasing soil nutrient concentration and light.

Partial ordination indicated that the predictor variables captured little of the total variation in species composition and functional groups cover. The relatively dynamic and complex nature of the Kilombero grasslands, including a high spatial variability in land use history and micro-topography may have contributed to these results (Starkey et al. 2002). Other sources of low explained variation is discussed in detail elsewhere (e.g. Økland 1999; Palmer 2012). Nevertheless, the results still indicate the relative importance of spatial position of plots, natural environmental conditions and human disturbance particularly plots spatial position (x), cow dung, TOC, altitude, distance to the river and distance to the kraal for this ecosystem. Future studies should incorporate those factors as they appear to be important drivers of the species composition and functional structure of inundated tropical grasslands.

Implications for management of the Kilombero Ramsar site

Our study has identified relationships between spatial position of plots (x), cow dung, TOC, altitude, distance to the river and distance to kraal and wetland plant communities of Kilombero. Such relationships provide valuable information for wetlands restoration and effective management strategies, particularly for Kilombero Ramsar site and other protected areas with similar ecological and management settings. Because of the abundance and availability of water throughout the year and the fertile soils, the Kilombero floodplain attracts livelihood activities which may destroy critical habitats and thereby impair biodiversity. Increase in cattle grazing effects such as trampling, gap openings and nutrient inputs my accelerate the spread of invasive species (e.g. *P. paniculata*) which consequently changes plant species composition and functional structure (Rea and Storrs 1999; DiTomaso 2000). The number and cattle movements should therefore be controlled in order to restore the integrity of the Kilombero Valley. Shrub and forb species were most abundant on high altitude indicating that maintenance of micro-topography within the floodplain is important for the Kilombero grassland ecosystem.

Overall, spatial position of plots, human disturbance and natural environmental conditions determine the spatial heterogeneity in the species composition and functional structure of Kilombero grasslands. Therefore, changes in natural environmental conditions and increases of human activities (e.g. livestock keeping, agriculture) would contribute to an accelerated change in the vegetation. This could have far-reaching implications for ecosystem services and ultimately lead to reduced biodiversity and rural livelihood. Therefore local communities, wetland managers and policy makers should discourage all human activities that compromise sustainability of the wetland ecosystems and overall biodiversity. Development of land use plans could supplement those efforts. Long-term monitoring of the grassland communities is recommended as the environment changes and increased human activities likely will increase the abundance of invasive species.

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Appendix

Relative cover, RC (%) of species recorded from the grasslands of Kilombero Valley, Morogoro, Tanzania. The RC is the ratio of individual species total cover (from all the quadrats and all the plots) and the total cover of all species combined together from all the quadrats and all the plots given in percentages. Species with no RC had <0.1 % relative cover. Short form represents species names for abbreviations used in Figs. 2 and 4. Species marked * and ** are weeds and invasive plant species, respectively.

RC	Short form	Species by families	RC	Short form	Species by families
		Acanthaceae			Labiatae
1.5	Hygauri	*Hygrophila auriculata**		Baspoly	*Basilicum polystachyon**
	Jushete	*Justicia heterocarpa*	0.5	Pycruan	*Pynostachys ruandensis*
		Aizoaceae			Liliaceae
	Gisphr	*Gisekia pharnaceoides*		Corolit	*Corchorus olitorius**
		Asteraceae		Diplong	*Dipcadi longifolium*
0.1	Vernspp	*Vernonia* spp.			Malvaceae
	Sonlux	*Sonchus luxurians*	0.5	Pavflav	*Pavonia flavoferruginea*
		Boraginaceae	0.1	Hibispp	*Hibiscus* spp.
	Helund	*Heliotropium undulatifolium**		Sidovat	*Sida ovata*
		Commelinaceae	0.4	Sidrho	*Sida rhombifolia*
	Anespp1	*Aneilema* sp1.			Onagraceae
	Anespp2	*Aneilema* sp2.		Ludere	*Ludwigia erecta*
		Convolvulaceae			Pedaliaceae
0.1	Ipomspp1	*Ipomoea* sp1.		Sesangu	*Sesamum angustifolium*
	Iposp2	*Ipomoea* sp2.			Poaceae
	Ipoobsc	*Ipomoea obscura*	1.7	Bracoma	*Brachiaria comata*
		Cucurbitaceae	0.1	Braeruc	*Brachiaria eruciformis*
	Mukmade	*Mukia maderaspatana*	3.6	Bridefl	*Brachiaria deflexa**
		Cyperaceae		Cenbifl	*Cenchrus biflorus*
0.4	Couassi	*Courtoisina assimilis*	0.8	Dacaegy	*Dactyloctenium aegyptium**
0.3	Cypcomp	*Cyperus compressus**	1.5	Digcil	*Digitaria ciliaris**
0.9	Cyptenu	*Cyperus tenuispica*	5.1	Diglong	*Digitaria longiflora*

Appendix continued

RC	Short form	Species by families	RC	Short form	Species by families
	Fimhis	*Fimbristylis hispidula**	4.1	Digter	*Digitaria ternata**
	Pyccai	*Pycreus capillifolius*	9.9	Digvelu	*Digitaria velutina**
0.7	Cypmara	*Cyperus maranguensis*	19.8	Echcol	*Echinochloa colona**
0.1	Cypnive	*Cyperus niveus*	1.7	Echhap	*Echinochloa haplocloda*
1.0	Cyprotu	*Cyperus rotundus**	0.1	Eleind	*Eleucine indica*
0.1	Fimdich	*Fimbristylis dichotoma*		Eracilia	*Eragrostis ciliaris*
4.5	Fimexil	*Fimbristylis exilis*	0.2	Eracilne	*Eragrostis cilianensis*
	Kylel	*Kyllinga elata Steud*	0.2	Schizspp	*Schizachyrium* sp.
		Euphorbiaceae	0.1	Agrospp	*Agrostis* spp.
	Phyreti	*Phyllanthus reticulatus*	2.5	Cynnlem	*Cynodon nlemfuensis*
	Euphirt	*Euphorbia hirta*	0.1	Digabys	*Digitaria abyssinica**
		Fabaceae	0.3	Digmacr	*Digitaria macroblephara*
0.2	Aesindi	*Aeschyonomene indica*	1.8	Digmila	*Digitaria milanjiana*
	Aesschi	*Aeschyonomene schimperi*		Ennconc	*Enneapogon conchroides*
1.4	Crotsp1	*Crotalaria* sp1.		Eratrem	*Eragrostis tremula**
0.1	Crotsp2	*Crotalaria* sp2.	0.1	Fesafi	*Festuca africana*
0.1	Crotsp3	*Crotalaria* sp3.	0.2	Hellanc	*Helictrotrichon lachnanthum*
0.1	Crotsp4	*Crotalaria* sp4.		Hetcont	*Heteropogon contortus*
0.1	Crotsp5	*Crotalaria* sp5.	0.6	Hypcymb	*Hyparrhenia cymbaria*
	Eriospp	*Eriosema* spp.	0.1	Impespp	*Imperata* spp.
0.1	Eripsor	*Eriosema psoraleoides*	5.1	Melmin	*Melinis minutiflora**
0.1	Mimpi	*Mimosa pigra***	4.1	Orypun	*Oryza punctata**
0.3	Tepline	*Tephrosia linearis*		Pancolo	*Panicum coloratum*
	Alyrugo	*Alysicarpus rugosus*	1.1	Panflu	*Panicum fluviicola*
	Alyvag	*Alyscarpus vaginalis*		Pangenu	*Panicum genuflexum*
0.1	Chamimo	*Chamaecrista mimosoides**	1.4	Panmax	*Panicum maximum*
	Macun	*Macrotyloma uniflorum*		Panpop	*Panicum pophyrrhizus*
	Desmsp	*Desmodium* spp.	0.5	Panrepe	*Panicum repens*
	Desset	*Desmodium setigerum*	11.3	Passcr	*Paspalum scrobiculatum**
0.6	Indsp1	*Indigofera* sp1.	0.4	Sacafri	*Sacciolepis africana*
0.2	Indisp2	*Indigofera* sp2.		Setspha	*Setaria sphacelata*
	Indisp3	*Indigofera* sp3.	1.4	SpoIocl	*Sporobolus ioclados*
	Indisp4	*Indigofera* sp4.	2.1	Spopyr	*Sporobolus pyramidalis**
	Indschi	*Indigofera schimperi*	2.6	Uromoss	*Urochloa mossambicensis**
0.2	Indvolke	*Indigofera volkensii*			Scrophulariaceae
	Smiel	*Smithia elliotii*		Linoli	*Lindenia oliveriana*
	Tellab	*Teramnus labialis*		Rusequi	*Russelia equisetiformis*
		Polygalaceae		Pseuspp	*Pseudosopubia* spp.
	Polpani	*Polygala paniculata***		Scodulc	*Scoparia dulcis**
		Portulacaceae	0.1	Strasia	*Striga asiatica***
	Portspp	*Portulaca* spp.	0.1	Strforb	*Striga forbesii*
		Rubiaceae			Solanaceae
	Kohasp	*Kohautia aspera*		Phyangu	*Physalis angulata*

Appendix continued

RC	Short form	Species by families	RC	Short form	Species by families
	Kohvir	*Kohautia virgata*	0.1	Physpp	*Physalis* spp.
	Oldaffi	*Oldenlandia affinis* subsp. *fugas*			Sterculiaceae
			0.1	Walind	*Waltheria indica*

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