Species communities and associations formed by the family Cyperaceae Juss. in some of Uganda's wetlands

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Abstract

This study was conducted between August 2000 and April 2001 in ten wetlands areas of Uganda and these included Lakes Bisina, Nakuwa and Opeta, including the Doho Rice Scheme in the Lake Kyoga basin; Mabamba and Lutembe bays, Lake Nabugabo, Musambwa islands and Lutoboka peninsula in the Lake Victoria basin; and Nyamuriro swamp in Kigezi region. This study focused on *Cyperaceae* because of their known abundance in wet or damp areas. The aim was to assess the diversity and examine the communities and associations formed by sedges. Floristic data were collected using quadrats along transects. Cluster analysis was used to analyse for species associations. Principal components analysis was used to determine the descriptive species of the sites of the wetlands. A total of 113 taxa in 107 species belonging to 17 genera and classified into seven tribes were identified. The most rare species included *Eleocharis dulcis* (Burm. f.) Henschel and *Cyperus iria* L. Using cluster analysis the ten sites of the wetlands were classified into sedge assemblages that generally reflected ecoregional differences between the Lake Kyoga and Victoria basins. The three distinct clusters formed from cluster analysis also revealed species assemblages that represented associations of these sedges found in the sites of each cluster.

Key words: associations, communities, Cyperaceae, wetlands

Introduction

Swamps tend to be dominated for large tracts by a single, vigorous species which in most cases are sedges (Moss, 1980). Visser (1960) recognized that 60% of the permanent swamps of Uganda consist of *Cyperus papyrus* L., which agrees with the more recent observation by Moss (1980). Carter (1956) also recognized four succession zones in the swamps of Uganda and observed the presence of members of family Cyperaceae in each zone with one zone being dominated entirely by *C. papyrus*.

Members of Cyperaceae, also called sedges, are dominant in wetlands (Ssegawa *et al.*, 2004) and some tropical grasslands (Lye, 2001). Worldwide, Cyperaceae has 104 genera and 5000 species. In East Africa, there are as many as 30 genera and 450 species (Goetghebeur, 1998; Lye, 2001). Uganda has a very large sedge flora with 223 species, with the majority recorded in the central and southern regions of the country (Lye, 2001).

The diversity of sedges in Uganda was studied by Haines & Lye (1983) and Wadenya (1996). However, little is still known about the sedge species communities and associations in the various habitats and sites. This study, therefore, identifies the community types and associations of sedges in the various habitats in which they are found including the characteristic or descriptive species for each community identified.

Materials and methods

Study areas

The wetlands under investigation are present in three major areas in Uganda. The first is the Lake Victoria basin which comprises Musambwa islands and Lake Nabugabo in the extreme west of Lake Victoria. Lutoboka peninsula is found on one of the main islands that comprise the 84 islands that make up the Ssese islands in Lake Victoria while Lutembe and Mabamba bays are found in the northern shores of Lake Victoria. The vegetation is predominantly *C. papyrus* with *Miscanthus violaceus* (K. Schum.) Pilg. dominant in other areas (Byaruhanga, Kasoma & Pomeroy, 2001). The second is the Lake Kyoga basin with the wetlands around Lakes Bisina and Opeta on

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the north-eastern side of Lake Kyoga; Doho Rice Scheme area on the eastern side of the Lakes Kyoga, while Lake Nakuwa forms an arm of Lake Kyoga on the southern side. The dominant vegetation community is *Vossia cuspidata* (Roxb.) Griff. interspersed with the tree *Aeschynomene cristata* Vatke. Occasionally *Oryza longistaminata* A.Chev. & Roehr. is abundant on the shorelines (Byaruhanga *et al.*, 2001). The third is the Nyamuriro swamp found in the mountainous region of Kigezi in south-western Uganda at a relatively higher altitude.

The sampling points within the selected wetlands were determined to cover a wide range of vegetation categories where possible. Gradsects were used to capture as many environmental gradients as possible. The sizes of the wetlands varied, ranging from about 1 km^2 for Musambwa islands to 566 km^2 for Lake Opeta wetlands. Accordingly, the number of sampling points in the wetlands was staggered using the species–area relationship ($S = cA^z$) to reflect this difference.

Data collection

Transects up to 800 m were used because of access problems and the size of wetlands. At each sampling point, four circular plots of 1 m radius were located equidistant from the sampling point and from each other at a distance of 2 m. Points were located at 10-m intervals. This is a modification of the point frequency method (Okland, 1990) and the method used by Wettstein & Schmid (1999). All sedges found in these quadrats were recorded with their respective percentage cover (Okland, 1990; Kent & Coker, 1994) and vouchers collected for identification.

Data analysis

The presence of sedge species was recorded in binary (presence or absence) format for each of the ten wetlands investigated. To determine similarity of sites, the 112×10 array was used to calculate the simple matching coefficient (SM) (Ludwig & Reynolds, 1988) for each pair (A and B), where $SM = a/(a + b + c)$, where a is the number of species that sites A and B have in common, b the number of species present in site A but absent from site B, and c the number of species present in site B but absent from site A. The SM ranged from near 0 (for a site pair highly dissimilar with respect to sedge species) to near 1 (site pair very similar) and a minimum SM of 0.28 was used for defining clusters.

To place species into meaningful assemblages, the similarities for all combinations of species pairs were summarized into three arrays or similarity matrices of sizes 3021×76 (cluster A), 1264×18 (cluster B), 4162×62 (cluster C) with rows as quadrats and species as columns, which corresponded to site clusters A–C. Three separate cluster analyses (weighted centroid) using Multivariate Statistical Package (MVSP) (Kovach, 1999) were conducted to produce dendrograms which grouped sedge species. A minimum SM of 0.0 was used to define sedge assemblages. As with the cluster analysis of the sites, other measures of similarity among species were attempted along with several different methods of clustering. All techniques provided similar results, with the SM and weighted centroid clustering making the most sense ecologically. Principal component analysis (Gauch, 1982; Pielou, 1984; Ludwig & Reynolds, 1988) was used to determine the descriptive species that defined the various groups of sites determined from cluster analysis.

Results

Flora

The ten wetlands yielded 113 taxa in 107 species belonging to seventeen genera, classified into seven tribes of Cyperaceae (Table 1) based on the species concept and classification of Goetghebeur (1998) and Haines & Lye (1983). The seven tribes had varying numbers of species of which Cypereae represented the largest proportion of species (61.2%) followed by Abildgaardieae (14.2%), Sclerieae (11.5%), Fuireneae (5.2%), Eleocharideae (3.5%), Schoeneae (3.5%) and Cariceae (0.9%). These represented about 50% of those recorded in Uganda by Haines & Lye (1983). The commonest genus was *Cyperus* and included species such *C. papyrus*, *C. denudatus*, *C. digitatus*, *C. cyperoides* and *C. pectinatus.* The rarest species were of the genus *Bulbostylis* and included *B. cardiocarpoides* and *B. coleotricha*. Other rare species were of the genus *Cyperus* and included *C. compressus*, *C. iria* and *C. diffomis*. Species collected through inventory sampling accounted for 23% of the total species recorded.

Sedge assemblages

Figure 1 shows that Mabamba bay (MBB) and Lutembe bay (LTB) had the highest similarity of 0.88. Other sites clustered at lower values. Three distinct groups of sites A, B

Table 1 The loadings of the original descriptive variables (i.e. species) for the ten wetlands and their distribution in the respective wetlands. Suprageneric classification is based on Goetghebeur (1998)

Species	Principal component 1 (PCI)	Principal component 2 (PCII)	BSN	DHO	LTB	LUT	MBB	MSW	NBG	NKW	NYR	OPT
Tribe Abildgaardieae												
Abildgaardia ovata (Burm. f.) Kral	0.073	−0.08	√	–	–	–	–	–	–	–	–	–
Bulbostylis cardiocarpoides K. Lye	0.126	**0.211**	–	–	–	–	√	–	√	–	–	–
Bulbostylis clarkeana Bordard	**0.239**	0.147	–	–	√	–	√	–	√	–	–	–
Bulbostylis hispidula (Vahl) R. Haines	**0.287**	**0.257**	–	–	√	√	√	–	√	–	–	–
Bulbostylis coleotricha (A. Rich.) C.B.Cl.	0.08	0.024	–	–	√	–	–	–	–	–	–	–
Bulbostylis microelegans (K. Lye) R. Haines	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Bulbostylis oritrephis (Ridley) C.B.Cl.	**0.159**	0.123	–	–	–	–	√	–	√	–	–	–
Bulbostylis pusilla (A. Rich.) C.B.Cl.	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Bulbostylis ugandensis (K. Lye) R. Haines	**0.287**	**0.257**	–	–	√	√	√	–	√	–	–	–
Fimbristylis complanata (Retz.) Link	**0.311**	−0.088	–	–	√	–	√	–	–	√	–	√
Fimbristylis dichotoma (L.) Vahl.	**0.511**	−0.126	√	√	√	–	√	–	√	√	–	√
Fimbristylis madagascariensis Boeck.	**0.15**	0.02	√	–	–	–	–	–	√	–	–	–
Fimbristylis miliacea Vahl. ssp. *macroglumis* K. Lye	0.05	−0.058	–	√	–	–	–	–	–	–	–	–
Fimbristylis miliacea (L.) Vahl. ssp. *miliacea*	0.076	−0.066	–	–	–	–	–	–	√	–	–	√
Fimbristylis robusta K. Lye	0.077	0.101	–	–	–	–	–	–	–	–	–	–
Fimbristylis subaphylla Boeck.	**0.384**	**−0.169**	√	–	√	–	√	–	–	√	–	√
Tribe Cypereae												
Ascolepis capensis (Kunth) Ridley	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Cyperus alopecuroides Rottb.	0.073	−0.069	–	–	–	–	–	–	–	√	–	–
Cyperus articulatus L.	**0.272**	**−0.273**	√	√	–	–	–	–	–	√	–	√
Cyperus atroviridis C.B.Cl.	0.053	−0.036	–	–	–	–	–	–	–	–	√	–
Cyperus circumclusus (C.B.Cl.) Kuk.	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Cyperus compressus L.	0.073	−0.069	–	–	–	–	–	–	–	√	–	–
Cyperus cyperoides (L.) Kuntze ssp. *cyperoides*	0.28	**0.164**	–	–	–	√	√	–	√	√	–	–
Cyperus denudatus L.f. var. *denudatus*	**0.539**	0.029	–	√	√	√	√	–	√	√	√	√
Cyperus denudatus L.f. var. *lucenti–nigricans* Kuk.	0.053	−0.036	–	–	–	–	–	–	–	–	√	–
Cyperus dereilema Steudel	0.05	−0.058	–	√	–	–	–	–	–	–	–	–
Cyperus dichroostachyus A. Rich.	0.05	−0.058	–	√	–	–	–	–	–	–	–	–
Cyperus difformis L.	0.123	−0.127	–	√	–	–	–	–	–	√	–	–
Cyperus digitatus Roxb. ssp. *auricomus* Kuk.	**0.279**	−0.18	√	√	√	–	–	–	–	–	–	√
Cyperus distans L. f.	**0.415**	−0.015	–	√	√	–	√	–	√	√	√	–

Table 1 (Continued)

Species	Principal component 1 (PCI)	Principal component 2 (PCII)	BSN	DHO	LTB	LUT	MBB	MSW	NBG	NKW	NYR	OPT
Cyperus dives Del.	**0.325**	**−0.309**	√	√	–	√	–	–	–	√	√	√
Cyperus dubius Rottb. ssp. *coloratus* (Vahl) Lye	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Cyperus dubius Rottb. ssp. *macrocephalus* K. Lye	0.049	0.11	–	–	√	–	–	–	–	–	–	–
Cyperus esculentus L.	0.127	0.043	–	–	–	–	–	–	√	–	–	–
Cyperus flavoculmis K. Lye	0.081	0.022	–	–	–	–	√	–	–	–	–	–
Cyperus fluminalis Ridley	**0.206**	**0.235**	–	–	√	√	–	–	√	–	–	–
Cyperus glaucophyllus Boeck.	0.049	0.11	–	–	–	√	–	–	–	–	–	–
Cyperus halpan L.	0.05	−0.058	–	√	–	–	–	–	–	–	–	–
Cyperus imbricatus Retz.	**0.325**	0.006	√	√	–	√	–	–	√	–	–	√
Cyperus iria L.	0.149	−0.135	–	–	–	–	–	–	–	√	–	√
Cyperus latifolius Poir.	**0.564**	−0.162	√	√	√	–	√	–	√	√	√	√
Cyperus maculatus Boeck.	0.191	**0.347**	–	–	–	√	–	√	√	–	–	–
Cyperus papyrus L.	**0.629**	−0.026	√	√	√	–	√	√	√	√	√	√
Cyperus pectinatus Vahl	**0.514**	−0.104	√	–	√	–	√	–	√	√	√	√
Cyperus procerus Rottb.	0.076	−0.066	–	–	–	–	–	–	–	–	–	√
Cyperus pustulatus Vahl	0.076	−0.066	–	–	–	–	–	–	–	–	–	√
Cyperus renducus Boeck.	0.05	−0.058	–	√	–	–	–	–	–	–	–	–
Cyperus renschii Boeck.	**0.178**	**0.175**	–	–	–	√	–	–	√	–	√	–
Cyperus rigidifolius Steudel.	0.053	−0.036	–	–	–	–	–	–	–	–	√	–
Cyperus rotundus L. ssp. *merkeri* C.B.Cl.	0.149	−0.135	–	–	–	–	–	–	–	√	–	√
Cyperus rotundus L. ssp. *rotundus*	**0.438**	−0.057	√	√	√	–	√	–	√	–	–	√
Cyperus rubicundus Vahl	0.149	−0.146	√	–	–	–	–	–	–	–	–	√
Cyperus sp.1	0.05	−0.058	–	√	–	–	–	–	–	–	–	–
Cyperus sp.2	0.073	−0.069	–	–	–	–	–	–	–	√	–	–
Cyperus sphacelatus Rottb.	**0.352**	0.393	–	–	√	√	√	√	√	–	–	–
Cyperus squarrosus L.	0.073	−0.08	√	–	–	–	–	–	–	–	–	–
Cyperus tenax Boeck.	0.126	**0.211**	–	–	–	√	–	–	√	–	–	–
Cyperus tenuiculmis Boeck. var. *tenuiculmis*	**0.153**	0.035	–	–	–	–	–	–	√	–	–	√
Isolepis costata A. Rich.	0.053	−0.036	–	–	–	–	–	–	–	–	√	–
Kyllinga aurata Nees	0.126	0.211	–	–	–	√	–	–	√	–	–	–
Kyllinga bulbosa P. Beauv.	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Kyllinga chrysantha K. Schum.	**0.157**	0.125	–	–	√	–	–	–	√	–	–	–
Kyllinga colorata (L.) Druce	0.133	−0.011	–	–	√	–	–	–	–	–	√	–
Kyllinga elatior Kunth	**0.363**	**0.191**	–	–	√	√	√	–	√	–	–	√
Kyllinga erecta Schumacher	**0.229**	−0.111	–	–	√	–	–	–	–	√	–	√
Kyllinga melanosperma Nees	0.05	−0.058	–	√	–	–	–	–	–	–	–	–
Kyllinga odorata Vahl	0.05	−0.058	–	√	–	–	–	–	–	–	–	–
Kyllinga pumilla Michx.	**0.212**	−0.011	–	√	√	–	√	–	–	–	–	–
Kyllinga sphaerocephala Boeck.	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Lipocarpha chinensis (Osb.) Kern	**0.436**	0.122	–	–	√	√	√	–	√	√	–	√
Oxycaryum cubense (Poepp. & Kunth) E.Palla	**0.231**	0.056	–	–	√	–	–	–	√	√	–	–
Pycreus capillifolius (A. Rich.) C. B. Cl.	0.073	−0.069	–	–	–	–	–	–	–	√	–	–

Table 1 (Continued)

Species	Principal component 1 (PCI)	Principal component 2 (PCII)	BSN	DHO	LTB	LUT	MBB	MSW	NBG	NKW	NYR	OPT
Pycreus flavescens (L.) Reichenb.	**0.431**	**−0.17**	√	√	–	–	√	–	√	√	–	√
Pycreus lanceolatus Poir.	0.076	−0.066	–	–	–	–	–	–	–	–	–	√
Pycreus macrostachyos (Lam.) J. Rayn.	**0.328**	−0.059	–	√	√	√	–	–	–	√	–	√
Pycreus mundtii Nees	**0.485**	−0.094	√	–	√	√	√	–	–	√	√	√
Pycreus niger (Ruiz & Pav.) Cufod.	0.103	−0.094	–	√	–	–	–	–	–	–	√	–
Pycreus nitidus (Lam.) J. Rayn.	**0.514**	−0.104	√	–	√	–	√	–	√	√	√	√
Pycreus nuerensis (Boeck.) Hooper	0.149	−0.135	–	–	–	–	–	–	–	√	–	√
Pycreus pelophilus (Ridley) C. B. Cl.	0.076	−0.066	–	–	–	–	–	–	–	–	–	√
Pycreus permutatus (Boeck.) Napper	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Pycreus polystachyos Rottb.	0.149	−0.135	–	–	–	–	–	–	–	√	–	√
Pycreus polystachyos Rottb var. *laxiflorus* K. Lye	**0.363**	**0.191**	–	–	√	√	√	–	√	–	–	√
Pycreus unioloides (R. Br.) Urb.	**0.307**	−0.023	√	–	–	–	√	–	√	–	–	√
Tribe Eleocharideae												
Eleocharis acutangula (Roxb.) Schult.	**0.461**	−0.068	√	–	√	–	√	–	√	√	–	√
Eleocharis dulcis (Burm. f.) Henschel	0.076	−0.066	–	–	–	–	–	–	–	–	–	√
Eleocharis marginulata Steudel	**0.153**	0.035	–	–	–	–	–	–	√	–	–	√
Eleocharis variegata (Poir) Presl.	**0.388**	0.012	–	–	√	–	√	–	√	√	–	√
Tribe Fuireneae												
Fuirena pubescens (Poir.) Kunth	**0.384**	**−0.169**	√	–	√	–	√	–	–	√	–	√
Fuirena stricta Steudel ssp. *stricta*	**0.303**	**−0.193**	√	–	–	–	√	–	–	√	–	√
Fuirena umbellata Rottb.	**0.461**	−0.068	√	–	√	–	√	–	√	√	–	√
Schoenoplectus confusus (E. Br.) K. Lye	0.053	−0.036	–	–	–	–	–	–	–	–	√	–
Schoenoplectus corymbosus (Roem. & Schult) J. Rayn.	0.076	−0.066	–	–	–	–	–	–	–	–	–	√
Schoenoplectiella senegalensis (Steudel) Lye	0.05	−0.058	–	√	–	–	–	–	–	–	–	–
Tribe Schoeneae												
Cladium mariscus (L.) Pohl ssp. *jamaicense* (Crantz) Kük.	**0.162**	0.047	–	–	√	–	√	–	–	–	–	–
Rhynchospora angolensis Turrill	**0.239**	0.147	–	–	√	–	√	–	√	–	–	–
Rhynchospora candida (Nees) Boeck.	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Rhynchospora corymbosa (L.) Britt.	0.126	**0.211**	–	–	–	√	–	–	√	–	–	–
Rhynchospora gracillima Thw.	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Tribe Cariceae												
Carex cognata Kunth var. *congolensis* K. Lye	0.053	−0.036	–	–	–	–	–	–		–	√	–

Table 1 (Continued)

Species	Principal component 1 (PCI)	Principal component 2 (PCII)	BSN	DHO	LTB	LUT	MBB	MSW	NBG	NKW	NYR	OPT
Tribe Sclerieae												
Scleria achtenii De Willd.	**0.239**	0.147	–	–	√	–	√	–	√	–	–	–
Scleria boivinii Steudel	0.049	0.11	–	–	–	√	–	–		–	–	–
Scleria bulbifera A. Rich.	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Scleria catophylla C. B. Cl.	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Scleria distans Poir. ssp. *chondrocarpa* Nelmes	0.049	0.11	–	–	–	√	–	–		–	–	–
Scleria distans Poir. ssp. *distans*	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Scleria greigiifolia (Ridley) C. B. Cl.	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Scleria iostephana Nelmes	0.077	0.101	–	–	–	–	–	–	√	–	–	–
Scleria melanomphala Kunth	**0.239**	0.147	–	–	√	–	√	–	√	–	–	–
Scleria nyasensis C. B. Cl.	**0.239**	0.147	–	–	√	–	√	–	√	–	–	–
Scleria racemosa Poir.	0.08	0.024	–	–	√	–		–	–	–	–	–
Scleria sp.	0.081	**0.022**	–	–	–	–	√	–	–	–	–	–
Scleria verrucosa Willd.	0.081	**0.022**	–	–	–	–	√	–	–	–	–	–

The wetlands are Lake Bisina (BSN), Doho Rice Scheme (DHO), Lutembe bay (LTB), Lutoboka point in Ssese islands (LUT), Mabamba bay (MBB), Musambwa islands (MSW), Lake Nabugabo (NBG), Lake Nakuwa (NKW), Nyamuriro swamp (NYR), Lake Opeta (OPT) These species include those collected in quadrats and inventory sampling.
The loadings (correlations) in bold on PCI and PCII are used to identify the descriptive species.
–, absence; √, presence.

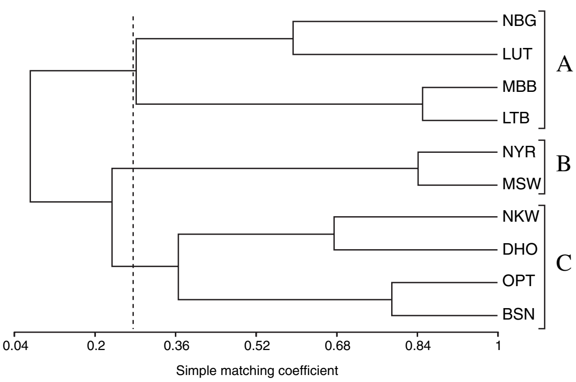

Fig 1 Cluster analysis of 10 wetlands based upon the presence or absence of 112 sedge species. The letters (A–C) indicate clusters defined by using a minimum simple matching coefficient of 0.28 (dotted line).

and C are evident in Fig. 1. Species richness for cluster A was 76, cluster B 18, and cluster C 62.

The cluster pair of Lake Nabugabo (NBG) and Lutembe bay (LUT) are remotely similar to the Mabamba bay (MBB) and Lutoboka peninsula (LTB) cluster pair in cluster A in terms of presence or absence of species (Fig. 1). In cluster B, Nyamuriro swamp (NYR) and Musambwa islands (MSW) clustered together and have the second greatest similarity. In cluster C, Lakes Opeta (OPT) and Bisina (BSN) had a closer similarity compared with the Doho Rice Scheme (DHO) and Lake Nakuwa (NKW) cluster pair in the subgroup.

The loadings (correlations) of the original descriptive variables (species) on principal component axes 1 (PCI) and 2 (PCII) for the ten wetlands are shown in Table 1. These are used to determine the species most important in defining groups of sites. The first two principal components (PCI and PCII) from the PCA accounted for 58% of variance in the binary species data. The decomposition of these axes provided insight into the species most responsible for defining groups of sites, as the loadings (=correlations) of the individual species (variables) on a PCA axis are an indication of the contribution of each original variable to the new PCA axis (Table 1).

Species with relatively high loadings (≥0.15) on the PCI (Table 1) were descriptive of sites with high scores, such as the MBB, NBG and LTB (Table 2), all of which are members of cluster A in the cluster analysis (Fig. 1). There were

Table 2 Scores of 10 wetlands on principal components axes 1–4 (PC1–PC4) and percent of total variance in species richness explained by each PC axis

Wetland	Axis 1	Axis 2	Axis 3	Axis 4
Lake Bisina (BSN)	0.308	−0.338	0.023	−0.145
Doho Rice Scheme (DHO)	0.222	−0.256	−0.593	−0.533
Lutoboka point (LTB)	0.401	0.121	0.201	0.275
Lutembe bay (LUT)	0.204	0.463	−0.195	−0.068
Mabamba bay (MBB)	0.403	0.11	0.272	0.205
Musambwa islands (MSW)	0.111	0.233	−0.409	0.23
Lake Nabugabo (NBG)	0.41	0.534	0.031	−0.359
Lake Nakuwa (NKW)	0.351	−0.331	0.103	0.12
Nyamuriro swamp (NYR)	0.2	−0.135	−0.527	0.597
Lake Opeta (OPT)	0.385	−0.335	0.198	−0.146
Variance	44.7	12.9	8.3	6.6
Cumulative variance	44.7	57.6	66.0	72.6

neither species with loadings ≤−0.15 on PCI (Table 1), nor sites with negative PCI scores (Table 2). Species with loadings ≥0.15 on PCII were descriptive of sites with high scores, such as NBG and LUT (Table 2), members of cluster A (Fig. 1). Species with loadings (≤−0.15) on the PCII (Table 1) were descriptive of sites with high negative scores, such as the BSN, OPT and NKW (Table 2), all of which are members of cluster C in the cluster analysis (Fig. 1).

Species association analyses

The three distinct clusters of sites produced by cluster analysis were used to place the sedge species into assemblages which represented common associations of sedges found in the sites of each cluster. The Friedman test (Zar, 1984) showed that the three clusters were significantly different ($\chi^2_{0.05(2)} = 8.14$, $P < 0.05$). This meant that in terms of sedge species present, the sites within each cluster were considered unique from all others for analyses of species associations which follow hereafter. Seventy-six species occurred at >4% of the 3021 sampling quadrats in the sites of cluster A (Fig. 1). The species paired by cluster analysis as derived from the species association analyses are shown in Figs 2–4. Species were paired by cluster analysis at a simple matching coefficient >0.0.

Species paired by cluster analysis, which had simple matching coefficients ≥0.75 included *Kyllinga erecta* Schumacher and *Scleria racemosa* Poir., *Fuirena pubescens* (Poir.) Kunth. and *Fimbristylis subphylla* Boeck., *Scleria achtenii* De Willd. and *Cyperus rotundus* L. ssp. *rotundus*, *Bulbostylis oritrephis* (Ridley) C.B.Cl. and *Pycreus flavescens* (L.) Reichenb, *Cyperus imbricatus* Retz. and *Rhynchospora corymbosa* (L.) Britt. Using a minimum simple matching coefficient of 0.0 as an arbitrary cutoff point for defining clusters, eight sedge assemblages (i.e. A1–A8) for cluster A in Fig. 1 were produced by cluster analysis (Fig. 2). Assemblage A4 included those species that predominantly grow in permanently wet *Miscanthus/Loudetia*-dominated swamp. Assemblages A1–A3 and A6 had those species that grow on swamp edges, lake shorelines, disturbed habitats and forest patches or bushes within grasslands, i.e. broad habitat-range species. Assemblage A3 included those species that predominantly do well in seasonally flooded *Loudetia kagerensis* grasslands and wetter riparian forest fringes. Assemblages A5, A7 and A8 had those species associated with deeper water *C. papyrus/Miscanthus violaceus*-co-dominated swamps and *Alchornea/Phoenix*-co-dominated swamp fringes.

Cluster B of Fig. 1 consisted of 18 species that occurred at >4% of 1264 quadrats in sampling sites. Using a minimum SM of 0.0 as an arbitrary cutoff point for defining clusters, two sedge assemblages were produced by cluster analysis, including the lake sandy shoreline or disturbed/secondary regrowth, or swamp edge species (B1), and the predominantly high-altitude, afromontane species (B2).

Cluster C of Fig. 1 consisted of 62 species that occurred at >4% of 4162 quadrats in sampling sites. These species were paired by cluster analysis at SM > 0.75 using a minimum SM of 0.0 as an arbitrary cutoff point for defining clusters (Fig. 4). Assemblages C1, C2, and C6–C8 are characterized by disturbed/secondary regrowth areas and fringing *Hyparrhenia/Sporobolus* grasslands on wetlands, adjacent to the wooded *Acacia* grasslands and rocky outcrops, that are frequently grazed by cattle while assemblages C3–C5, C8, and C9 are characterized by deep water species in *C. papyrus* and *V. cuspidata* vegetation communities.

Discussion

Distribution patterns of sedges

The distribution patterns of the sedge species in the wetlands, revealed that *C. denudatus* var. *denudatus*, *C. papyrus*, *Pycreus mundtii* and *Fuirena umbellata* had relatively widespread distributions, occurring in at least in nine of the ten wetlands. Species whose distributions were either

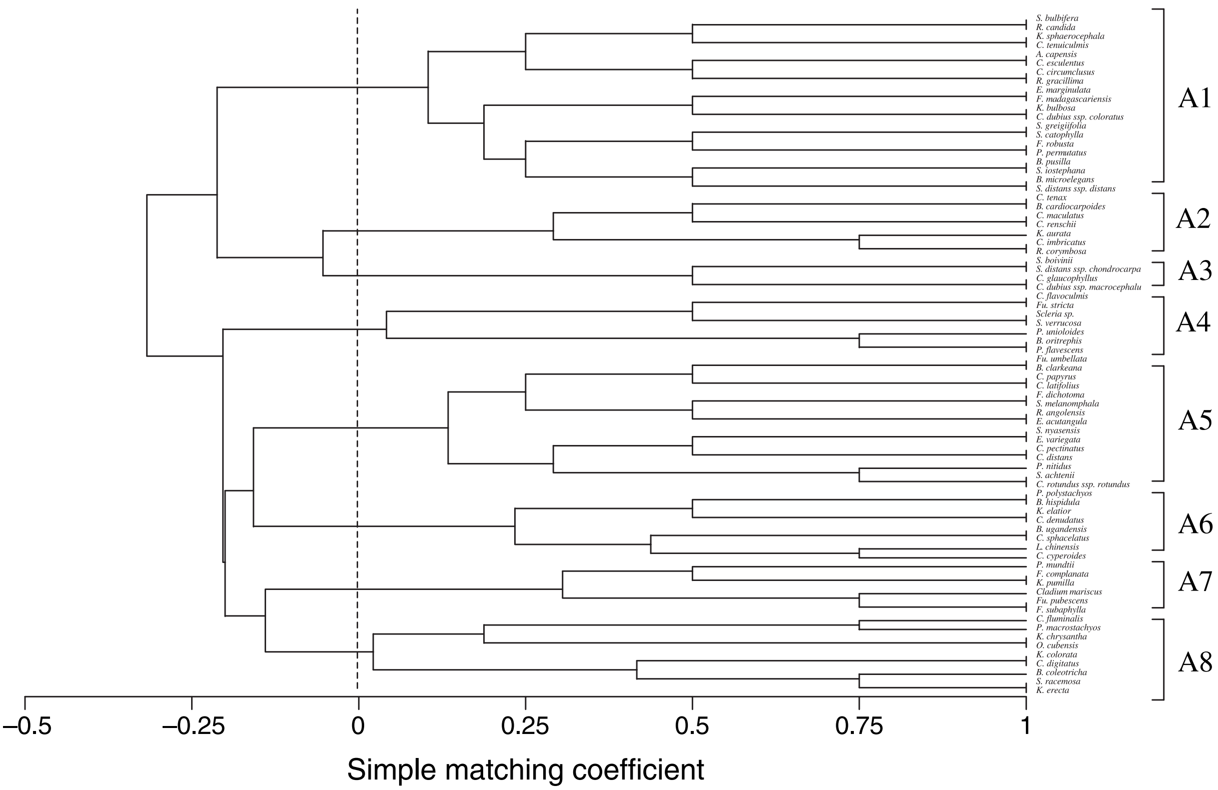

Fig 2 Species association analysis for sedges of the Lutembe bay (LUT), Mabamba bay (MBB), Lake Nabugabo (NBG) and Lutoboka peninsula (LUT) (cluster A of Fig. 1). Species assemblages (A1–A8) were defined using a simple matching coefficient of 0.0. A., *Ascolepis*; B., *Bulbostylis*; C., *Cyperus*; E., *Eleocharis*; F., *Fimbristylis*; Fu., *Fuirena*; K., *Kyllinga*; L., *Lipocarpha*; O., *Oxycaryum*; P., *Pycreus*; R., *Rhynchospora*; and S., *Scleria*.

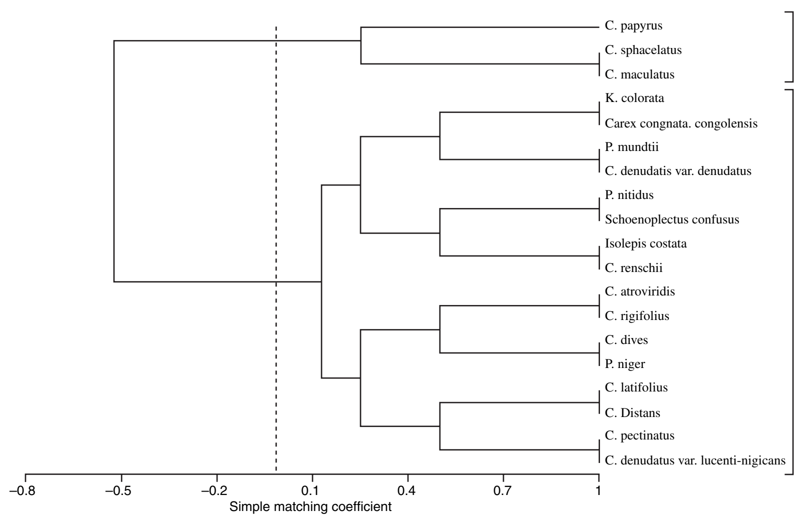

Fig 3 Species association analysis for sedge species of Nyamuriro swamp (NYR) and Musambwa islands (MSW) (cluster B of Fig. 1). Species assemblages (B1–B2) were defined using a simple matching coefficient of 0.0. (dotted line) C., *Cyperus*; P., *Pycreus*; K., *Kyllinga*.

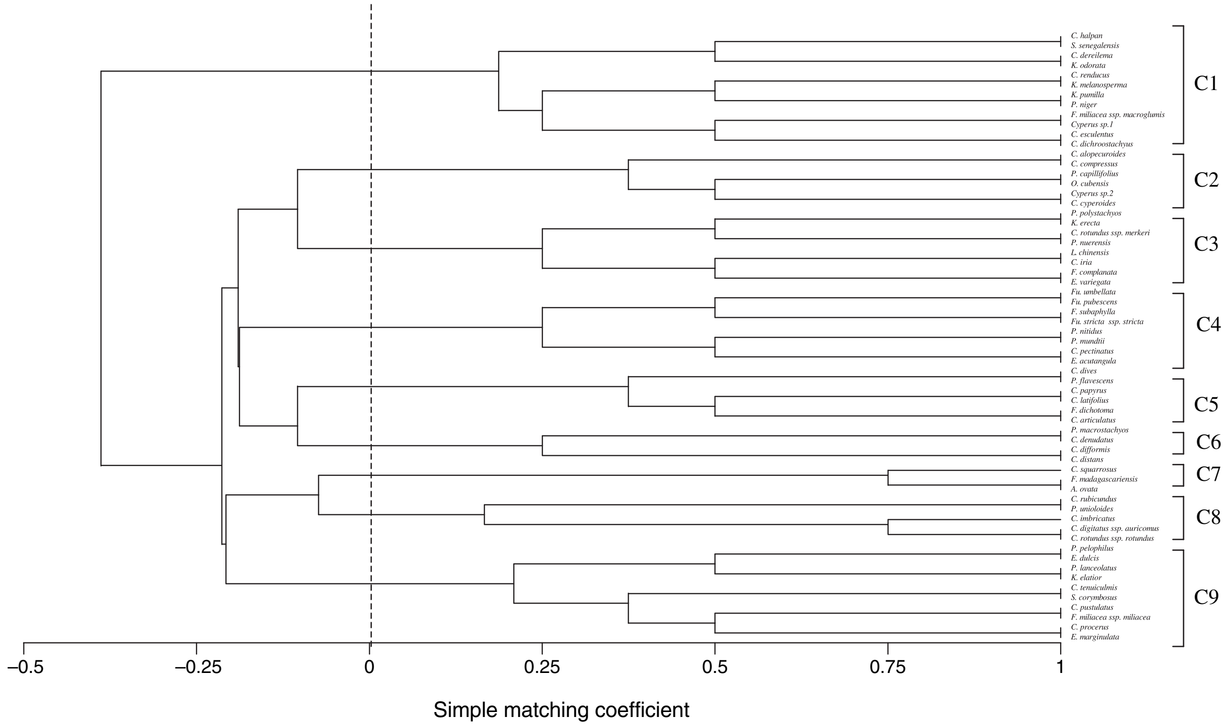

Fig 4 Species association analyses for sedges of Lake Nakuwa (NKW), Doho Rice Scheme (DHO), Lake Opeta (OPT) and Lake Bisina (BSN). Species assemblages (C1–C9) were defined using a simple matching coefficient of 0.0 (dotted line). Fu., *Fuirena*; C., *Cyperus*; S., *Schoenoplectus*; E., *Eleocharis*; O., *Oxycaryum*; P., *Pycreus*; A., *Abilgaardia*; K., *Kyllinga*; L., *Lipocarpha*; F., *Fimbristylis*.

mostly or entirely restricted to the Lake Kyoga basin included *Abildgaardia ovata*, *C. articulatus* and *Pycreus capillifolius*. Although Haines & Lye (1983) had many species recorded in the Lake Kyoga basin, we recorded several other species for the first time. These included *C. compressus*, *C. alopecuroides*, *C. dereilema*, *C. imbricatus*, *C. pectinatus*, *C. pustulatus*, *C. procerus*, *Eleocharis marginulata*, *Fimbristylis madagascariensis*, *K. erecta*, *Kyllinga melanosperma* and *Schoenoplectiella senegalensis.*

The observed difference in distribution of the species was probably influenced by the different processes of formation of the Lake Victoria and Lake Kyoga basin ecosystems, depicting ecoregional differences. The unique Nabugabo ecosystem, because of the high species richness, was originally part of Lake Victoria but later a sand bar developed and separated it from Lake Victoria when the water depths fell. This also led to the formation of various satellite lakes surrounded by *C. papyrus* swamps in the areas where Lake Victoria originally occupied. Wide elevational differences or range may also play a significant role in the distribution of sedge species. For instance, *Carex cognata* was only recorded from Nyamuriro swamp which had the highest elevation of 1900 m a.s.l. *Cyperus maculatus* was only recorded from the rocky/sandy region of Lake Victoria basin being more common on the sandy shores of Lake Victoria.

Comparison of wetlands based on sedge assemblages

The cluster of the ten wetland sites produced three distinct clusters (Fig. 1). Cluster A consisted of four wetlands all of which had relatively high species richness and were small in size. The analysis grouped Lake Nabugabo with Lutoboka peninsula, Mabamba and Lutembe bays, all found in the Lake Victoria basin. This was expected because all occur in the same geographic region with similar climatic conditions. This probably influences the species compositions in these sites in a similar way and hence the tendency to have similar species assemblages reflected in Fig. 1. Through PCA, the species typical of cluster A sites were determined. Descriptive species included *C. denudatus*, *C. latifolius*, *C. pectinatus*, *C. papyrus*, *P. nitidus*, *Eleocharis* *acutangula*, *F. umbellata* and *S. achtenii.* The species were common in these sites especially in the deeper water areas and can be used to accurately characterize these sites.

The two wetlands in cluster B included the Musambwa islands in Lake Victoria and Nyamuriro swamps in the Kigezi region. They had relatively poor species richness and far smaller in size compared to the cluster A sites. The clustering of Nyamuriro swamp with Musambwa islands is rather odd and could be attributed to its disturbed habitat because of cultivation when compared with other wetlands that were relatively intact and therefore representing fairly stable ecosystems. It can also be attributed to the sensitivity of the clustering technique to species richness such that a site with relatively fewer species will tend to be grouped with another of closest similarity depending on the species they have in common (Jongman, Ter Braak & Van Tongeren, 1995; Kovach, 1999).

Four wetlands form cluster C from the Lake Kyoga basin, namely Lake Nakuwa (NKW), Doho rice scheme (DHO), Lake Opeta (OPT) and Lake Bisina (BSN) from eastern Uganda. These sites were characterized by moderate species richness and large sizes. Within this cluster two subgroups were noted. NKW and DHO formed one subgroup indicating close floral similarity among these sites. OPT and BSN formed another subgroup. This separation suggests that differences in the sedge flora of sites may be due to the transition from one phytochoria to another (White, 1983). The former group represents the Lake Victoria regional mosaic while the latter is within the Sudanian regional centre of endemism.

Species associations of sedges

After placing sites into groups, the sedges occurring in each wetland site were used to associate species and create meaningful assemblages of sedges that are typically found in different regions of the basin. For cluster A sites (Fig. 1) 76 species were successfully placed into eight 'assemblages' (A1–A8) by cluster analysis as shown in Fig. 2, whereas for cluster B and C sites, two (i.e. B1 and B2) and nine assemblages (i.e. C1–C9) were created, respectively (Figs 3 and 4). The assemblages created depicted habitat types where the sedge species occurred predominantly. For instance, assemblage A4 included those species that are typical wet *Miscanthus/Loudetia*-dominated swamp.

Sites which are widely separated and very different in terms of habitat conditions, tending to have similar species sort into similar-species associations. Similar assemblages were noticed in the three groups of sites, but there were also several distinct differences among them. For instance, the assemblages produced from the sites of cluster C differed from those produced from cluster A sites. In assemblage A7 (Fig. 2), *P. mundtii* and *Fimbristylis complanata* were in the same species assemblage, whereas the same two species were completely unassociated in analysis of sedges in cluster C sites (Fig. 4). *K. erecta*, *Pycreus polystachyos*, *C. papyrus*, *C. latifolius* and *Fimbristylis dichotoma* however, are included in common assemblages in both analyses.

The assemblages produced by these analyses would appear to be a reflection of the species that have regularly occurred together in samples and evidently the assemblages cannot always be distinguished from one another on the basis of observed habitat preferences of sedges. Increasing the value of the simple matching coefficient, which was used to define assemblages helped to clarify some of the problems by coming up with more 'defined and distinct' assemblages.

Assemblages produced from sites of clusters A and C also differ somewhat from the results of cluster B, possibly because of the way that cluster analysis 'forces' pairing of species at low similarity even though they rarely occur naturally. Nevertheless, several meaningful assemblages were produced by these analyses. Most notable was assemblage A5 which consisted of *Scleria melanomphala*, *S. nyasensis*, *S. achtenii*, *Eleocharis variegata*, *E. acutangula*, *C. pectinatus* and *C. denudatus* var. *denudatus*. These species are typical of the sites in cluster A and are commonly found together mainly in the *Miscanthus/Loudetia*-dominated habitat type.

In conclusion, the wetlands studied support a diverse assemblage of sedges. They include 112 of the 223 species recorded in Uganda. This is a large number of species recorded because many other wetlands were not surveyed during this study. 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 (White, 1983). Distribution patterns of sedges indicated preferences of several species for certain portions of sites in the wetlands. 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. More botanical surveys need to be done as it is expected that more species would be recorded. This is in light of the fact that new records of species were made especially in the Lake Kyoga basin. This would also contribute to the already existing body of knowledge about the sedges in Uganda and thus fill gaps that existed.

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