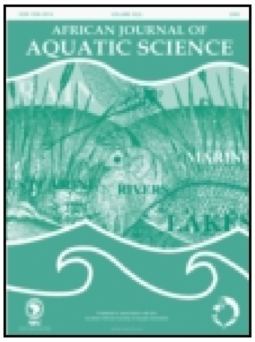

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A vegetation-based hierarchical classification for seasonally pulsed floodplains in the Okavango Delta, Botswana

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A classification scheme is presented for seasonal floodplains of the Boro-Xudum distributary of the Okavango Delta, Botswana. This distributary is subject to an annual flood-pulse, the inundated area varying from a mean low of 3 600 km² to a mean high of 5 400 km² between 2000 and 2006. A stratified random sample of 30 sites was surveyed for species composition and abundance in March–June 2007, using multiple quadrats along transects orthogonal to the floodplain long axis. A combination of indicator species analysis and ordination was used to derive a hierarchical classification system for floodplains, based on species assemblages. Indicator species analysis was used to identify ecologically meaningful levels of division, at four and nine classes. The four main classes of floodplain were: (1) Dry Floodplain Grassland (main indicators *Urochloa mosambicensis*, *Ipomoea coptica*, *Chloris virgata* and *Pechuel-Loeschea leubnitziae*); (2) Seasonally Flooded Grassland (*Nicolasia costata*, *Eragrostis lappula*, *Cyperus sphaerospermus* and *Setaria sphacelata*); (3) Seasonally Flooded Sedgeland (*Eleocharis dulcis*, *Leersia hexandra*, *Oryza longistaminata* and *Cyperus articulatus*); and (4) Seasonal Aquatic Communities (*Sacciolepis typhura*, *Eleocharis variegata*, *Fuirena pubescens* and *Cycnium tubulosum*). The resultant dendrogram provides an objective routine for classifying floodplains in the Boro-Xudum distributary in an ecologically meaningful way. This classification will assist in monitoring changes in vegetation resulting from hydrological change.

Keywords: ecological monitoring, indicator species, plant communities, wetland

Introduction

Wetlands provide a significant array of ecosystem services (Wilson and Carpenter 1999, Mitsch and Gosselink 2000) and, in developing countries, are relied on for the provision of direct services such as food, building materials, and medicines, in addition to the 'hidden' hydrological and biophysical services, such as flood amelioration and water quality improvement (Barbier 1994, Acharya 2000, National Conservation Strategy Agency 2000). The continued survival of wetlands is dependent in large part on maintenance of the hydrologic regime, and this is increasingly under threat globally, as a result not only of climate change but also of local changes such as surrounding land use, water abstraction, or changes to flow regimes due to damming for water and power supply. Sub-Saharan Africa is projected to be particularly affected by water stress resulting from climate change by 2025 (Postel 2000). Most southern African countries' economies depend on a significant contribution from natural resources, yet little is known about how climate changes will affect freshwater ecosystems and the flow of benefits from them.

Tropical wetlands are often subject to one or more distinct pulses in water supply as a result of rainfall seasonality, and are ecologically adapted to this varying hydrology (Junk and Piedade 1993, Bayley 1995, Junk 2000). Changes in rainfall, evapotranspiration and river flows may affect the flood-pulse in terms of timing, amplitude and duration, and consequently affect ecosystem properties. Understanding such changes and their likely effects is of critical relevance to land-use planning and management. Botswana's Okavango Delta is a large (16 000 km²), open wetland ecosystem, which has so far escaped major anthropogenic impact. However, hydrological change resulting from both development in the catchment and climate change is considered inevitable (Ashton and Neal 2003, Andersson et al. 2006). Knowledge of the baseline state and functioning of the system has, however, been limited largely due to its sheer size and inaccessibility. Consequently, the potential for monitoring the effects of hydrologic change on vegetation has been mainly restricted to remote sensing methods. Historically, these have been either of insufficient spectral resolution to distinguish differences between major floodplain vegetation types, or too expensive (Ringrose et al. 1988, Wolski and Murray-Hudson 2006) to apply in this large and dynamic wetland at high temporal resolution.

The Okavango Delta falls into the Zambezian Flooded Grasslands biome, characterised by low levels of endemism, but locally very high species richness, both in flora and fauna, including a number of endangered bird species (Junk et al. 2006, Ramberg et al. 2006, McGinley 2008). The richness per unit area of the Okavango flora is about one order of magnitude higher than the background value for Botswana as a whole — the species–area ratio for the Delta is about 0.054 km^{-2}, higher than all other biomes on the southern African subcontinent, with the exception of the Fynbos biome of the western Cape of South Africa, due in large part to the significant extent of perennially flooded areas (Snowy Mountains Engineering Corporation 1989). The Delta is a declared wetland of international importance — a RAMSAR site — and commitments to the 'wise use' principle embodied in the convention, and the Botswana Wetlands Policy and Strategy (National Conservation Strategy Agency 2000) require that management ensure the maintenance of ecosystem functioning and biodiversity (Jansen 2002). Adaptive management would be a logical framework to apply to the Delta and its development, but our basic understanding of the ecological organisation, and the drivers of that organisation is incomplete. A first step towards addressing this gap is gathering baseline ecological information, such as the distribution of different ecological communities (flora and fauna), and monitoring change.

Historically, the vegetation of the Delta has been qualitatively described by various authors (Snowy Mountains Engineering Corporation 1989, Ellery and Ellery 1997), with some more quantitative but localised work in the perennially flooded areas (Ellery et al. 1990, 2003), in the Xudum-Xwaapa system (Heemstra 1976), and on Chief's Island (Biggs 1979). Bonyongo et al. (2000) carried out a detailed phytosociological survey of a single floodplain in the middle Boro and recommended extension of their approach. The qualitative ecological zoning system developed by Snowy Mountains Engineering Corporation (1989) for the Delta as a whole was based on the vegetation specialist's extensive personal experience and observation of Delta floodplains. It provided the first full compilation of plant species, and some floristic and life form analysis of Delta plants by habitat, but had no quantitative basis. The checklist developed for that project has subsequently been updated and augmented by two consecutive rapid assessment studies carried out by Conservation International (2003), who also developed an overview of main vegetation groups from ordination of data from four sites in the Panhandle, western, central and northern Delta (Sliva et al. 2004). All of these studies are limited either in their geographic scope or their quantitative basis, effectively reducing their replicability.

This study describes the derivation of a simple hierarchical classification system for seasonally-pulsed floodplains in the Delta. The vegetation in different floodplains of the Boro-Xudum distributary was sampled in order to: (1) test for the presence of distinct species assemblages that could provide a classification system for floodplains; and (2) identify indicator species or groups of species that could be used to characterise different assemblages. A system of classification that is broadly applicable can be used to establish a baseline of floodplain vegetation distribution, and subsequently to monitor change with time. These data may then be used to inform policy development and management decisions.

Methods

Study area

The Boro-Xudum distributary (Figure 1) is approximately 6 000 km^2 in extent. Accession of water to the system is by over-bank flow from the main Okavango channel, after which the flow converges and heads south-east through multiple floodplains and channels.

Vegetation survey

Floodplains were divided into five strata of approximately equal area, based on historic flood frequency reconstructed from a time-series of satellite imagery (Wolski and Murray-Hudson 2006), and six sites were randomly selected within each stratum. Sites were surveyed between March and June 2007. A synopsis of sites is given in the Appendix, including the acronyms used here. Species composition and relative abundance were sampled along transects oriented orthogonally to the long axis of the floodplain, using 1 m^2 quadrats spaced 20 m apart; geographic coordinates for each quadrat were recorded in the field. Species–area curves from a preliminary survey (MM-H unpublished data) were used to determine the required sample area as ≥25 m^2; consequently, a minimum of 30 quadrats per site was surveyed. Species were identified in the field, where possible. Samples of unknowns were taken and pressed in the field, and those that could not be identified from the Peter Smith Herbarium (PSUB) collection at the Okavango Research Institute, Maun, Botswana, were sent to the Royal Botanic Gardens, Kew, UK, for identification. Nomenclature followed Germishuizen and Meyer (2007). The field sampling campaign was timed to maximise availability of inflorescences so as to facilitate identification. This resulted in sampling on the rising limb of the hydrograph. Thus many sites had just received, or were about to receive, floodwater from the 2006–2007 inflow.

Statistical analysis

Multivariate data analyses were carried out with routines in PCOrd 5.1 (McCune and Mefford 2006), and EstimateS (Colwell 2006) was used for analysis of richness and diversity parameters. Species frequencies per site were calculated from their proportional presence in quadrats (frequency). Hierarchical cluster analysis (flexible β linkage, $\beta = -0.25$, Sorensen distance) of sites was carried out on a data set comprising only species that occurred at more than three sites, based on their frequency distribution among quadrats (84 species). To test the hypothesis of no differences between clusters, a multi-response permutation procedure (MRPP) statistical test included in PCOrd was carried out using Sorensen distance and rank-transformed data. MRPP is a data-dependent routine that requires no assumptions about the underlying distribution structure of the population (Biondini et al. 1988). The weighted mean within-group distance ($\delta = \sum_{i=1}^{g} C_i x_i$ for g groups, where x_i is the average within-group distance, C is a weight derived from the number of species in the groups, and smaller values of δ indicate tighter clustering within groups), was calculated. The probability p of δ being less than or equal to this calculated value is estimated against a Pearson type III distribution (which accommodates the potential

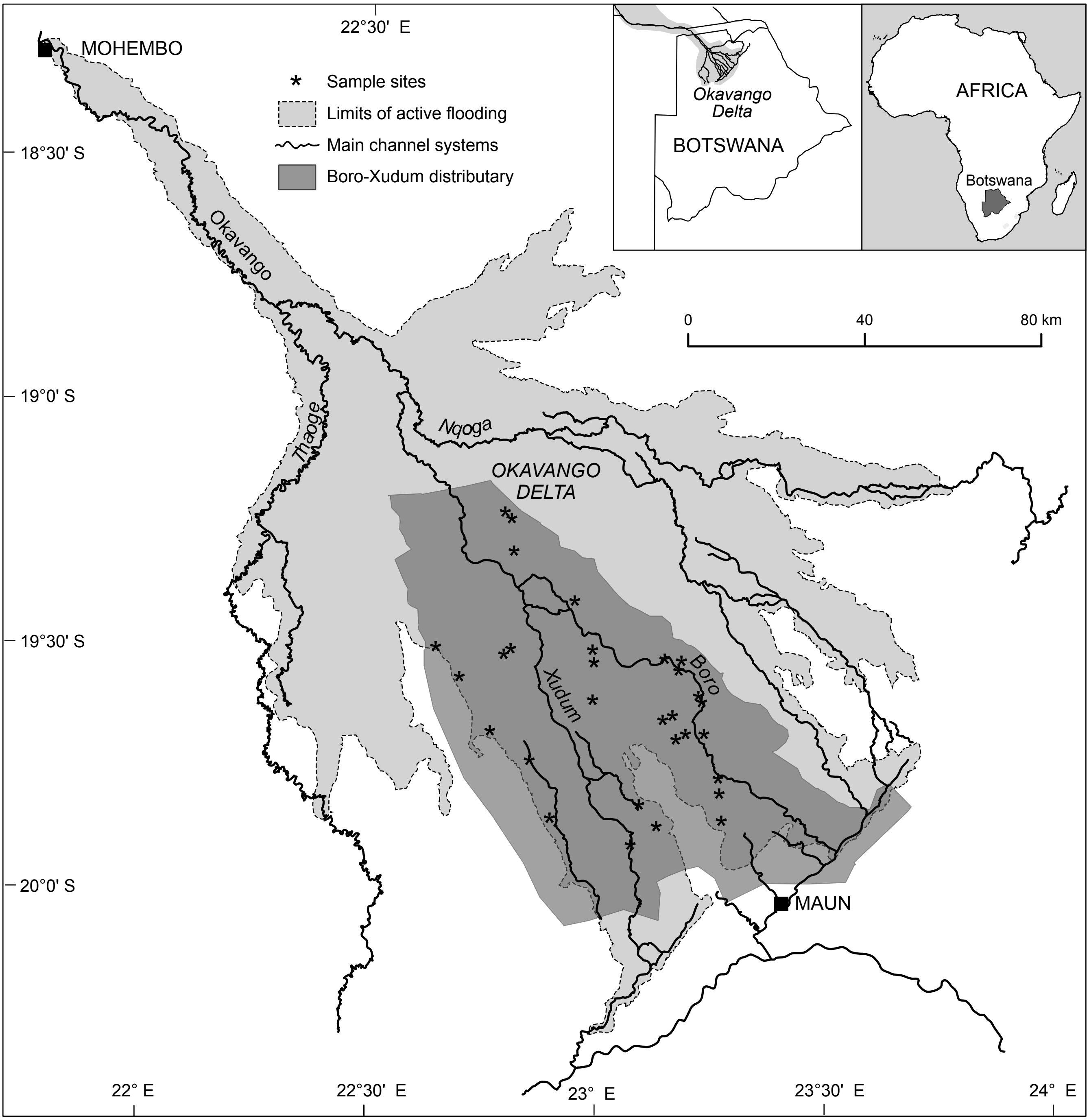

Figure 1: Study area showing the Boro-Xudum distributary and locations of survey sites

skewness of the underlying permutation distribution); this gives the probability of a type I error under the null hypothesis of no difference between groups. The test statistic $T = (\delta_{obs} - \delta_{expected})/\sigma_\delta$ describes the separation between groups, with more negative values indicating stronger separation. Effect size is provided by the chance-corrected within-group agreement $A = 1 - (\delta_{obs} / \delta_{expected})$; this describes within-group homogeneity.

Indicator species analysis (ISA; Dufrêne and Legendre 1997) was used to identify levels for defining classes. This routine calculates indicator values (IVs) for species based on fidelity and relative abundance in *a priori* defined groups, and evaluates the statistical significance of the IVs by comparison with IVs generated by Monte Carlo randomisation of the data set. Ecologically meaningful levels for defining classes were determined by applying ISA iteratively to an increasing number of divisions (Figure 2) and plotting the overall number of species identified as significant (at $p < 0.05$) indicators, and the overall average p-value at each level of division. Where the mean p-value is minimised or the number of significant indicator species is maximised, this represents a maximum of ecological information.

Non-metric multidimensional scaling (Kruskal 1964, Mather 1976) was used to ordinate the sites–species matrix (Sorensen distance, random starting configuration, 250 runs real and randomised, final selection of two-dimensional representation based on stress <10), to investigate intersite relationships. Species characteristic of clusters were determined by ISA.

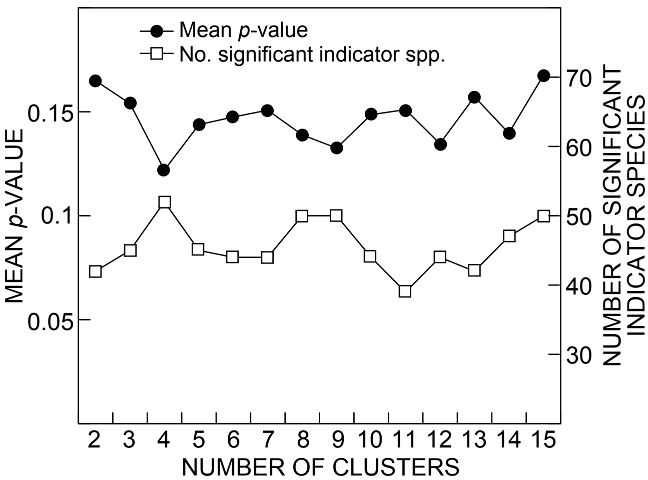

Figure 2: Changes in mean p-value and number of significant indicator species ($p < 0.05$) from indicator species analysis, with increasing number of clusters. Minima in mean p-values occur at four and nine, and maxima in number of indicators at four, eight and nine clusters, respectively

Results

A total of 166 positively identified species were recorded in the seasonal floodplains sampled, including 53 grasses, 31 sedges and 33 aquatic herbs. Adjusted jackknife 1 and 2 estimates (Colwell 2006) of potential total richness were 227 and 269, respectively. The data set used for ordination and clustering was reduced to 84 species by excluding those species that occurred at less than three sites.

Classification

There is a coincident minimum of ISA p-value and maximum of number of significant indicator species at four divisions (Figure 2). At six divisions, the first single site class appears (MOC), and a second appears at seven divisions (XHA). A further coincident indicator species maximum and p-value minimum occurs at nine classes, indicating a suitable ecological level for subclass definitions. The four main ecological classes are designated Dry Floodplain Grasslands (DFG), Seasonally Flooded Grasslands (SFG), Seasonally Flooded Sedgelands (SFS), and Seasonal Aquatic Communities (SAC), based on their main species.

The ordinated sites (Figure 3) fall into discrete clusters; envelopes correspond to the four classes defined in Figure 4. One major gradient captured most of the variance in the floodplain communities, the first dimension containing 82.8% and the second 6.7% of the information in the data set (cumulative = 89.5%). Here the relationship of the sites MOC and XHA to the other members of their class (which causes them to fall out as single site classes at higher cluster levels) can be seen. Despite the apparent large distances between these sites and their cluster centroids, all sites are within two standard deviations of the mean of ordination distance, and consequently did not

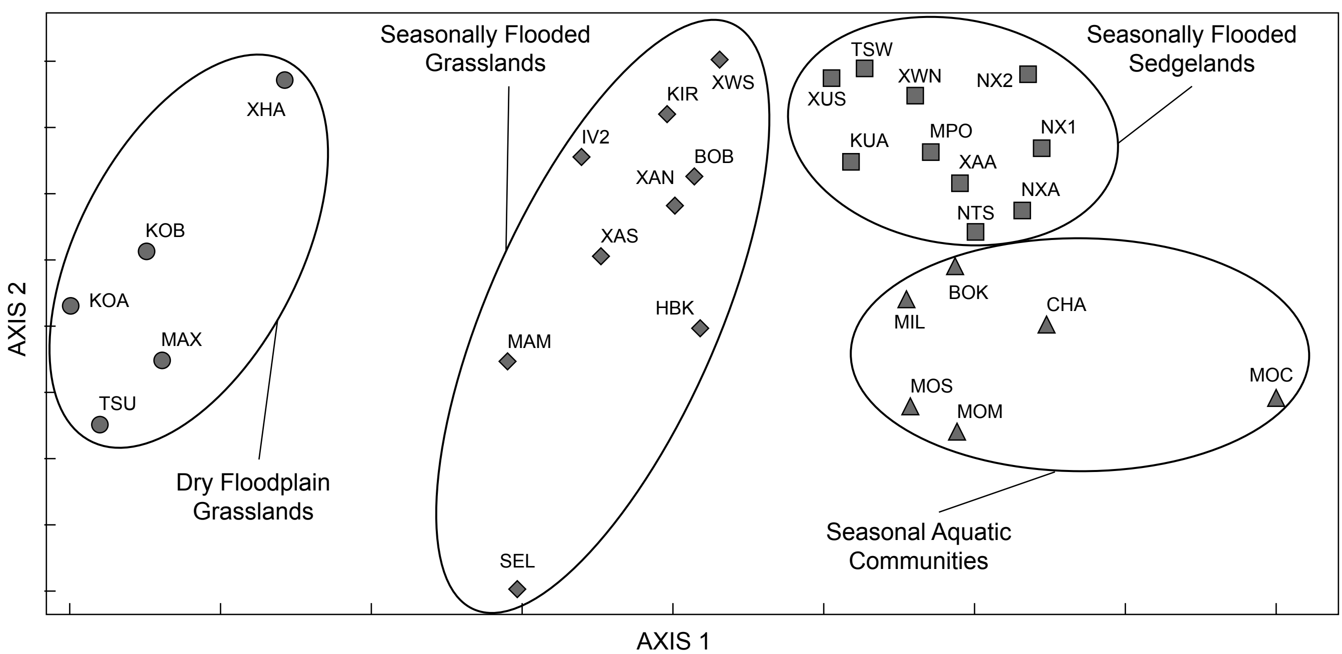

Figure 3: Non-metric multidimensional scaling ordination of sites by species. Envelope groupings correspond to the classes shown in Figure 4

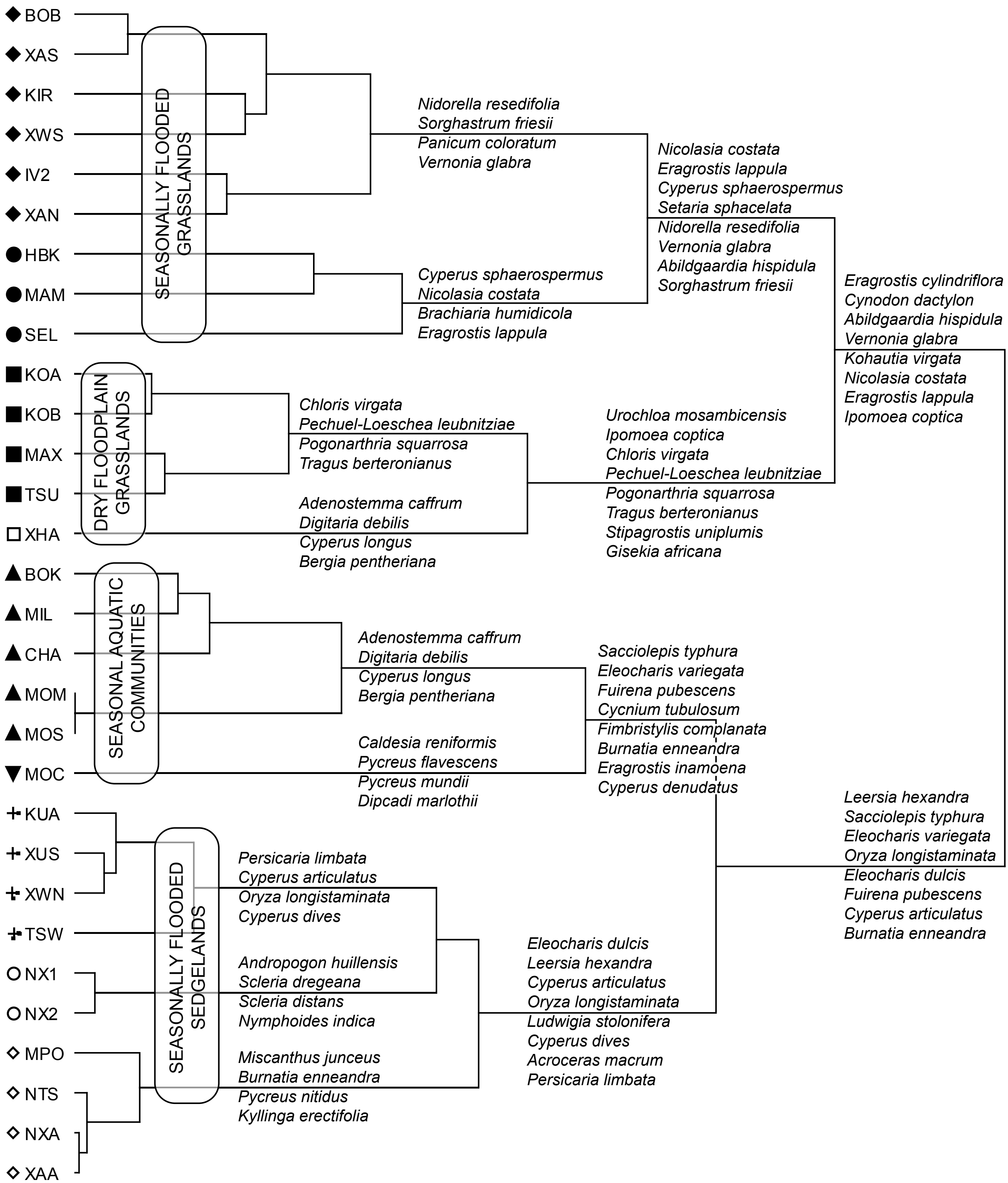

Figure 4: Dendrogram of sites clustered by species (flexible β linkage, β = −0.25, Sorensen distance). Four primary classes (oval envelopes) and nine subclasses of sites are shown (◆, ●, ■, □, ▲, ▼, +, ○ and ◇), based on analysis of changes in indicator strength. At levels six and seven of division, single site classes are generated: MOC ▼ and XHA □. Site codes are elaborated in the Appendix

meet the criterion used to identify outliers. MRPP tests of the four-class division showed a chance-corrected within-group agreement $A = 0.535$, with the probability of a smaller or equal δ (the weighted mean within-group distance) $p < 1E-8$; that is, the hypothesis of no difference between groups can be rejected. Pairwise comparisons between clusters likewise all resulted in p-values < 0.001 (Table 1).

Further subdivision into nine sub-classes, as mentioned above, results in the appearance of two single site classes. Once these are excluded, two of the remaining classes can be meaningfully subdivided, specifically the larger groups of seasonally flooded grasslands and sedgelands. MRPP of these subdivisions also showed a strong within-group agreement ($A = 0.710$, $p < 1E-8$), which implied classes are different.

Class characteristics

Floodplains of the distal Okavango Delta are generally in the order of 50–200 m wide, and the total topographic difference between thalweg and island margin is 1–2 m. They are not typically terraced as 'classic' alluvial floodplains, but form a complex mosaic within which flooding generally decreases in frequency, duration and depth with increasing distance from major channel supply systems.

The four main classes of floodplain vegetation distinguished can be roughly considered as two groups, drier and wetter, and these can be separated on the basis of a threshold in the mean duration of flooding of approximately five months (MM-H unpublished data). Most of the floodplain communities are characterised by a dominance of grasses and sedges; only the driest class supports any woody shrubs or trees.

Ratios of annual to perennial plants (A:P), sedge:grass (Cyp:Gram) ratios and Shannon diversity indices (calculated from the full data set) are presented in Table 2. The A:P ratio values are lowest in the Seasonal Aquatic Communities, increasing through the two intermediate classes and reach a maximum in the Dry Floodplain Grasslands, the inverse of the pattern followed by the sedge:grass species ratio. Mean diversity indices (richness, evenness, Shannon and Simpson indices) were lowest in the DFG class, intermediate in SFG and SAC, and highest in the SFS class, but none of these differences are statistically significant.

An annotated dendrogram (Figure 4) is structured as a dichotomous key; major indicator species are included to allow separation of each division, and identification of the nine floodplain subclasses. Table 3 lists the major indicator species of the four primary classes, their indicator values, p-values, and their life cycle and growth form.

Dry Floodplain Grassland

These communities are characterised by the (mainly) annual grasses *Urochloa mosambicensis* and *Chloris virgata*, the herb *Ipomoea coptica*, and the perennial forb *Pechuel-Loeschea leubnitziae*. Additional common species of annual grass include *Pogonarthria squarrosa*, *Tragus berteronianus* and *Stipagrostis uniplumis*. In those areas that have not received recent flooding, shrubs and small trees may have become established, with *Acacia erioloba*, *A. nigrescens* and *Combretum imberbe* being among the more common. There are also many annual herb species

Table 1: MRPP pairwise comparisons of between-cluster differences for floodplain species in the Boro-Xudum distributary in 2007. t = test statistic, A = chance-corrected within-group agreement, p = probability of a smaller or equal δ. Note: p is not corrected for multiple comparisons

Classes	t	A	p
SFG vs SAC	−7.847	0.361	0.00005
SFG vs DFG	−7.416	0.416	0.00017
SFG vs SFS	−9.397	0.328	0.00001
SAC vs DFG	−6.090	0.454	0.00092
SAC vs SFS	−6.029	0.228	0.00011
DFG vs SFS	−8.235	0.398	0.00005

Table 2: Class life-cycle characteristics and Shannon diversity of floodplain classes in the Boro-Xudum distributary in 2007

Class	Annual: perennial	Sedge: grass	No. of herb spp.	Mean H'
DFG	1.2	0	7	2.76
SFG	0.27	0.36	4	2.81
SFS	0.14	0.57	5	2.98
SAC	0.045	2.0	6	2.80

found in this community. On average these communities are flooded for less than a month. They are essentially rain-sustained grasslands that receive just sufficient flooding to maintain them as grasslands and to prevent succession to woodland.

Seasonally Flooded Grasslands

Dominant species where flooding is more frequent include the herbs *Nicolasia costata* and *Nidorella resedifolia*, the grasses *Eragrostis lappula* and *Setaria sphacelata*, and the sedge *Cyperus sphaerospermus*. Frequently, there is also a scattering of the diminutive annual sedge *Abildgaardia hispidula*. These grasslands seldom have any woody seedlings or saplings. These grasslands are flooded for between one and five months.

Seasonally Flooded Sedgelands

Here, the characteristic plants are mainly sedges (as the class name implies; *Eleocharis dulcis* and *Cyperus articulatus*), and aquatic grasses such as *Leersia hexandra* and *Oryza longistaminata*. Herbs are water-tolerant perennials such as *Ludwigia stolonifera* and *Persicaria limbata*. Mean duration of flooding in these sedgelands is five to eight months.

Seasonal Aquatic Communities

These communities are characterised by a predominance of sedges and numerous floating-leaved and submerged aquatic herbs. Typical grasses and sedges include *Sacciolepis typhura*, *Eleocharis variegata* and *Fuirena pubescens*. Herbs such as *Cycnium tubulosum*, and the floating-leaved *Nymphaea nouchali* and *Nymphoides indica*, develop once the short (<three months, on average) seasonal dry period is over. During the dry period, short-sprouting herbs such as *Burnatia enneandra* come into leaf, flower and seed.

Table 3: Indicator species parameters for the four-class division of floodplains in the Boro-Xudum distributary in 2007. Indicator values and their *p*-values are derived from indicator species analysis (Dufrêne and Legendre 1997); life cycle and growth form data are from Germishuizen and Meyer (2007). P = Perennial, A = annual, (a) = occasionally annual, (p) = occasionally perennial

Primary class	Indicator value	*p*-value	Life cycle	Growth form
		Dry Floodplain Grasslands		
Urochloa mosambicensis	98.9	0.0002	P	Graminoid
Ipomoea coptica	89.3	0.0002	A	Herb
Chloris virgata	80.0	0.0002	A (p)	Graminoid
Pechuel-Loeschea leubnitziae	80.0	0.0002	P	Shrub
Pogonarthria squarrosa	80.0	0.0002	P (a)	Graminoid
Tragus berteronianus	80.0	0.0002	A	Graminoid
Stipagrostis uniplumis	79.4	0.0002	P (a)	Graminoid
Gisekia africana	73.3	0.0012	A (p)	Herb
Eragrostis cylindriflora	71.2	0.0004	A	Graminoid
Cynodon dactylon	66.4	0.0004	P	Graminoid
Bergia pentheriana	62.7	0.0018	P	Herb
Corchorus tridens	60.0	0.0024	A	Herb
Aristida meridionalis	60.0	0.0026	P	Graminoid
Hermannia quartiniana	60.0	0.0026	P	Herb
Tephrosia purpurea	60.0	0.0026	A (p)	Herb
Melinis repens	60.0	0.0028	A (p)	Graminoid
Eragrostis viscosa	60.0	0.0032	A	Graminoid
Acacia erioloba	60.0	0.0034	P	Shrub, Tree
Sporobolus ioclados	53.6	0.0054	P	Graminoid
Kohautia virgata	48.6	0.0266	A (p)	Herb
Combretum imberbe	31.5	0.0488	P	Shrub, Tree
Acacia nigrescens	24.6	0.1314	P	Tree
Digitaria debilis	11.8	0.7179	A	Graminoid
Gomphocarpus fruticosus	5.9	0.9494	A (p)	Herb, Shrub
		Seasonally Flooded Grasslands		
Nicolasia costata	73.9	0.0016	P	Herb
Eragrostis lappula	69.1	0.0012	P	Graminoid
Cyperus sphaerospermus	60.4	0.0046	P	Cyperoid
Setaria sphacelata	54.6	0.0006	P	Graminoid
Nidorella resedifolia	51.5	0.0044	A	Herb
Vernonia glabra	48.2	0.03	P	Herb
Abildgaardia hispidula	40.3	0.177	A	Cyperoid
Sorghastrum friesii	33.9	0.0892	P	Graminoid
Aristida junciformis	33.3	0.0474	P	Graminoid
Panicum coloratum	33.3	0.0622	P	Graminoid
Schoenoplectus erectus	33.3	0.0666	A	Cyperoid
Trachypogon spicatus	32.1	0.1366	P	Graminoid
Paspalum scrobiculatum	26.5	0.3167	P	Graminoid
Digitaria eriantha	23.3	0.195	P	Graminoid
Kohautia caespitosa	21.4	0.193	A (p)	Herb
Sporobolus spicatus	14.8	0.6173	P	Graminoid
Cenchrus ciliaris	12.8	0.4131	P	Graminoid
		Seasonally Flooded Sedgelands		
Eleocharis dulcis	69.7	0.0016	P	Cyperoid
Leersia hexandra	64.2	0.0002	P	Graminoid
Cyperus articulatus	62.5	0.0008	P	Cyperoid
Oryza longistaminata	62.4	0.001	P	Graminoid
Ludwigia stolonifera	61.5	0.0068	A (p)	Herb
Cyperus dives	50.0	0.0098	P	Cyperoid
Acroceras macrum	46.5	0.0276	P	Graminoid
Persicaria limbata	45.9	0.0126	P	Herb
Paspalidium obtusifolium	44.1	0.0416	P	Graminoid
Schoenoplectus corymbosus	40.8	0.016	P	Cyperoid
Vossia cuspidata	39.8	0.0328	P	Graminoid
Potamogeton thunbergii	37.3	0.1186	P	Herb
Brachiaria humidicola	35.3	0.1316	P	Graminoid
Phragmites australis	30.0	0.1032	P	Graminoid
Sesbania microphylla	26.3	0.1326	A	Herb
Nesaea radicans	7.9	0.8752	P	Herb

Table 3: (cont.)

Primary class	Indicator value	*p*-value	Life cycle	Growth form
		Seasonal Aquatic Communities		
Sacciolepis typhura	80.7	0.0002	P	Graminoid
Eleocharis variegata	76.4	0.0002	P	Cyperoid
Fuirena pubescens	69.1	0.0006	P	Cyperoid
Cycnium tubulosum	67.3	0.0014	P	Herb
Fimbristylis complanata	65.9	0.0002	P	Cyperoid
Burnatia enneandra	65.0	0.0016	P	Herb
Eragrostis inamoena	56.7	0.0018	P	Graminoid
Cyperus denudatus	52.8	0.0008	P	Cyperoid
Utricularia sp.	47.8	0.022	P (a)	Herb
Nymphoides indica	47.6	0.0342	P	Herb
Miscanthus junceus	46.0	0.0212	P	Graminoid
Pycreus nitidus	44.0	0.0376	P	Cyperoid
Panicum repens	43.8	0.0078	P	Graminoid
Nymphaea nouchali	41.7	0.071	P (a)	Herb
Sphaeranthus flexuosus	39.4	0.0624	A (a)	Herb
Rhynchospora holoschoenoides	36.5	0.1394	P	Cyperoid
Scleria dregeana	35.4	0.0614	P	Cyperoid
Cyperus longus	35.1	0.2925	P	Cyperoid
Imperata cylindrica	34.4	0.2058	P	Graminoid
Andropogon huillensis	30.0	0.1052	P	Graminoid
Scleria distans	30.0	0.1106	P	Cyperoid
Fuirena umbellata	24.6	0.4379	P	Cyperoid
Digitaria eylesii	21.3	0.3521	P	Graminoid
Kyllinga erecta	17.5	0.3807	P	Cyperoid
Kyllinga intricata	13.9	0.5191	P	Cyperoid
Sopubia mannii	7.7	0.8828	P	Herb

Discussion

In general, the vegetation of the floodplains is characterised by short-lived herbaceous (non-woody) plants. Where long-term environmental changes are most pronounced (Dry Floodplain Grasslands), these are more likely to be opportunistic, fast-growing annuals, while in areas that are regularly flooded, perennial species and those with vegetative reproductive strategies are likely to dominate.

Floodplain communities and species ecology

The overall results of this classification exercise correspond in a broad sense with the qualitative categorisation of Snowy Mountains Engineering Corporation (1989). There is also close correspondence with two of the main vegetation groups identified in the more quantitative assessment of Sliva et al. (2004): SFS is equivalent to the *Schoenoplectus corymbosus*–*Cyperus articulatus* communities, and DFG to the *Urochloa mosambicensis*–*Pechuel-Loeschea leubnitziae* communities. SFG falls into their category 'communities of the aquatic–terrestrial transition zone' and corresponds roughly to '*Panicum repens* grassland communities'. Although based on cluster analysis, that study was not designed to develop a classification system, and consequently no quantitative basis for selecting indicator species was given. In the present study, for example, we found that the two species used for characterising the seasonal sedgelands in most previous work (Snowy Mountains Engineering Corporation 1989, Bonyongo et al. 2000, Sliva et al. 2004), *Schoenoplectus corymbosus* and *Cyperus articulatus*, seldom actually occur as codominants. Although both are recognised as significant indicators for this class in our analysis, *C. articulatus* in fact only emerges as a primary indicator (with the highest IV) at the sixth level of division. *Schoenoplectus corymbosus* never achieves an IV greater than 63 and, in this instance (three classes), is ranked eleventh in importance as an indicator. These species are both conspicuous, tall, emergent sedges that tend visually to mask their diminutive but statistically more important neighbours, such as *Leersia hexandra* or *Eleocharis dulcis*. The SFG and SFS classes are better represented in the survey data set (*n* = 9 and *n* = 10, respectively) and there are good indications (Figures 2 and 3) that these classes can profitably be subdivided. It is also in these classes that most of the species diversity is concentrated.

The single site classes MOC and XHA are clearly defined by small suites of species not found at other sites. In the case of MOC, these species are primarily aquatic herbs, and it seems likely that this site represents an end-member of seasonal flooding, in which both frequency and duration are close to 100%. XHA is a dry floodplain grassland site, but the presence of *Cyperus longus* suggests that the flooding regime is slightly longer or more frequent than the mean for this class. This possibility is corroborated by the position of XHA within its envelope in ordination space (Figure 3).

The estimates of overall species richness of these seasonal floodplains agree closely with the Snowy Mountains Engineering Corporation (1989) estimate of 240. It appears that only a small subset of these species is distributed widely enough to make useful indicators for floodplain classification at the distributary scale. Between-group differences in annual:perennial and sedge:grass ratios are a good reflection of differences in hydroperiod between sites. The DFG class of floodplain is characterised by annual grasses and herbs adapted for rapid seasonal growth and seed production during the short rainy season; there are also three woody species, one of which (*Acacia erioloba*) emerged with an IV of 60 for this group. This may be interpreted as follows: the low frequency of flooding in these sites results in flood events assuming the role of major ecological disturbances and, between such events, successional processes are those operating in the surrounding savanna woodlands — an initial burst of fast-growing annual, or short-lived perennial, species, followed by a slow intrusion of woody species. SFG floodplains are characterised by perennial grasses; some sedges and herbs are annual, and their presence may be related to rainy season growth. The decline in the proportion of annual species with increasing hydroperiod in the SFS and SAC classes may simply be attributable to the lack of a sufficiently long window for germination and growth.

Most of the floodplains sampled in this study exhibited zonation of vegetation along the topographic gradient from upland to thalweg; to remove noise from ecotones, only quadrats more than 40 m from upland areas were used in the analysis. There is evidence from other studies that species assemblages may be replicated in such zones within single floodplain sites. Bonyongo et al. (2000) studied floodplain vegetation in a single floodplain in the Boro system and described three vegetation types that were further divided into a total of eight communities. From their data, under the classification proposed here, the overall designation of this floodplain would be SFS, while the fringe type '*Setaria sphacelata–Eragrostis inamoena*' corresponds to class SFG. These vegetation types behave as mobile assemblages and their distribution appears to reflect the hydroperiod conditions of the recent past. Thus a sequence of large floods will result in a net movement up-catena of, for example, the afore-mentioned two grass species and their associated assemblage. Timing of sampling in relation to plant phenology was also a factor in our survey work: several herbaceous species (e.g. *Abildgaardia hispidula* and *Nicolasia costata*) apparently take advantage of space opened up by the die-back of hydrophytes as the flood retreats, and grow rapidly in aerobic soils in response to increased day-length and rainfall. These opportunists do not survive prolonged inundation, but are found (up to 20% of cover in some quadrats) in regularly flooded areas immediately prior to and during the early stages of the rising flood. If sampling was carried out after the flood peak, no evidence of their presence would remain except, probably, propagules. Such effects are characteristic of the bimodal nature of ecological production in this hydrologically asynchronous system. Bonyongo et al. (2000) note that grazing by large mammals was most prevalent in the *Paspalidium obtusifolium–Panicum repens* community in the floodplain they studied, in both wet and dry seasons, as *P. repens* responds to the advent of both local (summer) rain and winter floods.

Applicability of the classification

Perhaps the most difficult obstacle to overcome with regard to mapping and modelling vegetation distribution in large wetlands is accommodating the dynamics of composition. Remote sensing is often the approach of choice for mapping vegetation, given the constraints of access and size, but is itself constrained by cost, temporal, spatial and spectral limitations. McCarthy et al. (2005) identified 12 ecoregion classes in the Delta, based on remote sensing of seasonally flooded wetlands. They defined these in terms of gross vegetation structure, although they identified examples of key species. This classification was done at a pixel resolution of 28.5 m, which is well-suited to the grain of spatial variation in vegetation. They noted, however, that the 'class definitions are ambiguous, even if distinct species composition is suggested by Ellery and Ellery (1997) for example' (McCarthy et al. 2005: 4354). This inability to ascribe distinct species composition to spatially fixed 'ecoregion' classes arises because there is constant adjustment to hydrological variation: vegetation communities in pulsed wetlands are very seldom spatially static; likewise, geographic locations very seldom show stable plant species composition. The ecoregions that McCarthy et al. (2005) identified cannot be equivalent to vegetation communities; unless such ecoregion maps are produced on an annual basis from new data, they remain snapshots of a particular instant in the successional history of the vegetation in a particular location, and are essentially maps of physiography, or 'potential habitat'. Correlations must be sought between physiography, hydrological variation and floodplain species assemblages to accommodate the dynamic interactions between species composition and its drivers in order to maximise the utility of such remote sensing approaches.

Monitoring floodplain species composition through simplified ground survey requires only that a common classification system is employed. Describing and defining such classes is a vital step in mapping and monitoring change in the Okavango Delta, where national policies and international conventions mandate ecological monitoring, but the country lacks the capacity to do it (Jansen 2003). The knowledge required to recognise the few indicator species involved in classification is easily acquired; with two weeks of training, the field assistants involved in this field study became adept at the sampling methodology and identification of the most common species. It is likely, however, that a more economical method of sampling could be used, such as one large fixed quadrat, and repeated measures taken to observe trends.

Further applications of this classification system include its potential for use in the development of modelling applications for comparing, for example, the differences in distribution and extent of communities that might arise as a result of changes in hydroperiod. Class relationships with spatially defined hydrological parameters could be used as input to a spatial model, and these hydrological parameters manipulated to simulate the effects of climate change or human activities in the catchment.

Conclusions

This study has made possible a repeatable and relatively simple classification of seasonally-pulsed floodplains in the Okavango Delta based on the presence of different suites of indicator species and a dichotomous key. The classification can be used to map the extents and distributions of different floodplain classes to allow monitoring of change, and thus to inform management.

Analysing change in the strength of species indicator value and significance with changing number of classes provides a robust method for identifying an ecologically optimum number of classes and where to make further subdivisions.

Floodplain classes identified from quantitative analysis of frequency of occurrence data for herbaceous species correspond to some extent with earlier qualitative classifications, although indicator species identified in this study did not necessarily correspond with the dominant or conspicuous species used to define classes in earlier studies.

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Appendix: Vegetation survey site data

Site code	Coordinates: UTM Zone 34 S Datum WGS 84		Date completed	Locality name	Frequency stratum	Number of transects	Total number of quadrats	Number of core quadrats	Flood state at time of survey
	Easting	Southing							
BOB	724069	7825022	17 Apr 2007	Bobo	2	3	40	27	Dry
BOK	732931	7821944	16 May 2007	Bokoro	4	2	35	25	Wet
CHA	703725	7851938	13 Jul 2007	Chao	5	1	35	31	Wet
HBK	672444	7841718	12 Apr 2007	Horseback	3	1	33	28	Wet
IV2	725917	7825856	14 Mar 2007	Ivory 2	1	3	38	26	Dry
KIR	708023	7829330	28 Mar 2007	Kiri	3	5	38	18	Dry
KOA	728756	7821640	18 Apr 2007	Kolobahatse A	1	5	34	15	Dry
KOB	726729	7820543	19 Apr 2007	Kolobahatse B	1	4	38	22	Dry
KUA	736725	7808128	20 Apr 2007	Kunoga	3	4	37	21	Dry
MAM	684705	7822605	24 Apr 2007	Mamoxinxha	2	3	35	23	Wet
MAX	736266	7811652	03 May 2007	Maxhanasesunda	1	3	38	26	Dry
MIL	727828	7837924	25 May 2007	Nxaraga	3	3	30	28	Wet
MOC	689481	7863255	23 Mar 2007	Mombo central	5	3	33	22	Wet
MOM	688267	7871024	21 Mar 2007	Mombo	5	2	37	28	Wet
MOS	689680	7870351	22 Mar 2007	Mombo south	4	2	32	25	Wet
MPO	732434	7829186	17 May 2007	Moporota	5	3	35	23	Wet
NTS	724322	7838584	24 May 2007	Ntswi	4	3	39	27	Wet
NX1	689164	7841330	03 Apr 2007	Nxabega 1	5	3	36	24	Wet
NX2	688060	7839986	04 Apr 2007	Nxabega 2	5	3	36	24	Wet
NXA	727489	7836509	18 May 2007	Nxaraga	4	3	40	28	Wet
SEL	678014	7835038	11 Apr 2007	Selby	2	5	34	14	Dry
TSU	737079	7802066	04 May 2007	Tsutsubega	1	2	30	22	Dry
TSW	693444	7815862	25 Apr 2007	Tshwaramasepa	4	3	34	22	Wet
XAA	731970	7830521	23 May 2007	Xaa	4	5	37	18	Wet
XAN	708319	7840463	16 Mar 2007	Xaxaba north	2	2	39	31	Dry
XAS	708120	7837970	27 Mar 2007	Xaxaba south	2	2	37	29	Dry
XHA	697992	7802480	26 Apr 2007	Xhanyani	1	3	35	23	Dry
XUS	716610	7796727	10 May 2007	Xudum south	3	2	34	26	Wet
XWN	718409	7805718	08 May 2007	Xwaapa north	3	3	38	26	Wet
XWS	722345	7801062	09 May 2007	Xwaapa south	2	3	35	23	Dry