Diversity and distribution of sedges on multivariate environmental gradients

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Abstract

Relationships between environmental factors and the distribution patterns of sedges were studied in the wetland important bird areas of Uganda. Vegetation data were collected using the transect and quadrat methods. Four quadrats were located at each sampling point at 10 m intervals along the transect from dry land to open water. Relative abundances of sedges were recorded in each quadrat. Inventory sampling was done to record species that were not recorded on the transects so as to generate near complete species lists. Human influences on vegetation such as harvesting, fire and vegetation modification were examined along the transects. Soil samples were collected along the transects for analysis of P, K, Na, Ca, Mg and organic matter. Other parameters recorded from water samples included water levels, pH and water conductivity. Rainfall and altitude were also recorded. Canonical correspondence analysis was used to correlate the relative abundances of the species to measured environmental variables. Linear correlation of the environmental variables with principal components indicated that water levels, altitude and rainfall were major factors that influenced the abundance and occurrence of sedges in the different bird areas. Sedge distribution patterns are a function of local geological and edaphic factors; and human-induced exogenous disturbances.

Key words: canonical correspondence analysis, Cyperaceae, diversity, wetland

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Introduction

Members of Cyperaceae, also commonly known as sedges, are dominant in wetlands and tropical grasslands. Worldwide, the Cyperaceae has 104 genera and 5000 species, with as many as 30 genera and 450 species in east Africa (Goetghebeur, 1998; Lye, 2001). According to Lye (2001), the total number of species in tropical Africa is about 800, while the number in tropical east and north-east Africa is 497. Lye further reports that tropical east Africa has 450 species while 268 species are known from tropical north-east Africa.

Although Uganda has a very large sedge flora with 223 species, it has only two country endemics (Lye, 2001): *Isolepis ruwenzoriensis* (Lye & Haines, 1974) and *Kyllingiella ugandensis* (Haines & Lye, 1978).

Cyperaceae is one of the families with members that are dominant in the wetland bird areas under study and therefore is a good candidate for this investigation.

The diversity of sedges in Uganda has been mainly studied by Haines & Lye (1983); however, little is known about the species diversity, distribution and abundance at various habitats and sites; and the factors that influence their distribution. It is expected that this study will contribute information in this regard within the selected bird areas in Uganda.

Materials and methods

Study sites

This study was carried out between August 2000 and May 2001 and was conducted in three major regions; the Lake Victoria basin that comprised Lutembe and Mabamba bays, Lutoboka point and Musambwa islands, and Lake

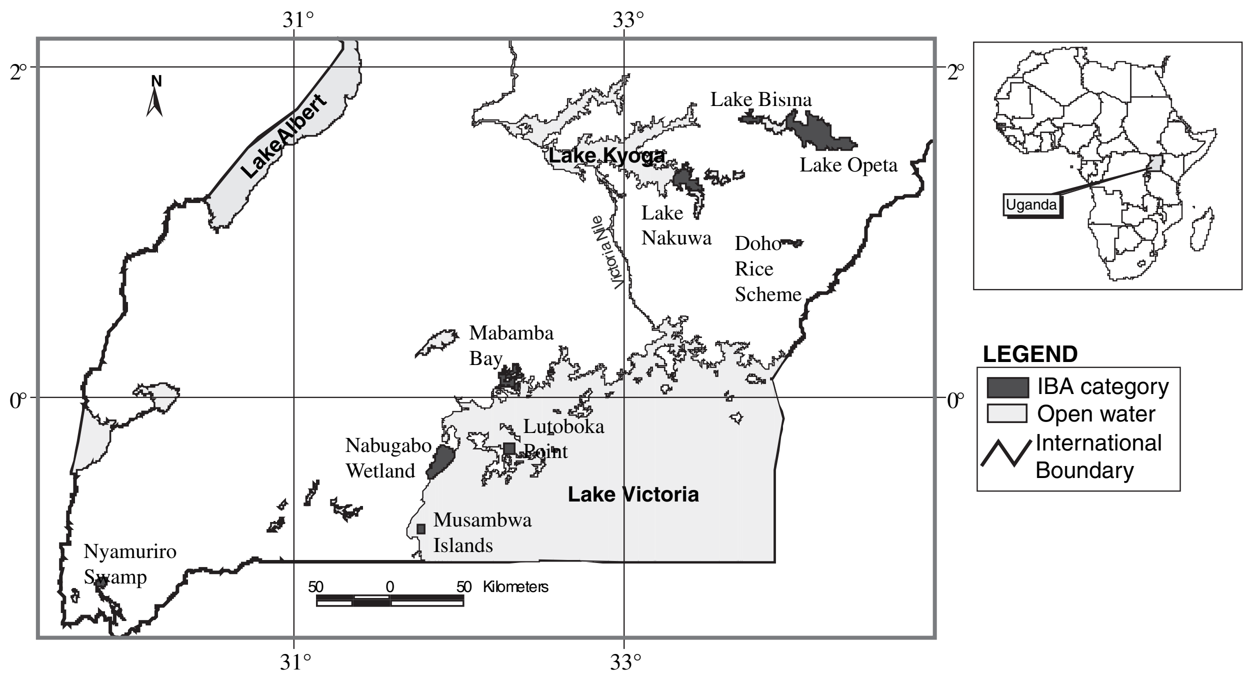

Fig 1 Location of wetland bird areas in Uganda.

Nabugabo on the eastern side of Lake Victoria. The Lake Kyoga basin includes the Lakes Opeta and Bisina in the north-east, the Doho rice scheme in the east and Lake Nakuwa forming an arm in the southern section. The Kabale region includes the Nyamuriro swamp which forms part of the extensive swamp that interconnects Lake Mutanda and Lake Bunyonyi (Fig. 1). These bird areas form part of the 30 important bird areas identified in Uganda as critical to the conservation of birds and were selected using internationally agreed scientific criteria (Byaruhanga, Kasoma & Pomeroy, 2001).

Sampling design

It was decided to capture as many habitat types and environmental gradients as possible in the different vegetation types that were identified. The relatively larger bird areas were divided into sites as part of the sampling design. This was done to ensure that there was consistency in sampling effort that was proportional to the size of the bird area, since all the bird areas were of varied size ranging from about 1 km^2 for Musambwa islands to 566 km^2 for Lake Opeta.

Transect lengths up to 800 m were used in wetlands because of access problems and, in some cases, the size of the wetlands. These followed habitat types that characterize each site as much as possible. Line transects and circular quadrats were used to collect the diversity data. Sampling points were located at 10-m intervals. Using the sampling point, four circular quadrats, of 1-m radius, were located equidistant from the sampling point and from each other at a distance of 2 m. This is a modification of the point frequency method (Okland, 1990) and the method used by Wettstein & Schmid (1999). Four quadrats were used to capture as many sedge species per sampling site as possible. All Cyperaceae species found in these quadrats were recorded with the percentage relative abundance (Okland, 1990; Kent & Coker, 1994) and specimens collected for identification were assigned collection numbers.

pH, conductivity and dissolved oxygen were measured directly in the field using the pH, conductivity and dissolved oxygen meters of Hanna Instruments; models HI 9023C, HI 9033 and HI 9142, respectively. These variables were measured at 50-m intervals wherever there was visibility and enough water to allow measurement.

Soil samples were collected for analysis for Ca, Mg, Na, K, P and organic matter. The samples were collected at intervals of 100 m along the transect and the vegetation type of the sample sites was recorded. Water depths were estimated at 50-m intervals (to the nearest 5 cm). Altitude was determined using a global positioning system at various points in the study site and later averaged. Rainfall values were obtained from the nearest weather stations.

The levels of vegetation disturbance and modification were determined subjectively. The levels are those suggested by Sheil (1996). Each level was determined on a linear scale of 0–4. For instance, a value of '0' corresponded with 'near natural', while '4' corresponded with 'near artificial' modification level. Vegetation disturbance was rated as none, limited, moderate, heavy and very heavy. Subjectivity in judgement was minimized by repeating the procedure at 100-m intervals and also by on-the-spot observations by the author to ensure that the level of accuracy and consistency increased as successive samples were taken.

Pastoralism and associated bush burning is a land-use practise that is fairly frequent in both protected and unprotected bird areas like Lutembe bay. A scale of 0–4 was used subjectively to measure the grazing intensity and 0–3 for burning in plots and at site level. Evidence of vegetation cutting or harvesting was recorded. This was done at 100-m intervals.

General collections were made outside the demarcated plots. Data on species richness and other variables not included on the site data form but worth recording were also made. The purpose of acquiring these data sets, in combination with data from demarcated plots, was to generate as complete lists as possible.

Data analysis

Species-sample plot matrices as proposed in Okland (1990) were developed for each bird area and used as the primary matrices. These were based on the presence/absence of sedge species in the sample plots. Ten species matrices were developed to represent the different bird areas. The rows of the matrices represented the sample (quadrat) vectors and the columns represented the species vectors. The matrices consisted of Doho rice scheme, 420 × 14; Lake Bisina, 721 × 19; Lake Nabugabo, 430 × 37; Lake Nakuwa, 2152 × 26; Lake Opeta, 869 × 30; Lutembe bay, 615 × 27; Lutoboka point, 70 × 13; Mabamba bay, 1906 × 29; Musambwa islands, 19 × 03; and Nyamuriro swamp, 1245 × 14.

Analyses including calculations of the diversity index and species richness estimations were performed using the computer programme *EstimateS* (Colwell, 1997). The index seeks to characterize the diversity of a sample or community by a single number (Magurran, 1988). Most indices that have been proposed to measure biodiversity try to encompass the two dimensions of the concept: richness and evenness.

To measure the different aspects of variability between the different bird areas, Simpson's index of diversity (D) was used (Magurran, 1988); however, to determine whether there were significant differences between the diversity of the different sites, Friedman test was used (Zar, 1984).

Two species richness estimators were used to estimate species richness from the bird areas. An estimator (S2*, or Chao2) of the true number of species in an assemblage based on presence/absence data in a sample [according to Colwell & Conddington (1994)] was used. $S2^* = S_{obs} + (L^2/2M)$, where L is the number of species that occur in only one sample ('unique' species), and M is the number of species that occur in exactly two samples ('duplicate' species).

A jackknife estimator of species richness (Jack1) was also used to estimate the true number of species (Palmer, 1995). The first-order jackknife estimator Jack1 (Palmer, 1991) was calculated from $\text{Jack1} = S + r1(n-1)/n$, where S is the observed number of species, $r1$ is the number of species occurring in one sample unit, and n is the number of sample units.

Species accumulation curves have been used to evaluate the adequacy of a sample size in a community data set. These were drawn for each bird area using the programme *EstimateS* (Colwell, 1997) after 100 randomizations.

Species–area relationship

The effect of size of bird areas on species richness was examined using the simple regression analysis. A species richness log area relationship was considered using the formula: $S = CA^z$ where S is the number of species, A is the area, C is a parameter that varies widely depending upon the taxa or taxon being considered and the unit of area measurement, and z is a constant (Gleason, 1922). The independent variable was log-transformed to ensure a normal distribution. Species richness was entered as the dependent variable. Significance of the linear model produced was determined by the ANOVA F-value and associated probability.

Gradient analyses

To determine the effects of some ecological variables and human-induced activities on the distribution of sedge species, bird areas were divided into three major ecoregions using the ecoregion classification developed by Omernik & Gallant (1988). These were the Lake Victoria basin, the Lake Kyoga basin and the predominantly sandy/rocky regions of Lake Victoria – the 'Nabugabo complex'. The bird areas were further subdivided into sites for the purposes of surveying based mainly on area and vegetation distinctiveness.

Environmental characterization of sites

Among the ecological variables considered were water depth (cm), water depth along a transect from the swamp edges to the open water; pH (pH units), from above the ground-level water (where present); conductivity (μS cm^{-1}); and dissolved oxygen, [(DO) (mg L^{-1})]; from the soil (in most cases peat within the root zone) measures of average phosphorus (p.p.m. as P); potassium [Me/(100 g)$^{-1}$ as K]; sodium [Me/(100 g)$^{-1}$ as Na]; organic matter (% as O.M.); calcium [Me/(100 g)$^{-1}$ as Ca]; and magnesium [Me/(100 g)$^{-1}$ as Mg]. The exchangeable Ca, Mg, Na and K were extracted with an excess of ammonium acetate solution, 1 M NH_4OAc. The amounts of exchangeable Na and K were then determined by flame photometry, and Ca with Mg by atomic absorption spectrophotometry (Okalebo, Gathuna & Woomer, 1993). Analysis of total P using wet acid oxidation was based on Kjeldahl oxidation to leave a sulphuric acid solution. To determine P, the sample digest solution was followed by a colometric procedure with pH adjustment. Human-induced activities measured on a nominal scale at 100-m intervals were, harvesting, cultivation, grazing, fire, vegetation disturbance and vegetation modification.

Species–environment relationship

Canonical correspondence analysis used to determine species–environment relationships was conducted using the MVSP 1999 computer programme of Jongman, Ter Braak & Van Tongeren (1995). The purpose of using canonical correspondence analysis was to find the relationship between the relative abundances of the species to measured environmental variables. Input was by means of 18 variables and 39 species from the sampling quadrats of the environmental variables. The ecological variables were ranged and log transformed using the Excell programme, $Z'_{kj} = (Z_{kj} - Z_{k,min})/Z_{k,max} - Z_{k,min})$, where Z'_{kj} is the ranged value, Z_{kj} is the observed variable, $Z_{k,min}$ is the lowest value of the variable *k* encountered over *n* sample plots, and $Z_{k,max}$ is the highest value of the variable *k* encountered over *n* sample plots. Ranging transforms variables onto a 0–1 scale without altering the relative positions of the observations along the scale. This is done to compare variables measured using different units and scales by giving them the same weight. Logarithmic transformation was done to facilitate comparison in the statistical sense by achieving univariate normality for each individual observation, $\ln(1 + Z_{kj})$, where ln is the natural logarithm and Z_{kj} is the observed variable. This standardization removes arbitrariness in the units of measurement of the environmental variables and makes the canonical coefficients comparable with each other, but does not influence aspects of the analysis (Jongman *et al.*, 1995).

The Multivariate Statistical Package produced two biplots that placed each species in multidimensional (environmental) space. Species that had particularly strong correlations with the environmental gradients were discussed to define species assemblage composition. Species were also compared with one another to determine which are most tolerant or intolerant to certain factors.

Results

Field studies of the 10 bird areas yielded 112 species belonging to 17 genera and classified into seven tribes of the Cyperaceae. The account below is based on the species concept and classification of Goetghebeur (1998) and Haines & Lye (1983). The seven tribes had varying number of species of which Cypereae represented 61.2%; Abildgaardieae 14.2%; Sclerieae 11.5%; Eleocharideae 3.5%; Schoeneae 3.5%; and Cariceae 0.9%. These represented about 51% of those recorded in Uganda by Haines & Lye (1983). The frequently recorded species included *Cyperus papyrus* L., *Cyperus denudatus* L.f. var. *denudatus, Cyperus digitatus* Roxb. var. *auricomus* Kuk, *Cyperus cyperoides* (L) Kuntze, *Cyperus pectinatus* Vahl. and *Fuirena umbellata* Rottb. The least recorded included *Bulbostylis cardiocarpoides* K. Lye, *Bulbostylis coleotricha* (A. Rich.) C. B.Cl., *Cyperus compressus* L., *Cyperus iria* L., and *Cyperus diffomis* L. Species collected elsewhere other than in quadrats along transects at a particular site (through

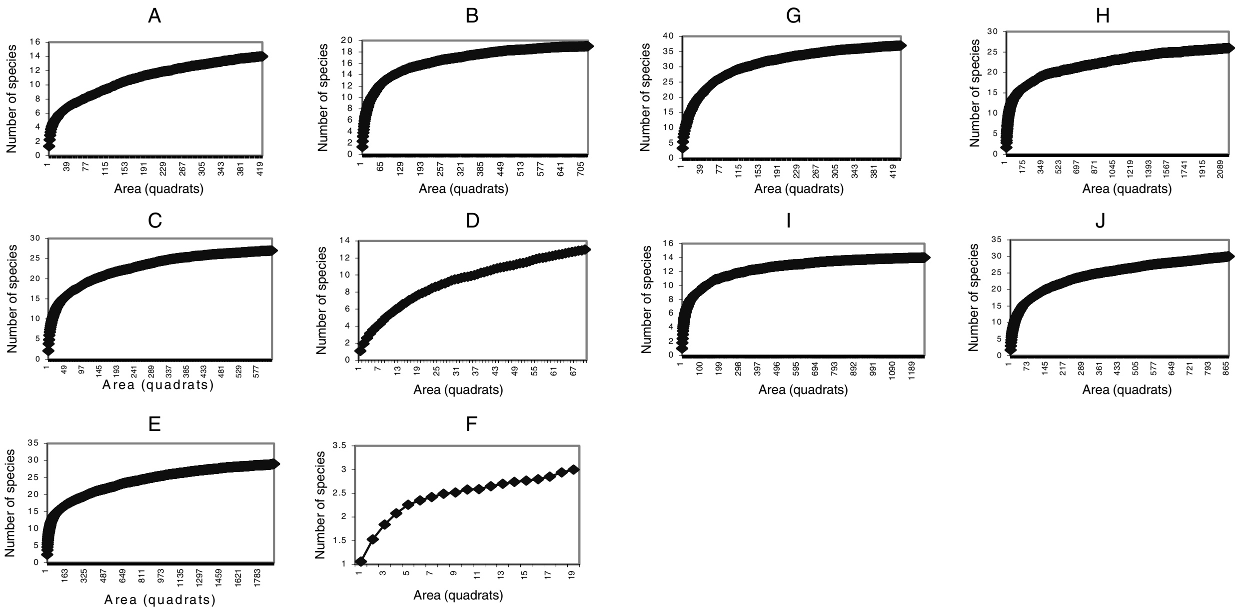

Fig 2 Species accumulation curves for (A) Doho Rice Scheme (DHO); (B) Lake Bisina (BSN); (C) Lutembe Bay (LTB); (D) Lutoboka Peninsula (LUT); (E) Mabamba Bay (MBB); (F) Musambwa Islands (MSW); (G) Lake Nabugabo (NBG); (H) Lake Nakuwa (NKW); (I) Nyamuriro Swamp (NYR); and (J) Lake Opeta (OPT). Drawn using the programme *EstimateS* after 100 randomizations.

opportunistic sampling) accounted for 23% of the total species recorded. The total number of species recorded for Lake Bisina was 22; Doho rice scheme, 25; Lutembe bay, 37; Lutoboka point, 22; Mabamba bay, 36; Musambwa islands, 3; Lake Nabugabo, 56; Lake Nakuwa, 31; Nyamuriro swamp, 17; and Lake Opeta, 41.

The species accumulation curves show the change in species richness with increasing numbers of quadrats (i.e. area) sampled as shown in Fig. 2. Lake Nakuwa, Nyamuriro swamp, Lake Bisina and Mabamba bay had fairly adequate sampling effort since the curves were tending towards their asymptotes, while Lake Nabugabo, Musambwa islands and Doho Rice Scheme had the lowest sampling effort.

Using Chao2 and first-order Jack1 as species richness estimators shown in Table 1, Lake Nabugabo had the highest species richness while Musambwa islands had the lowest. Lake Nabugabo still scored the highest species diversity based on Simpson's diversity index, and Musambwa islands had the lowest.

The Simpson's index being a dominance index is weighted towards the abundances of the commonest species rather than providing a measure for species richness (Magurran, 1988). As D increases diversity decreases though when the reciprocal form of Simpson's is adopted, the value of the index increases with increasing diversity. Lake Nabugabo has the value of $1/D = 9.17$ (Table 1), denoting a high species diversity and very low dominance of species. The abundance of species tended to be fairly uniform as compared with Lake Nakuwa with $1/D = 4.33$ due to *Cyperus papyrus* as the dominant species and as such had relatively lower diversity. The Friedman test (Zar, 1984) showed that diversity was significantly different between the bird areas $\chi^2_{0.05[9]} = 30.03$, $P < 0.05$. There was a recognizable consistency in pattern between the Simpson's diversity index and the species richness estimators.

Environmental variables

Data from the analysis of soil samples and other measured environmental variables determined is given in Table 2.

Observed species richness in sample quadrats of bird areas ranged from 3 for Musambwa islands to 37 for Lake Nabugabo. The area of bird areas considered ranged from 1 km^2 for Musambwa islands to 566 km^2 for Lake Opeta. There was an increase in species richness of bird areas with an increase in area. Fifty-nine percent of the total

Table 1 Total species richness as estimated by Chao2 and the Jackknife estimator (Jack1) and diversity determined using the Simpson index

	BSN	DHO	LTB	LBK	MBB	MSW	NBG	NKW	NYR	OPT
Quadrats	721	420	615	70	1906	19	430	2151	1245	869
Spp. Obs.	19	14	27	13	29	3	37	26	14	30
Uniques	1	3	3	5	4	1	5	4	1	6
Duplicates	1	1	2	1	4	0	2	3	0	2
Chao2	19	17	29	21	31	4	42	29	15	37
Jack1	20	17	30	18	33	4	42	30	15	36
Simpson	6.01	4.33	8.23	4.86	5.7	2.04	9.17	4.33	4.47	6.47

BSN, L. Bisina; DHO, Doho rice scheme; LTB, Lutembe bay; LBK, Lutoboka point; MBB, Mabamba bay; MSW, Musambwa islands; NBG, L. Nabugabo; NKW, Lake Nakuwa; NYR, Nyamuriro swamp; OPT, L. Opeta.

Table 2 Results of some of the various environmental factors recorded in the study sites in each of the bird areas

	w.d. (cm)	pH (pH units)	Cond. (μS cm^{-1})	DO (mg L^{-1})	% P	% K	% Na	% O.M	% Ca	% Mg	Alt. (m)	Rainfall
Bisina												
Mean	41.1	6.8	240	1.7	7.44	1.41	0.24	8.81	9.13	2.87	1051	1265
SE	3.76	0.03	33.2	0.1	1.22	0.05	0.006	0.4	0.24	0.16	7.05	85
SD	28.4	0.1	99.61	0.4	5.73	0.24	0.03	1.89	1.11	0.75	14.1	120.2
Range	90	0.1	189	0.7	15.4	0.66	0.09	5.6	3	1.94	34	120
Minimum	10	6.7	135	1.3	3.88	0.92	0.19	5.1	8.2	2.16	1034	1180
Maximum	100	6.9	324	2	19.3	1.58	0.28	10.7	11.2	4.1	1068	1350
Lutembe												
Mean	20.5	6.9	79.23	1.9	0.31	0.21	0.02	24.1	0.5	0.23	1168	1775
SE	0.84	0.01	2.79	0.03	0.01	0.01	0.0008	0.91	0.02	0.009	3.62	194.18
SD	7.64	0.1	20.32	0.3	0.1	0.09	0.007	7.49	0.17	0.08	7.23	388.37
Range	20	0.4	62	0.8	0.28	0.3	0.03	29.1	0.58	0.26	17	900
Minimum	10	6.8	54	1.5	0.18	0.1	0.01	8.9	0.2	0.1	1159	1300
Maximum	30	7.1	116	2.3	0.46	0.4	0.04	38	0.78	0.36	1176	2200
Nyamuriro												
Mean	5.56	6.1	125.9	1.2	0.47	0.34	0.07	22.2	6.98	1.57	1936	1025
SE	2.17	0.01	6.69	0.1	0.02	0.02	0.007	0.5	0.35	0.12	18.6	177.36
SD	9.22	0.1	28.4	0.4	0.09	0.11	0.03	2.44	1.73	0.58	37.1	307.2
Range	20	0.1	67	0.8	0.18	0.3	0.07	5.2	3.8	1.22	89	575
Minimum	0	6	82	0.8	0.39	0.2	0.02	19.6	5.2	0.96	1898	675
Maximum	20	6.1	149	1.8	0.57	0.5	0.09	24.8	9	2.18	1987	1250
Nabugabo												
Mean	27.2	5.3	19.11	3.1	0.2	0.29	0.03	8.24	8.1	1.76	1150	1075
SE	0.72	0.02	0.42	0.1	0.04	0.04	0	1.28	0.5	0.04	4.33	90.4
SD	9.19	5.4	5.38	1.4	0.14	0.14	0	5.13	0.71	0.16	7.51	156.12
Range	35	18	18	5.3	0.28	0.28	0	9.93	1	0.31	15	300
Minimum	5	8	8	1.7	0.06	0.15	0.03	3.27	7.6	1.61	1143	950
Maximum	40	26	26	7	0.34	0.43	0.03	13.2	8.6	1.92	1158	1250

w.d., water depth; Cond., conductivity; DO, dissolved oxygen; Alt., altitude. Variables measured from the soil samples collected included phosphorus (P) expressed in p.p.m.; potassium (K) expressed in Me (100 g)$^{-1}$; sodium (Na) expressed in Me (100 g)$^{-1}$; organic matter (O.M) expressed as a percentage; calcium (Ca) expressed in Me (100 g)$^{-1}$; and magnesium (Mg) expressed in Me (100 g)$^{-1}$. Rainfall measured as mean annual rainfall to the nearest 25 millimetres; figures obtained from the nearest rainfall station. Other variables recorded but on a nominal scale included harvesting, grazing, cultivation, fire, vegetation disturbance and modification.

variability in species richness was accounted for by regression with area ($R^2 = 0.5921$). The analysis showed significant (ANOVA test, $P = 0.01$) dependence of species richness on the independent axis.

The canonical correspondence analysis (CCA) was done for Nyamuriro swamp, Lake Bisina, Lutembe bay and Nabugabo. The choice was based on the bird areas with the most complete data set. There were incomplete data sets for some bird areas because (a) there was no medium to base measurements on, e.g. neither water readings nor soil samples were taken for Musambwa islands because the respective media, i.e. water and soil were nonexistent; (b) it did not make sense to measure variables for water-based transects as there would be no gradient to follow at all such as the open water-based transects; (c) in some cases it was not possible to get at least three consecutive readings of a particular parameter under investigation.

The first two axes of the CCA ordination (CC1 and CC2) explained the species–environment relationship well and accounted for 50% of the variation in the weighted averages of the 39 species with respect to 18 environmental variables.

Eigenvalues for the first four constrained axes as generated by a CCA of all plots explained by the species data and of the species–environment relation were 0.466, 0.369, 0.22 and 0.204, respectively.

According to Ter Braak (1986), the 'weighted average' indicates the 'centre' of a species distribution along an environmental variable. For this study, the weighted average of each species was the average value of each environmental variable in quadrats where the species occurs; the weighting of each quadrat was proportional to the species frequency of occurrence. Arrows indicating the relative importance and direction of the 18 environmental variables were placed on the axes using the statistical package MVSP by Kovach (1999) as shown in Fig. 3.

Each arrow points in the direction of maximum variation in value of the corresponding variable, and each may be extended in both directions from the origin of the plot (origin being the grand mean of each environmental variable). The length of the arrow represents the degree to

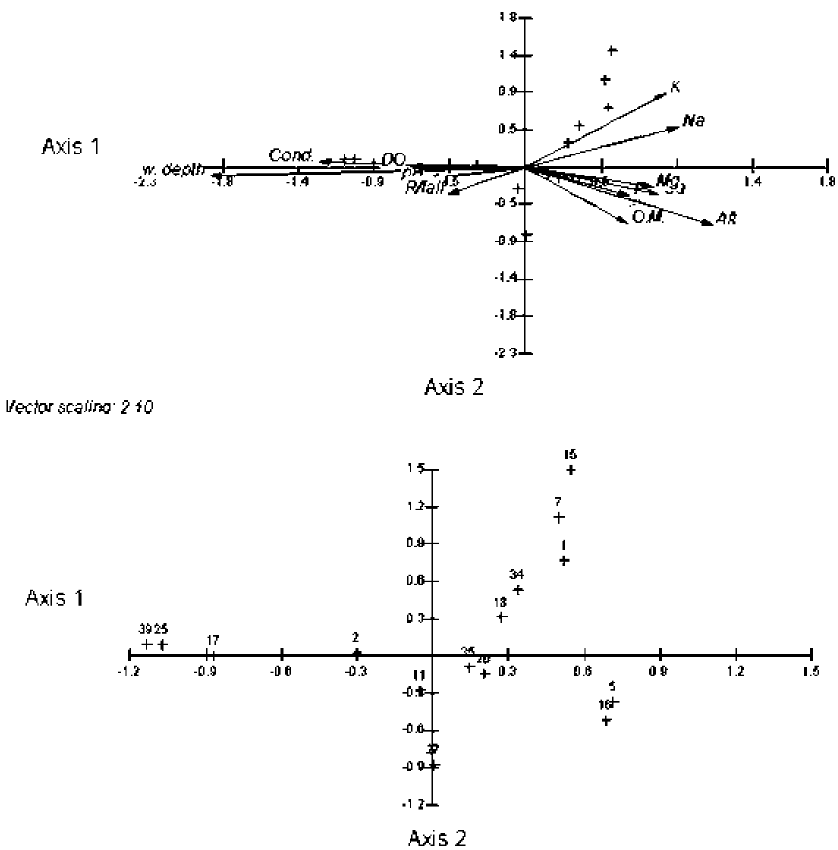

Fig 3 Canonical correspondence analysis ordination diagram showing environmental variables (arrows) most strongly correlated with axes CC1 and CC2 and all species distributions on these axes represented by numbers. Only those species that showed strong correlations with the environmental variables are shown.

which each is correlated with the CCA axes. Therefore, important environmental variables (in terms of predicting species assemblage composition) have longer arrows than less important ones. It can be seen from Fig. 3 that *Eleocharis acutangula* (Roxb.) Schult. 25, *Scleria nyasensis* C.B.Cl. (39) and *Cyperus pectinatus* Vahl. (17) were strongly correlated with water depth, whereas *Rhynchospora angolensis* Turrill (34) and *Ascolepis capensis* (Kunth) Ridley (1) were the least influenced by water depth in their distribution. It can also be seen that *Cyperus papyrus* (16) was more strongly correlated with altitude and hence their distribution was greatly influenced by altitude, whereas *Eleoocharis acutangula* (25), *Scleria nyasensis* (39) and *Cyperus pectinatus* (17) are the least influenced by altitude in their distribution. The majority of the species not represented in the ordination diagrams grew in habitats with average conditions of the environmental variables investigated.

The environmental variables most important in explaining species distributions were determined by examining correlations with the axes. The first axis was important in explaining 28% of variance, and was most strongly correlated with water depth. The second axis explains 22% of the variance and was most strongly correlated with %K. The third and fourth axes explain only 13% and 12% and were not considered further since the first two axes explain at least 50% of the variation that is recommended according to Ter Braak (1986).

In the analysis it was found that the eigenvalues and the correlations with environmental variables of these axes based on CCA are relatively allowing for ecological interpretation. They show that the environmental axes are strongly related to the first two axes of CCA.

The results of the global permutation test judge the significance of the relation between species and the environment (Ter Braak, 1986; Ter Braak & Smilauer, 1998). This process chooses variables that explain significant ($P \leq 0.05$) and independent directions of total variation in the distribution of the species, in a manner that is analogous to the selection process found in stepwise multiple regression (Christie & Smol, 1993). The test of the significance is based on the eigenvalue of the first axis.

The first canonical eigenvalue is 0.466 and the F-ratio is 11.016. The resulting P-value is 0.005, indicating that the first canonical axis is statistically significant at the 0.5% level. The test based on the sum of all canonical eigenvalues (the trace) is 2.579, with an F-ratio of 3.506 (P-value = 0.005), demonstrating that the relation between the species and the environmental variables is highly significant ($P < 0.01$).

Table 3 shows the results of the automatic forward selection procedure of environmental variables by the CANOCO programme by Ter Braak (1986, 1996). Part A of the table lists the individual environmental variables and the variance they explain singly, i.e. when that particular

Table 3 CCA forward selection of environmental variables

Variable	Var. N	λ-1	λ-A	P	F
A. Marginal effects					
Water depth (cm)	7	0.45			
Altitude (m)	17	0.39			
Vegetation disturbance	5	0.33			
Rainfall (mm)	18	0.27			
Grazing	1	0.25			
Cultivation	2	0.23			
Vegetation modification	6	0.22			
Water conductivity (μS cm^{-1})	9	0.22			
K [Me (100 g)$^{-1}$]	12	0.21			
Na [Me (100 g)$^{-1}$]	13	0.2			
Organic matter (%)	14	0.17			
Fire	4	0.16			
Mg [Me (100 g)$^{-1}$]	16	0.15			
Ca [Me (100 g)$^{-1}$]	15	0.15			
PH (pH units)	8	0.14			
DO (mg L^{-1})	10	0.14			
P [Me (100 g)$^{-1}$]	11	0.08			
B. Conditional effects					
Water depth (cm)	7		0.45	0.005*	9.24
Altitude (m)	17		0.31	0.005*	6.61
Rainfall (mm)	18		0.26	0.005*	5.71
Vegetation disturbance	5		0.22	0.005*	4.63
% K	12		0.19	0.005*	4.31
Vegetation modification	6		0.19	0.005*	4.26
Cultivation	2		0.17	0.005*	3.66
Fire	4		0.12	0.01*	2.71
Organic matter (%)	14		0.11	0.005*	2.55
Grazing	1		0.08	0.06	1.94
PH (pH units)	8		0.08	0.02*	1.78
P [Me (100 g)$^{-1}$]	11		0.07	0.135	1.53
Na [Me (100 g)$^{-1}$]	13		0.07	0.115	1.59
DO (mg L^{-1})	10		0.06	0.115	1.46
Ca [Me (100 g)$^{-1}$]	15		0.06	0.295	1.23
Mg [Me (100 g)$^{-1}$]	16		0.09	0.025*	2.17
Water conductivity (μS cm^{-1})	9		0.05	0.33	1.13

Vegetation disturbance, vegetation modification, grazing, cultivation and fire all recorded on a nominal scale.

variable is used as the only environmental variable (λ-1 column). In this case other environmental variables are ignored. Most of the variance is explained by water depth (0.45) while the least is explained by phosphorus (0.08). Part B of the table shows the environmental variables in order of their inclusion in the model, together with the additional variance each variable explains at the time it was included (λ-A) and the significance of the variable at that time (*P*-value) together with the test statistic (*F*-value).

The variables marked with asterisks in part B of Table 3, with *P*-values ≤ 0.05, contribute significantly (at 5% significance level) to the model of already included variables. These variables are, in order of importance, water depth, altitude, rainfall, vegetation disturbance, potassium, vegetation modification, cultivation, fire, organic matter, pH and %Mg.

Discussion

Environmental factors

The water depths, altitude, and rainfall were the most important environmental variable correlates of sedge assemblage structure in the bird areas studied. Water depths have been reported to be one of the most important factors that influence vegetation distribution and species assemblages (Lind & Visser, 1962) in wetlands; however, certain species for instance *Cyperus papyrus* tend to have broader habitats as long as the habitat is sometimes flooded (Lind, 1956). Another important factor is altitude. Although earlier studies of Hall & Swaine (1976), Friis (1992) and Hamilton (1975) focused on woody plant species in forest ecosystems, they generally agreed that altitude is an important factor in influencing species distributions. Rainfall has been found to be important as far as the species assemblage composition and distribution are concerned because a floristic impoverishment is expected as precipitation decreases; a factor that probably contributes to variations of floristic richness in the Lake Victoria basin and Lake Kyoga basin. Lye (2001) implies that rainfall greatly influences the distribution and diversity of sedges although he argues this on a regional/country scale. Friis (1992) reports that critical rainfall limits exist for different groups of taxa, although he further cautions that interactions between altitude and rainfall make correlations with diversity complex.

Other factors such as fire, cultivation, organic matter, amount of potassium, vegetation disturbance and modification were also important in regulating assemblage composition. These results do not preclude the fact that both abiotic (physiochemical factors) and biotic factors are important in characterizing sedge assemblages in sites. In fact, there are general factors that influence species distributions and diversity in terrestrial ecosystems, these include climate (Currie, 1991; Lye, 2001), habitat structure and productivity (Rozenzweig & Abramsky, 1993; Lye, 2001), nutrient poor sediments such as the almost pure silica-sand on the north-west side of Lake Victoria (Lye, 2001), seasonal water logging or flooding that keeps trees and shrubs away (White, 1977; Lock, 1998) thus providing optimal conditions for rare sedges (Lye, 2001), and biogeographical factors such as habitat area and isolation (MacArthur & Wilson, 1967; Connor & McCoy, 1979). All these factors are increasingly influenced by human activities (Wettstein & Schmid, 1999); however, the results of this study highlight the fact that areas with high species richness were characterized by fairly low water depths, high rainfall and low elevations. For species growing in permanent wetlands, fluctuation of rainfall from year to year is less critical. On the other hand, areas of high altitude may receive more rainfall, making it hard to differentiate the two parameters. Water depth is also linked to rainfall and fluctuates from season to season.

Nutrient enrichment, availability and sedge species diversity

The activities in the catchment areas of the bird areas investigated have different effects at varying levels on the vegetation composition and structure in the wetlands. The activities influence the nutrient enrichment and availability to the plants that utilize the wetland area as nutrient sources. Therefore the activities that take place in the catchment areas may be critical in determining the vegetation structure and composition of the wetlands. This consequently may influence the type of vegetation community and species that grow in that community, including species richness. Although there has been a lot of scientific work done (Whittaker, 1965), the nature of the relationship between nutrient availability and plant species diversity in wetlands and other ecosystems is still a major subject for ecologists (Bridgham *et al.*, 1996; Marrs, Grace & Gough, 1996; Hooper & Vitousek, 1998). Changes in species composition, loss of overall plant diversity, conversion of a unique flora to that dominated by a few common species, and replacement of native species by exotics (as in Doho Rice Scheme) have been reported in connection with nutrient enrichment in several types of wetlands (Aerts & Berendse, 1988; Verhoeven *et al.*, 1988). Due to the strong interdependence between species richness and productivity (Tilman & Pacala, 1993) and between nutrient supply and productivity, the presumed link between nutrients and species composition is the effect of nutrient enrichment on productivity.

For relatively undisturbed wetlands, comparative studies have shown that high species diversity is frequently associated with low nutrient status, and that species rich wetlands typically have moderate productivity and standing crop (Vermeer & Berendse, 1983; Moore & Keddy, 1989). This was particularly true for Lake Nabugabo that did not seem to be as nutrient rich as Lake Bisina but recorded far higher species richness. Although Nalubega & Nakawunde (1995) report that phosphorus is an important nutrient that sustains the growth of *Cyperus papyrus* dominated vegetation community, it was not evident in this study as shown in Table 3. In fact this study highlights that there is a threshold value of potassium that is required for the proliferation of *Cyperus papyrus* below which it will be a poor stand.

The relationships between nutrient enrichment, productivity and species richness in wetlands are not always consistent however. Changes in species composition and species richness are not always associated with increases in productivity (Verhoven *et al.*, 1993). In some ecosystems nutrient additions have been known to reduce plant species diversity (Schlesinger, 1994).

The inquiry into which nutrients limit plant growth and productivity in wetlands is not conclusive (Bridgham *et al.*, 1996). Many wetlands especially freshwater wetlands tend to be nitrogen limited (Bowden, 1987). Mosses, e.g. *Sphagnum* as was observed in Mabamba bay and Lake Nabugabo, appear to be more responsive to alkalinity-acidity gradients than to nitrogen or phosphorus gradients (Vitt & Chee, 1990; Vitt, Li & Belland, 1995); however, it can be misleading to interpret results based solely on the nutrient availability since nutrient gradients tend to be complex and incorporate other variables related to species diversity (Day *et al.*, 1988; Grace & Pugesek, 1997). It should also be noted that uncommon and rare species are positively associated with low-to-intermediate biomass, species rich sites, but don't occur at high biomass values (Moore & Keddy, 1989; Johnson & Leopold, 1994). This was particularly true for Lake Nabugabo, which had a relatively low biomass and was species rich as compared with Lake Nakuwa, which had a higher biomass consisting mainly of *Cyperus papyrus* and was species poor, the size of the latter notwithstanding. Bedford *et al.* (1999), however, argues that understanding effects of nutrient enrichment on ecosystem productivity may not be sufficient to predict effects on species diversity. This is because species may be lost due to a particular nutrient limitation. Bedford *et al.* (1999) further suggested that studies involving both ecosystem properties and individual species responses should be undertaken.

The results of this study help to explain the highly restricted distribution patterns of many species and reveal the limiting factors affecting sedges in the bird areas under investigation. Large differences were noted in the way species of the same family, and even the same tribe and genera responded to the physiochemical variables. There were some species that were recorded in habitats with levels of environmental variables at or near the averages for those variables (the centroid of the plots). Other species preferred habitats with levels either much below or much above averages for the bird areas. In contrast there are some species that have widespread distribution patterns in the bird areas. These species occur in areas with habitats that are average in their water depths, altitude and water conductivity levels. These habitat 'generalists' are much more capable of adapting to and surviving changing environmental conditions at sites in the bird areas than species that are more specialized in their habitat requirements.

Several species of sedges were found to be broadly distributed but never abundant where they were found; others were narrowly distributed and abundant where they were found; and others were narrowly distributed and not abundant where they were found. All these represented different forms of rarity and local endemism. Fiedler (1987) argues that rarity in relation to vascular plants is about geographical distribution and population sizes of a particular species. According to Fiedler & Ahouse (1992), geographical distributions of rarity can also include a temporal dimension, such that a rare species is defined by its abundance, distribution and persistence through evolutionary time. Rarity is important in the conservation of biodiversity for several reasons, including the restrictions imposed by having fewer area-options available for narrowly distributed species when attempting to represent as many species as possible for conservation (Williams *et al.*, 1996b).

The use of estimated species richness (which takes into account rare species) and diversity indices as biodiversity–value surrogates (Williams *et al.*, 1996a) for the selection of priority areas for conservation of sedges is one of the popular quantitative methods. Conservationists have always sought areas in which the maximum number of species are represented as high priorities for managing biodiversity (Scott *et al.*, 1987). Species richness can also be justified as a direct measure of one popular aspect of biodiversity (Noss, 1990), although it depends a lot on size of sampling area (Mares, 1992) and on the sampling effort deployed within the area (Palmer, 1990; Bullock, 1991; Prendergast *et al.*, 1993b; Colwell & Coddington, 1994). This study revealed that Lake Nabugabo, Lake Opeta and Mabamba bay had the highest estimated species richness as shown in Table 1. They would form a set of bird areas that would be appropriate for conservation of sedges.

Another important aspect in conservation is endemism. Endemism is important in conservation for two reasons. First, the most narrowly distributed species indicate unique complements and hence irreplaceable areas (Williams *et al.*, 1996b). The second reason is that in some cases there may be a link between small range sizes and vulnerability (threat). This relationship, however, is not always universal (Robinson & Redford, 1990). This study revealed that Lake Nabugabo recorded the highest number of endemics. It was also observed that a lot of human activity is taking place in the seasonal wetlands adjacent to the lake. This constitutes a threat to the survival of sedges whose habitat is being destroyed. This would rank Lake Nabugabo high on the priority list for conservation initiatives. Other bird areas also affected by human activities but with species richness lower than that of Lake Nabugabo and therefore with fewer 'interest' species include Lake Bisina, Lake Opeta, Nyamuriro swamp and Musambwa islands.

Efficiency in the selection of priority areas for conservation is important however. This is because the area of land available for conservation is usually limited and there is often competition between conservation and incompatible land uses for managing particular areas. Conservation goals have to be attained within only a limited part of the landscape because of competition from other land uses (Kirkpatrick, 1983; Pressey, 1994). The purpose of identifying priority areas is not to dictate the only areas with conservation value, neither is it proposed that they are sufficient for conservation on their own. The idea is instead to identify a necessary foundation for biodiversity conservation, based on a particular and clearly stated goal. Selection of maximum-coverage sets for representing as much diversity as possible within a given number of areas can be used basing on optimization techniques (Csuti *et al.*, 1997). Prioritization to determine which sites among the chosen sites has the greatest urgency for applying conservation management would be based on the diversity complement and threats (Williams *et al.*, 1996a, b). This is catered for still if the bird areas considered above are selected.

Conclusions

The bird areas studied support a diverse assemblage of sedges. They include 112 of the 223 species recorded in Uganda. This is a fairly large number of species recorded given the fact that a lot more wetlands were not surveyed during this study. This would put the bird areas at a high ranking for the conservation of plants, particularly sedges. There were marked differences between the species assemblages recorded in the Lake Victoria basin and the Lake Kyoga basin that could be attributed to differences in climate and geology of the two basins that lie in two different phytochoria.

Distribution patterns of sedges indicated preferences of several species for certain portions of sites in the bird areas. Species that had wide geographical ranges did not necessarily have high local abundances. Likewise, species with narrow geographical ranges did not necessarily have low local abundances. In many cases, however, species exhibited ecoregional groupings. Water depths, altitude and rainfall were found to be the most important variables for explaining sedge assemblage composition.

The results of this study further reveal that although nutrients are important for the distribution of plant species, human-induced factors can override the importance of these nutrients. This is particularly true for Nyamuriro swamp where cultivation has greatly reduced the wetland ecosystem to near agricultural land thus leading to loss of the plant diversity through habitat loss. This is so despite the relative richness in nutrients from the surrounding volcanic nutrient rich soils.

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