

Disaggregating Hydroperiod: Components of the Seasonal Flood Pulse as Drivers of Plant Species Distribution in Floodplains of a Tropical Wetland

Michael Murray-Hudson · Piotr Wolski · Frances Murray-Hudson · Mark T. Brown · Keotshephile Kashe

Abstract Wetland hydroperiod consists of different components, including frequency, duration and depth. A significant proportion of the seasonally flood-pulsed Okavango Delta is inundated for part of each year. Variation in hydroperiod, driven by the interaction of climate and ecological factors, results in a mosaic of vegetation communities. These communities are highly dynamic over temporal and spatial scales. This study aimed to identify quantitative relationships between hydroperiod components and floodplain vegetation, to better understand the potential effects of hydrological change. A stratified random sample of 30 floodplains was surveyed for species composition and abundance. Hydroperiod components for sample quadrats were estimated from remote sensing and field measurement. Ordination demonstrated strong correlations between species composition and flood frequency, duration, years-since-last-flood and depth. Eight statistically discrete vegetation communities were derived from cluster analysis. Generalized linear models of species distributions along hydrological gradients were used to derive frequency and duration optima. Means of these parameters differed significantly between communities. Increasing hydroperiod corresponded with a progression from grasslands through sedge-dominated to aquatic communities. Species in infrequently flooded areas indicated disturbance and a succession

trend towards open woodland. In the sedgeland, average depth was the strongest correlate, while in grasslands and aquatic communities, this was duration.

Keywords Wetland hydroperiod · Seasonal pulsing · Aquatic macrophytes · Flood frequency · Flood duration · Flood depth · Ordination

Introduction

Wetland hydroperiod is an intuitively simple concept which is remarkably difficult to define in strict terms: some practitioners define it for the purposes of their particular study as the duration of inundation in a given year (e.g., Crase et al. 2013; David 1996), while others try to incorporate the complexities that arise from seasonal, inter-annual and multi-decadal climate and hydrologic variation, and scale-dependent episodic events, to give a more general definition (e.g., Mitsch and Gosselink 2000). Such definitions must include the implicit effects of flood frequency (and its corollary, time elapsed since flooding occurred), duration and depth of inundation; they consequently need to be broad, such as that used by Nuttle (1997): “The pattern of water-level fluctuations in a wetland is its hydroperiod”. While these more general definitions are useful in that the temporal variation of hydroperiod is not lost, the different components of the concept – that is, frequency, time elapsed since previous flood, duration and depth – each have (sometimes subtly) different ecological effects.

Junk (2000) defines floodplains as complex dynamic systems of ecotones of different spatial and temporal scales, periodically crossed by a mobile ecotone, the moving littoral zone (the land-water boundary). The periodic inundations which occur in many tropical and subtropical wetlands are often relatively unimodal, being derived from strongly

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seasonal rainfall. They are also often of long duration and high amplitude, although in arid areas, many wetlands are ephemeral, and exhibit very large ranges of hydrologic variation and irregular inundation. Despite the variation, the flood regime in these systems may be the strongest factor affecting plant species richness, cover, and community composition (Capon 2005; Lenssen et al. 1999; Robertson et al. 2001; Bayley 1991). There is a large body of evidence that flood-pulsing is linked to high productivity and diversity (Junk and Piedade 1993; Brinson et al. 1981; Murphy et al. 2003), and that tropical wetland systems are well adapted to large variations as a result of the reproductive strategies and physiognomic characteristics of the plant species. Persistent, flood tolerant seed banks, the ability to reproduce both clonally and by seed, and to produce structure rapidly, typify tropical wetland plant communities (Alexander et al. 2008; Brock and Rogers 1998; Henry et al. 1996). Herbaceous wetland vegetation responses to hydrologic variation are usually relatively rapid (Junk and Piedade 1993; Junk 2002; Bagstad et al. 2005), since many plants have short life-cycles and many also may reproduce both from seed or clonally; as a result, the species composition is in a state of constant flux. Topographic gradients in wetlands often exhibit vegetation zoning, which is the response of the species pool to changing hydrology (Van Der Valk and Welling 1988); zones move with changing water levels (“mobile ecotones”). Niering (1987) suggests the term vegetative development for such compositional change, rather than succession. Our work suggests that in hydrologically dynamic tropical systems, vegetative adjustment may be a more appropriate term, as it lacks the directional implications of succession or development.

The floodplains of the Okavango Delta in northern Botswana (19°S, 23°E, Fig. 1) receive a large, essentially unimodal annual flood pulse, which because of the length and gradient of the catchment arrives during the dry season (March-May), and takes 3–4 months to traverse the system. The pulse surcharges the main channel and spreads out over a large alluvial fan which is a mosaic of islands and approximately 12,800 km² of wetlands, of which about 10,000 km² are seasonally inundated to varying degrees (Gumbricht et al. 2004). In addition to the inter-annual variation in pulse size and timing, Okavango Delta inflows exhibit multi-decadal sequences of relatively wetter or drier conditions (McCarthy et al. 2000; Mazvimavi and Wolski 2006). The periodicity of these sequences is in the order of 30 to 40 years. Of relevance to this study is the period 1989–2007; this period straddles the change from a multi-decadal drying phase, through the lowest flow on record in 1996, into a wetting phase from 1997 to the present. The inflow in 2011 was the fourth largest on record, while that in 2007, the year of the survey, was in the top 25th percentile (it exceeded 79 % of recorded inflows).

Seasonal floodplains in the Delta exhibit conspicuous vegetation zoning, and obvious compositional changes with

lateral and downstream distance from water sources. While the hydrology is relatively well understood (Wolski and Savenije 2006; Bauer et al. 2003; Wolski et al. 2006; Wilson and Dinçer 1976), the relationships between plant species composition and hydrology have not previously been quantified, although some qualitative descriptions have been made (e.g., Smith 1976). This is considered essential information for the development of management tools, and also for policy development for the Delta and other wetlands in Botswana (National Conservation Strategy Agency 2000). The need for such tools and for science to guide policy in this system is becoming increasingly urgent, as development pressures increase in the Okavango basin, which links three sovereign states, two of which have very limited water sources (Ashton and Neal 2003). In addition, the Delta thus far has not been affected by major anthropogenic impacts, and represents one of the few large open wetland ecosystems which are relatively untransformed globally. In this, it offers a rare opportunity to study wetland ecological processes away from the confounding influences of human activities.

This study investigated plant species distribution in relation to hydrological parameters in floodplains where the effects of pulsing are most strongly manifested, the Boro-Xudum distributary (Fig. 1), based on a field survey, and remote-sensing derived hydrological history. The aim was to identify which components of hydroperiod best explained compositional variation in the vegetation communities of these seasonal floodplains. Since different floodplains, and parts of floodplains, experience different degrees of inundation under a given flood pulse, we sought answers to the questions:

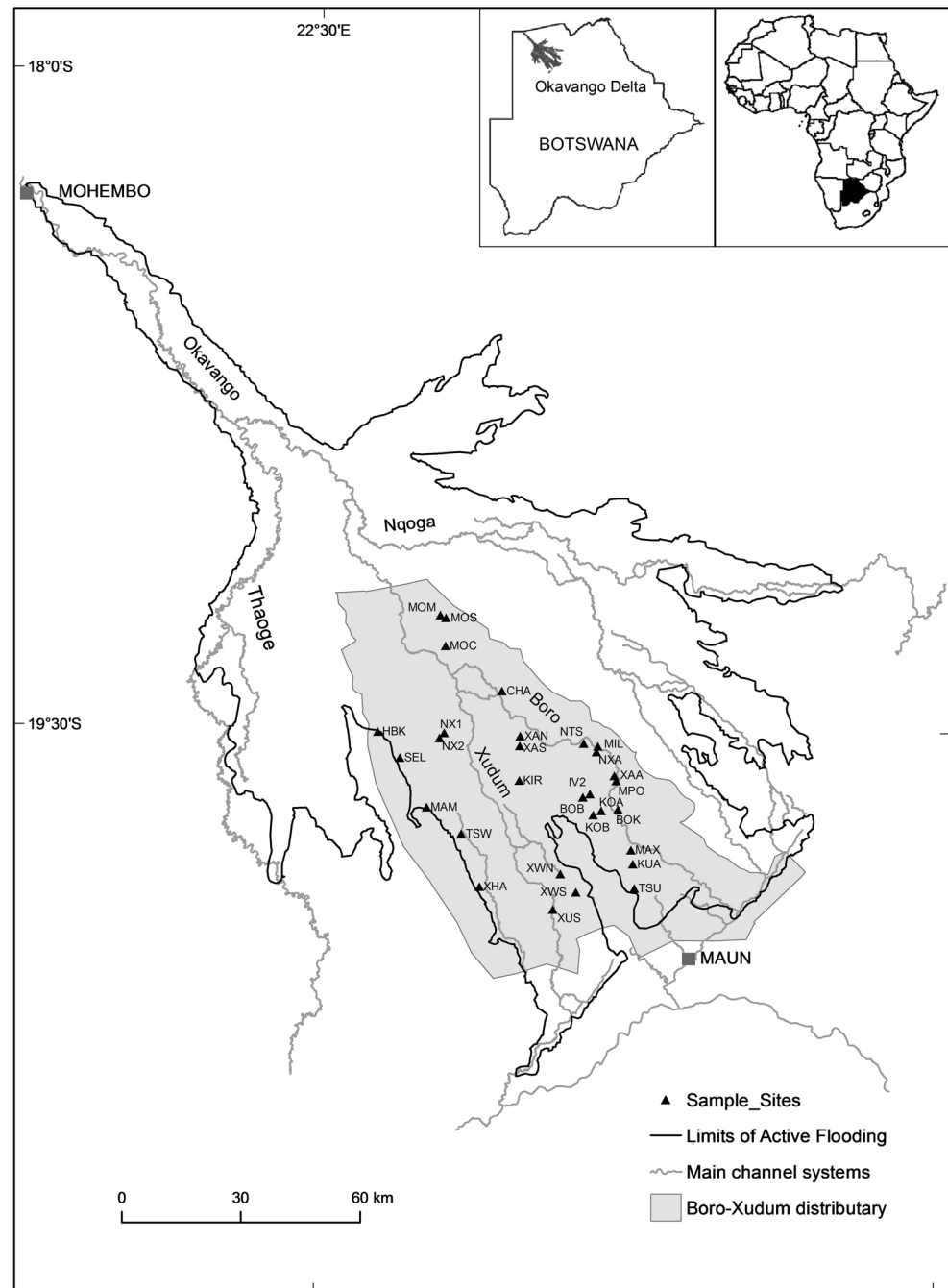
1. How are annual inundation frequency, intra-annual inundation duration and depth related in the seasonally pulsed parts of the Delta?
2. What are the relationships between these variables and species composition of floodplain macrophytes?
3. Are these relationships different at the scales of distributary to those at the scale of individual floodplains?

Methods

Hydrological Variables

Flood duration (hereafter, “dur”, the average number of months of inundation over the preceding 3, 4 and 7 years) in months was derived from an 8-year time series of MODIS (Moderate Resolution Imaging Spectroradiometer) imagery (spatial resolution 250 m) (Murray-Hudson et al. 2014),

Fig. 1 The study area, showing the Boro and Xudum distributaries, and the sample sites



while annual frequency (“frq”, the average of the proportion of 18 years that each quadrat at a site was inundated) and years elapsed since last flood (“ysl”) were derived from an 18-year record of Landsat TM imagery (spatial resolution 28.5 m) (Wolski and Murray-Hudson 2006). That study developed a routine for discriminating floodplain vegetation from active riparian vegetation, and for distinguishing dry and wet fire scars, through interpretation of Landsat images of annual maximum flood extent in the year 2002 against a reference set of 1:50,000 scale analogue aerial photography.

This allowed the identification of areas not prone to flooding in the medium to long term (notably riparian woodland), as well as an objective system for mapping annual maximum flood extent in a time-series of Landsat images from 1989 to 2007.

Water depth was recorded for those quadrats which were wet at the time of survey (1–4 months prior to peak flood) for each quadrat. Depth here is the average derived from multiple quadrats at each flooded site (17 of the 30 sites were flooded at the time of sampling). It does not represent the realized long

term average, nor the potential maximum depth, because the field campaign was carried out while the flood pulse was rising.

Vegetation Sampling

Floodplains in the Boro-Xudum distributary were divided into 5 frequency strata of approximately equal area (Table 1), based on historic flood frequency derived from Landsat imagery (Wolski and Murray-Hudson 2006), and 6 sites were randomly selected within each stratum using the ERDAS Imagine 9.1 clump routine (Leica-Geosystems 2006) and a random number generator. Sites were surveyed between March and June 2007. Species composition and relative abundance was sampled along transects oriented orthogonally to the long axis of the floodplain, using 1 m² quadrats spaced 20 m apart; geographic coordinates for each quadrat were recorded in the field. Transects traversed floodplains between island margins, starting and ending at the nearest mature (>4 m high) tree to the floodplain. Species area-curves from a preliminary survey (2006, unpublished data) were used to determine the required sample area as ≥ 25 m². Transect length varied with the dimensions of each floodplain, and so the number of transects at each site was increased until a minimum of 25 quadrats had been surveyed.

Species were identified in the field where possible; samples of unidentifiable plants were pressed in the field; those which could not be identified from the Peter Smith Herbarium collection at the Okavango Research Institute were identified by the Royal Botanic Gardens at Kew, England. Nomenclature follows Germishuizen and Meyer (2007). Species life-cycle attributes (life-span, growth form, reproductive strategy) were derived from the literature, primarily Snowy Mountains Engineering Corporation (1989), Conservation International (2003), Germishuizen and Meyer (2007), and the FAO Grassland Species database (2009).

Table 1 Areas of flood frequency strata used in sample site selection. Frequency classes were grouped to maximize similarity of area

Stratum	Number of pixels	Area km ²	Frequency class groups
1	1302836	1,058.2	1
2	1063578	863.9	2–3
3	1283557	1,042.6	4–7
4	1456122	1,182.7	8–12
5	1065975	865.8	13–14

Analysis

Species data were summarized for each sample site by the proportion of quadrats in which they were present; this metric is the relative frequency, and values were not transformed. Inter-species relationships were investigated using agglomerative cluster analysis to define floodplain vegetation communities (used here in the sense of the collection of plant species occurring in one place at one time), based on the 52 species occurring in more than 5 sites; this cut-off was selected to ensure that the most common species were used to characterize floodplain communities. Within-group and pairwise similarities for communities identified were tested with the multi-response permutation procedure (MRPP) in PCOrd v5.1 software (McCune and Mefford 2006).

To investigate patterns of species distribution in relation to flooding parameters, two separate approaches to ordination were carried out. The primary matrix was a 52 species by 30 site matrix, using only data from quadrats which were more than 40 m from island margins, while the environmental matrix was 30 sites with average flood frequency, mean flood duration of the 3, 4 and 7 preceding years, years since last flood, and average water depth in 2007. The two approaches were as follows:

- a) The first approach used non-metric multidimensional scaling (NMS) (Mather 1976; Kruskal 1964; McCune and Mefford 2006), which makes no assumptions of linear relationships among variables, but tends to linearize relationships between species space and environmental space. Sorensen distance was used with random starting configurations, and 250 runs each of real and randomized data; a 2 dimensional solution was selected from the rate of change in stress. This technique was used to investigate relationships between species and sites, and to derive a set of site classes based on hydroperiod;
- b) The second approach used canonical correspondence analysis (CCA) on the same data set; this procedure constrains the ordination by a multiple regression on environmental variables. The ordination was centered with unit variance to allow interpretation of fitted species abundances, with scaling to optimize species distances, and site scores derived from species (to get the best approximation of chi-squared inter-species differences). CCA was used to investigate the relationship of community structure and species distribution to a small set of hydrological variables. The strength of this relationship was tested against a multiple (Monte Carlo) randomization of the full dataset. Individual species distribution relationships with frequency and duration were derived subsequently from CCA ordination against these two

variables separately. Probabilistic species distribution parameters along these hydrological gradients were estimated using generalized linear models (GLMs) based on Gaussian logistic regression (Ter Braak and Looman 1986). This approach assumes a unimodal bell-shaped response curve, and allows the derivation of species optimum values (the value of the environmental variable at which the probability of occurrence is highest), tolerance (a measure of ecological amplitude, related to the breadth of the bell curve), and the maximum probability of occurrence. Distribution curves were generated from CANOCO v5.54 (Ter Braak and Smilauer 2006). One of the drawbacks with this method is that species whose optima lie outside the sampled range of the independent variable are not well modeled. In this study, species whose modeled flood duration optima were estimated at >12 months were set to 12 months, and those (dryland species) whose optima were <0 were set to 0; similar thresholds were imposed for distributions with annual flood frequency at 0 and 18.

This second approach was used to relate the communities identified through cluster analysis to inundation duration, and then to seek differences in relationships between community composition and the separate components of hydroperiod, frequency, years-since-last flood, duration and depth through a progressive reduction of the dataset. Further ordination and cluster analysis was carried out on two intermediate frequency and duration groups, (as determined from cluster analysis, see results section and Fig. 4), separately but based on the full complement of quadrats (i.e., including those quadrats within 40 m of island margins).

Results

Sites

The sites and their environmental characteristics are described in [Appendix 1](#).

Table 2 Correlations between hydrological variables

Variable	Average frequency	Average duration	Years since last flood	Average depth
Average frequency	1			
Average Duration	0.909	1		
Years since last flood	-0.617	-0.706	1	
Average depth	0.727	0.609	-0.335	1

Hydrology

The hydrological variables are strongly co-linear (Table 2). Thus floodplains (or parts of floodplains) which are more frequently flooded tend to be flooded for longer, with greater average depth.

Hydrology-Vegetation Relationships

The initial NMS ordination of the full dataset (Fig. 2) shows strong relationships between species composition and three hydrological variables (Table 3): 18-year average frequency (frq), 3-year average monthly duration (dur), and the number of years since last flood (ysl). Long-term flooding frequency is the strongest predictor of species composition for the full dataset. Different lengths (3, 4 and 7 years) of antecedent duration record were initially tested; the strongest correlation was found with an average of the 3 preceding years (coefficients of 0.74, 0.69 and 0.67 respectively). A weaker correlation was found with depth; since the survey was undertaken prior to the flood peak, while flood waters were still rising, this parameter is not a particularly robust variable.

The classes of sites in Fig. 2 are derived from agglomerative cluster analysis of sites in species space. They are, in order of increasing hydroperiod: Intermittently flooded, Regularly flooded short duration, Medium duration seasonally flooded, and Long duration seasonally flooded. The Intermittently flooded class on the far left (○) is strongly separated from the other sites, and is comprised of floodplains which have only received water in the very highest floods of the last 2 decades.

Cluster analysis of the 52 most common species (those occurring at more than 5 sites) illustrates 8 communities (Fig. 4). In order of increasing duration optima, these are: Dry Floodplain Grassland (DFG), Occasionally Flooded Grassland (OFG), Seasonally Flooded Grassland Margins (SFGM), Seasonally Flooded Grassland (SFG), Seasonally Flooded Sedgeland (SFS), Sedge Meadow (SM), Aquatic Community Margins (ACM) and Aquatic Community (AC). The ranges of inundation duration optima for the different groups are shown on each major branch. MRPP tests (Sorensen distance, flexible $\beta=0.25$) on all cluster-defined

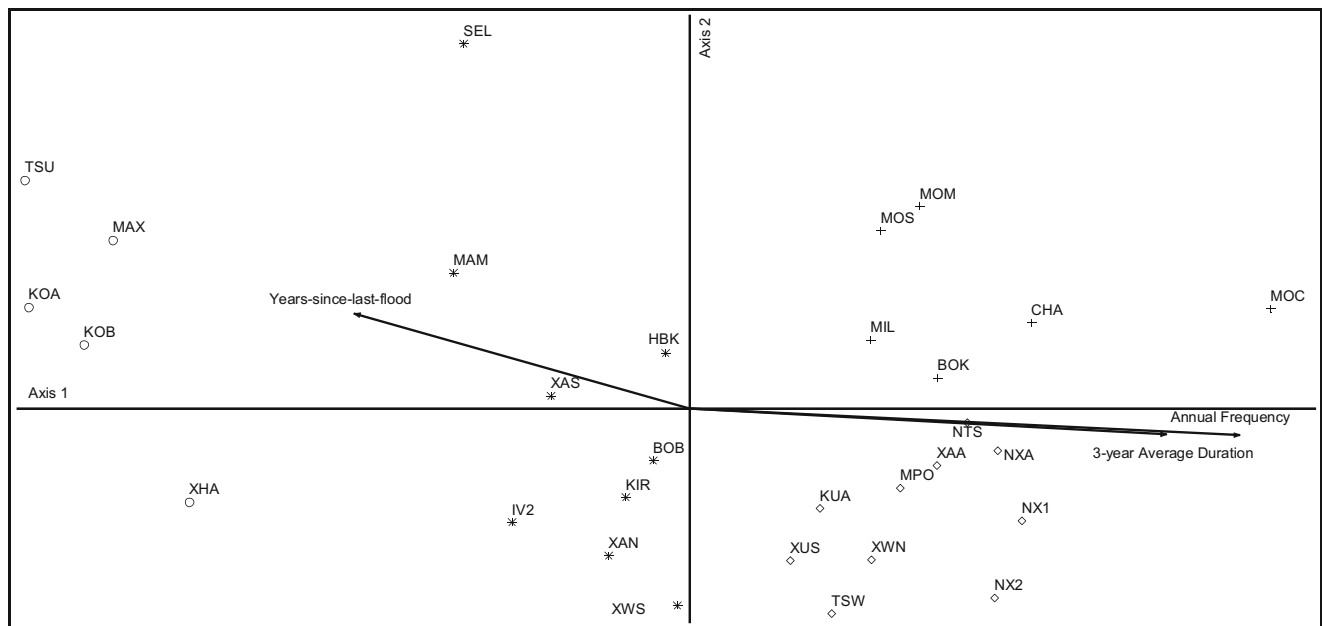


Fig. 2 Non-metric multi-dimensional scaling (NMS) ordination biplot of 30 sites against 52 species (species occurring in >5sites only), showing 4 major site classes (Intermittently flooded ○, Regularly flooded short duration *, Medium duration seasonally flooded ◇, and Long duration

seasonally flooded +) with long-term flood frequency, mean flood duration and time since last flood. Hydrological variables are indicated by arrows in the direction of increase

communities showed significant differences ($p < 0.001$); pairwise testing for difference between these 8 communities was also significant ($p < 0.05$). Descriptive names (ellipses) on the dendrogram branches interpret information on habitat preference for the 8 communities.

The differences between average duration optima for communities were significant ($p < 0.05$) at all levels tested, as were those of frequency optima. Among the 8 communities, average duration tolerance (as determined from the GLMs) margins were different at $p = 0.08$, indicating that the breadth of tolerance ranges is not very different between these communities. The lowest tolerance was in the DFG community, and this contributes most of the difference between communities at this level of clustering; exclusion of this group reduces the probability of significance to $p = 0.24$.

Table 6 lists the main life-cycle characteristics, and the hydrological parameters estimated from generalized linear

models, for all species occurring in more than 5 sites. Half of the species found in drier floodplains (frequency <20 %, duration <2 months) are annuals which propagate by seed; of these, about half exhibit graminoid and half herb growth form. As flood frequency and duration rises, the proportion of clonal perennials rises, as does the proportion of graminoid species, until frequency reaches about 80 %, when perennial aquatic herbs start to appear. An exception here is the perennial herb *Cycnium tubulosum*, which is a conspicuous component of the sedge meadow community (Fig. 4), where the mean frequency of inundation is only 67 %.

Hydroperiod Components as Drivers of Species Distribution

The next step in analysis was to seek differential effects between drivers. The effects of the ysl variable on species-distance relationships between sites is more evident when the

Table 3 Pearson correlation coefficients between NMS ordination axes and hydrological variables. The ordination was carried out on a 30 site by 52 species matrix

Axis:	1	2
Hydrological variable	r^2	r^2
Frequency	0.829	0.001
Average Duration	0.736	0.002
Years since last flood	0.589	0.097
Average depth of wet quadrats	0.46	0

data are subjected to CCA, which constrains the ordination with the environmental variables (Fig. 3), and like the NMS, indicates three distinct drivers: dur and frq, and ysl. Note the near-orthogonal relationship between the five labeled sites (which have not been flooded for at least 2 years) and the remainder. When these sites are removed from the dataset, the change in the correlations between species composition and environmental variables (Table 4) is marked; the simplified structure of ordination space results in a stronger primary relationship with frequency, and the co-linear relationship between frequency and duration is also clear. Table 5 gives the strengths of the relationship between species and hydroperiod (H_0 : no linear relationship). NMS analysis of sites dominated by SFG, SFG and AC communities shows clear differences in the strengths of effect of the different components of

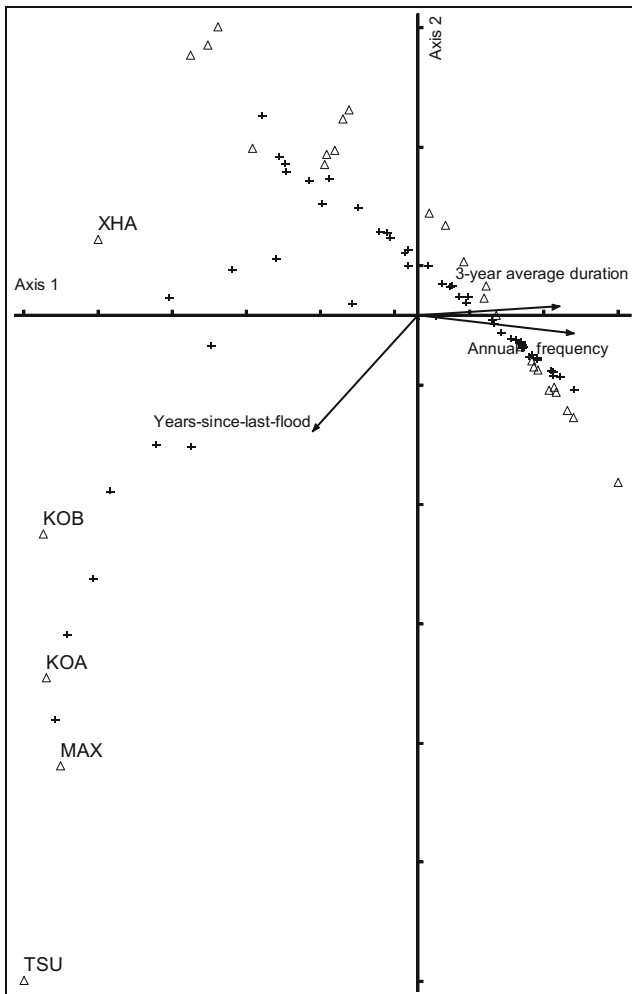


Fig. 3 CCA ordination joint plot of 30 sites and 52 species (species occurring in >5 sites only); scores are linear combinations of the hydrological variables. Hydrological variables are indicated as arrows, sites as Δ , and species as +. A clear distinction exists between regularly flooded sites (unlabeled) and sites in which dryland succession is occurring (labelled, along the left side of the plot)

Table 4 Comparison of Pearson correlation coefficients between site hydrological variables and CCA ordination axes for all sites ($N=30$) and for regularly flooded sites with <2 years since last flood ($N=25$)

Data set	Axis: Hydrological Variable	1 r^2	2 r^2	3 r^2
N=30	Frequency	0.743	0.192	0
	Average Duration	0.738	0.061	0.094
	Years since last flood	0.791	0.148	0
N=25	Frequency	0.998	0	0.003
	Average Duration	0.735	0.320	0

hydroperiod on species composition (Table 7). In SFG communities, duration is the strongest driver, with much weaker effects from years-since-last-flood and frequency; in SFS communities, average depth is the strongest driver, followed by duration, while in AC communities, duration again appears as the strongest, but is closely followed by frequency and depth.

Analyzing intra-community species distributions provides some insight into composition variation and overlap. Within the larger groups of intermediate hydroperiod floodplain communities (SFG including SFGM, and SFS), analysis of full transect data (i.e., including quadrats within 40 m of island margins) indicates that there are distinct “floodplain margin” communities of species which occupy the higher elevation floodplain zones in proximity to islands (Figs. 5 and 6). The margin community of floodplains which are dominated by SFS communities has a broad composition, with few flood-intolerant species; it includes many sedge and grass species which have a preference for short duration flooding. It is similar in composition to the sedge meadow community and the seasonally flooded grassland margins community (Figs. 4 and 5). Similarly, in floodplains dominated by SFG communities, the marginal (SFGM) community has species in common with DFG communities (Figs. 4 and 7). Both

Table 5 Monte Carlo Test Results – CCA Species-Environment Correlations for regularly flooded sites ($N=25$). Environmental variables are 18 year mean flood frequency and 3 year average flood duration

Axis	Real Data R^2	Randomized Data, 998 runs			
		Mean	Min	Max	p^a
1	0.910	0.687	0.492	0.874	0.001
2	0.739	0.652	0.427	0.892	

^a p =proportion of randomized runs with species-environment correlation greater than or equal to the observed species-environment correlation: i.e., $p=(1+\text{no. permutations} \geq \text{observed})/(\text{no. permutations} + 1)$; p is not reported for axis 2 because using a simple randomization test for this axis may bias the p values

Table 6 Life cycle characteristics and hydrological controls of species occurring in more than 4 sites

Code	Species	Life span ¹	Growth form ¹	Reproduction ¹	Optimum Frequency (% of years)	Optimum duration (months)	Tolerance (months)	Main community
Kohvir	<i>Kohautia virgata</i> (Willd.) Bremek.	A (p)	H	Seed	0.0	0	6.5	OFG
Eracyl	<i>Eragrostis cylindriflora</i> Hochst.	A	G	Seed	1.1	1	3.6	OFG
Uromos	<i>Urochloa mosambicensis</i> (Hack.) Dandy	P	G	Seed/ Clonal	5.8	0	2.1	DFG
Ipocop	<i>Ipomoea coptica</i> (L.) Roth ex Roem. & Schult.	A	H	Seed	7.3	0	3.2	OFG
Stiuni	<i>Stipagrostis uniplumis</i> (Licht.) De Winter	P (a)	G	Seed/ Clonal	7.5	0	2.1	DFG
Gisafr	<i>Gisekia africana</i> (Lour.) Kuntze	A (p)	H	Seed	7.9	0	2.3	DFG
Vergla	<i>Vernonia glabra</i> (Steetz) Vatke	P	H	Seed	9.1	3	4.2	OFG
Cyndac	<i>Cynodon dactylon</i> (L.) Pers.	P	G	Clonal/ Seed	12.0	1	4.7	OFG
Berpen	<i>Bergia penteriana</i> Keissl.	P	H	Seed	13.9	1	2.7	OFG
Digdeb	<i>Digitaria debilis</i> (Desf.) Willd.	A	G	Seed	18.9	1	2.8	OFG
Abihis	<i>Abildgaardia hispida</i> (Vahl) Lye	A	G	Seed	36.1	3	8	SFG
Cyplon	<i>Cyperus longus</i> L.	P	G	Clonal/ Seed	37.5	6	5.4	SM
Digeri	<i>Digitaria eriantha</i> Steud.	P	G	Seed	37.7	4	3	SFGM
Eralap	<i>Eragrostis lappula</i> Nees	P	G	Seed	39.2	3	2.6	SFG
Niccos	<i>Nicolasia costata</i> (Klatt) Thell.	P	H	Seed	39.2	3	2.4	SFG
Cypsph	<i>Cyperus sphaerospermus</i> Schrad.	P	G	Clonal/ Seed	41.1	3	3	SFG
Sorfri	<i>Sorghastrum friesii</i> (Pilg.) Pilg.	P	G	Clonal/ Seed	44.8	4	2.7	SFG
Traspi	<i>Trachypogon spicatus</i> (L.f.) Kuntze	P	G	Seed	46.0	4	2.9	SFG
Nidres	<i>Nidorella resedifolia</i> DC.	A	H	Seed	48.2	4	2.5	SFGM
Spospi	<i>Sporobolus spicatus</i> (Vahl) Kunth	P	G	Clonal/ Seed	50.0	4	6.8	SFGM
Impcyl	<i>Imperata cylindrica</i> (L.) Raeusch.	P	G	Clonal/ Seed	50.0	8	5.7	SM
Brahum	<i>Brachiaria humidicola</i> (Rendle) Schweick.	P	G	Clonal/ Seed	50.7	4	4.9	SFG
Setsph	<i>Setaria sphacelata</i> (Schumach.) Stapf & C.E.Hubb. Ex M.B.Moss	P	G	Clonal/ Seed	53.1	5	3.6	SFG
Passcr	<i>Paspalum scrobiculatum</i> L.	P	G	Clonal/ Seed	54.1	5	2.9	SFGM
Panrep	<i>Panicum repens</i> L.	P	G	Clonal/ Seed	63.6	6	3.8	SFS
Eraina	<i>Eragrostis inamoena</i> K.Schum.	P	G	Seed/ Clonal	73.5	8	4.4	SFS
Cypden	<i>Cyperus denudatus</i> L.f.	P	G	Clonal/ Seed	74.3	7	4	SFS
Fuiumb	<i>Fuirena umbellata</i> Rottb.	P	G	Clonal/ Seed	77.2	7	3.2	SM
Fimcom	<i>Fimbristylis complanata</i> (Retz.) Link	P	G	Clonal/ Seed	77.2	8	4.1	SM
Cyctub	<i>Cyrtium tubulosum</i> (L.f.) Engl.	P	H	Seed	79.2	8	3.3	SM
Cypart	<i>Cyperus articulatus</i> L.	P	G	Clonal/ Seed	79.5	8	3.2	SFS
Rhyhol	<i>Rhynchospora holoschoenoides</i> (Rich.) Herter	P	G	Clonal/ Seed	79.5	8	4.1	SFS
Pycnit	<i>Pycnopus nitidus</i> (Lam.) J.Raynal	P	G	Clonal/ Seed	80.1	8	3.3	ACM
Fuipub	<i>Fuirena pubescens</i> (Poir.) Kunth	P	G	Clonal/ Seed	80.5	7	3.7	SM
Misjun	<i>Miscanthus junceus</i> (Stapf) Pilg.	P	G	Seed	83.0	8	3	ACM

Table 6 (continued)

Code	Species	Life span ¹	Growth form ¹	Reproduction ¹	Optimum Frequency (% of years)	Optimum duration (months)	Tolerance (months)	Main community
Leehex	<i>Leersia hexandra</i> Sw.	P	G	Clonal/Seed	83.9	8	3.1	SFS
Digeyl	<i>Digitaria eylesii</i> C.E.Hubb.	P	G	Clonal/Seed	85.7	9	3.7	ACM
Burenn	<i>Burnatia enneandra</i> P.Micheli	P	H	Clonal/Seed	85.7	9	3	ACM
Sldre	<i>Scleria dregeana</i> Kunth	P	G	Clonal/Seed	85.7	9	3.1	ACM
Acrmac	<i>Acroceras macrum</i> Stapf	P	G	Clonal/Seed	86.6	8	3.3	SFS
Schcor	<i>Schoenoplectus corymbosus</i> (Roth ex Roem. & Schult.) J.Raynal	P	G	Clonal/Seed	88.5	8	4.6	SFS
Utricsp	<i>Utricularia</i> sp.	P (a)	H	Clonal/Seed	88.6	9	3.1	ACM
Orylon	<i>Oryza longistaminata</i> A.Chev. & Roehr.	P	G	Clonal/Seed	89.2	8	3.6	SFS
Elevar	<i>Eleocharis variegata</i> (Poir.) C.Presl	P	G	Clonal/Seed	91.2	8	3.2	SFS
Nymnou	<i>Nymphaea nouchali</i> Burm.f.	P (a)	H	Clonal/Seed	91.6	9	3.2	AC
Sactyp	<i>Sacciolepis typhura</i> (Stapf) Stapf	P	G	Clonal/Seed	91.9	9	3.3	SFS
Ludsto	<i>Ludwigia stolonifera</i> (Guill. & Perr.) P.H.Raven	A (p)	H	Seed/Clonal	100.0	9	9.3	AC
Nymind	<i>Nymphoides indica</i> (L.) Kuntze	P	H	Clonal/Seed	100.0	10	3.2	AC
Potthu	<i>Potamogeton thunbergii</i> Cham. & Schltld.	P	H	Clonal/Seed	100.0	11	4.3	AC
Pasobt	<i>Paspalidium obtusifolium</i> (Delile) N.D.Simpson	P	G	Clonal/Seed	100.0	12	4.2	AC
Eleacu	<i>Eleocharis acutangula</i> (Roxb.) Schult.	P	G	Clonal/Seed	100.0	8	3.9	AC
Eledul	<i>Eleocharis dulcis</i> (Burm.f.) Trin. ex Hensch.	P	G	Clonal/Seed	100.0	12	4.4	AC

¹ Data source: Germishiuzen and Meyer, 2007. *A* annual, *P* perennial, *A(p)* annual, sometimes perennial, *P(a)* perennial, sometimes annual; *G* graminoid (includes sedges), *H* herb

marginal communities also include a number of woody species, as shrubs (9 in the SFS and 5 in the SFGM).

Discussion

The co-linearity between hydrological variables reflects the hydro-geomorphological character of the Delta, in which topographic gradient is sufficiently low that the water surface gradient is effectively the same, and local floodplain-dryland relief differences are seldom greater than 2 m (Gumbrecht et al. 2004). The strong correlations found between these variables and species distributions indicate that hydrological variation indeed does exert a powerful and somewhat predictable influence on plants in

the seasonal floodplains. The multi-decadal sequences of wetter and drier years identified by Mazvimavi and Wolski (2006) will function to increase the relative flooding frequency during wetter and decrease it during drier sequences. The period 1989–2007 was thus characterized by a decreasing (1989–1996), then an increasing frequency (1996–2007). This may be the underlying reason that frequency was the strongest correlate with species composition.

This study found a clear distinction between communities of floodplains which had not been inundated for several years, and those which receive regular flooding under present hydrological circumstances, a finding corroborating that of Heintz et al. (2007). Once flooding drops below a threshold frequency (estimated as 20 %, or longer than 3 years without inundation, from Table 6), soil

Table 7 NMS Pearson correlations with hydrological variables for a) seasonally flooded sedgeland sites; b) seasonally flooded grasslands; c) seasonal aquatic communities. In a) and b), 2 ordination dimensions produced least stress in the data; 3 were required in c)

Axis:	1	2	3
Hydrological variable	r ²	r ²	r ²
a) Seasonally flooded grassland (9 sites, 43 spp)			
3-year Average Duration	0.358	0.077	–
Years since last flood	0.04	0.067	–
18-year Frequency	0.0004	0.005	–
b) Seasonally flooded sedgelands (10 sites, 53 spp)			
Average depth of wet quadrats	0.834	0.009	–
3-year Average Duration	0.307	0.408	–
18-year Frequency	0.037	0.342	–
c) Seasonal aquatic communities (6 sites, 32 spp)			
3-year Average Duration	0.267	0.546	0.009
18-year Frequency	0.066	0.461	0.006
Average Depth of wet quadrats	0.024	0.396	0.016

moisture is apparently insufficient to maintain wetland plant communities, and a successional trend is started towards open savanna woodland. The early stages of this succession are characterized by pioneer species such as *Pechuel-Loeschia leubnitziae*, *Pogonarthria squarrosa* and *Urochloa mosambicensis*. The later stages show woody species establishment as well. In this study, sites which received floods only in higher inflow years ranged in ysl from 18 through to 8 (KOA, KOB, MAX, TSU, Fig. 1). In these sites, shrub and shrub/tree species become established (e.g., *Acacia erioloba*, *Combretum imberbe*). Under renewed flooding, these opportunists will effectively be forced out, and a seasonally flooded grassland community develops. Personal observations (MM-H) from more distal parts of the Delta outside of our survey area indicate that *Acacia tortilis* is also a pioneer woody species on floodplains which have been dry for several years. Re-flooding by the large inflows of 2010 and 2011 resulted in very extensive mortalities of trees on these wooded relict floodplains. At this low frequency (<1 in 7 years), the flood pulse represents a major disturbance, and resets the dryland succession each time it occurs, opening them up to re-colonization by initially wetland, and eventually dryland species. The longevity of Delta wetland species propagules under prolonged dry conditions is unknown, although seed bank experiments in South Africa (Brock and Rogers 1998) have shown staggered germination of wetland species from an ephemeral wetland after a 5 year dry period in response to 2 wetting cycles; longer survival than 5 years is considered likely for both seed and clonal plants in

Delta conditions. In addition, rising floodwater is likely to carry with it seeds from upstream plants, so recruitment of water-adapted plants is likely to be relatively rapid.

Effects of the flood pulse at sites of intermediate levels of frequency and duration are not as distinct, although there are clear differences in species composition. The majority of species are grasses or sedges - emergent flood-tolerant (to varying degrees) plants. Most of the grasses in the seasonally flooded grassland communities (duration range 3.8–4.7 months) are tuft-forming perennials; these rely predominantly on seed for dispersal, although individual plants may live for several years (Germishuizen and Meyer 2007). In the seasonally flooded sedgelands, where duration is 4.7–6.3 months, all the main species are rhizomatous perennials (although most produce seeds as well). Few species have duration optima between 6 and 7 months; those that do tend to have broad tolerance ranges (e.g., *Brachiaria humidicola*, *Panicum repens*); instead these intermediate-hydroperiod communities are characterized by an admixture of flood-intolerant species, which are found on the ecotones between the floodplain core and island dryland communities, and flood-tolerant species which inhabit the core zone itself.

When species composition of classes of sites is related to hydroperiod components, separately, some discrimination of main effects appears to be possible (Table 7); in sites dominated by SFG, SFS and SAC, the overriding strength of frequency as a driver is replaced by a stronger response to duration (SFG and SAC), and depth (SFS). These latter variables function at the level of individual plant ecology and physiology, while long-term frequency is an integration of the long-term hydrological characteristics of Delta floodplains. In the case of the AC communities, longer duration of inundation probably helps the hydrophytes by excluding competition from species less tolerant of flooding, while in the SFG communities, species with higher water demands are favoured by short-duration flooding over dryland species. The sedgelands (SFS) are adapted to seasonal periods of wet and dry, and depth is likely to affect composition through the specific morphological and physiological adaptations of species to inundation.

Figures 5 and 6 show that there is overlap in species composition between drier zones (margins, more elevated sections) of SFS floodplains and SFG core communities; similar overlap occurs between SAC margins and SFS core communities. These results suggest that in all floodplains with intermediate flooding, similar collections of species will be found, with relative abundances reflecting the current short-term hydroperiod of the particular elevation zone within the floodplain. Proportions change as duration and depth change, and different optima are reached or tolerances exceeded. The time-scale for such adjustment will depend on the relative growth rates of the species, but the fact that an average of

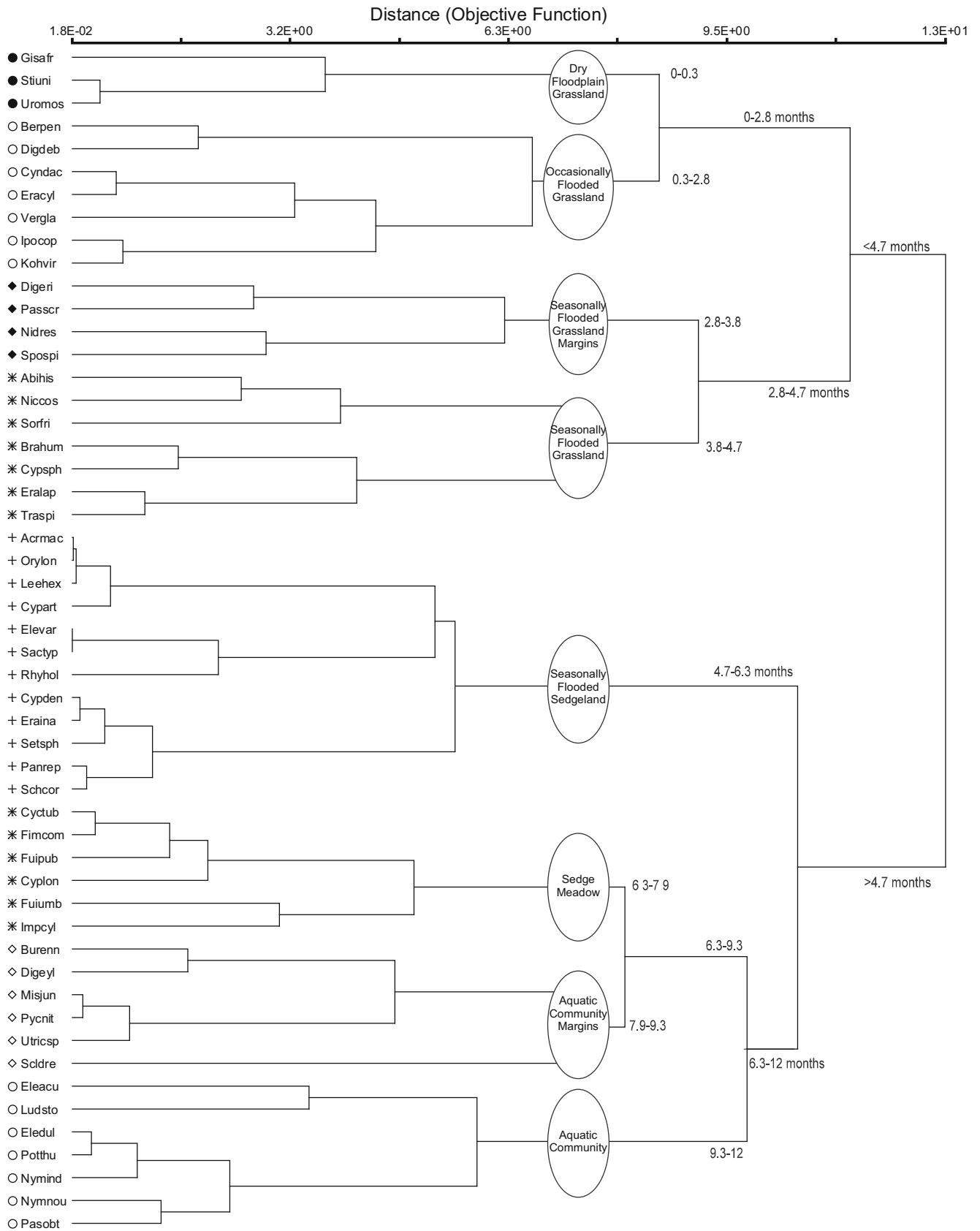


Fig. 4 Dendrogram of species communities based on those species occurring in more than 5 sites. Ranges of duration optima (numbers on branches – all in months) characterize 8 distinct assemblages. Six-letter

species codes are used for brevity; full species names, optima and tolerance ranges, and life cycle data are given in Table 6

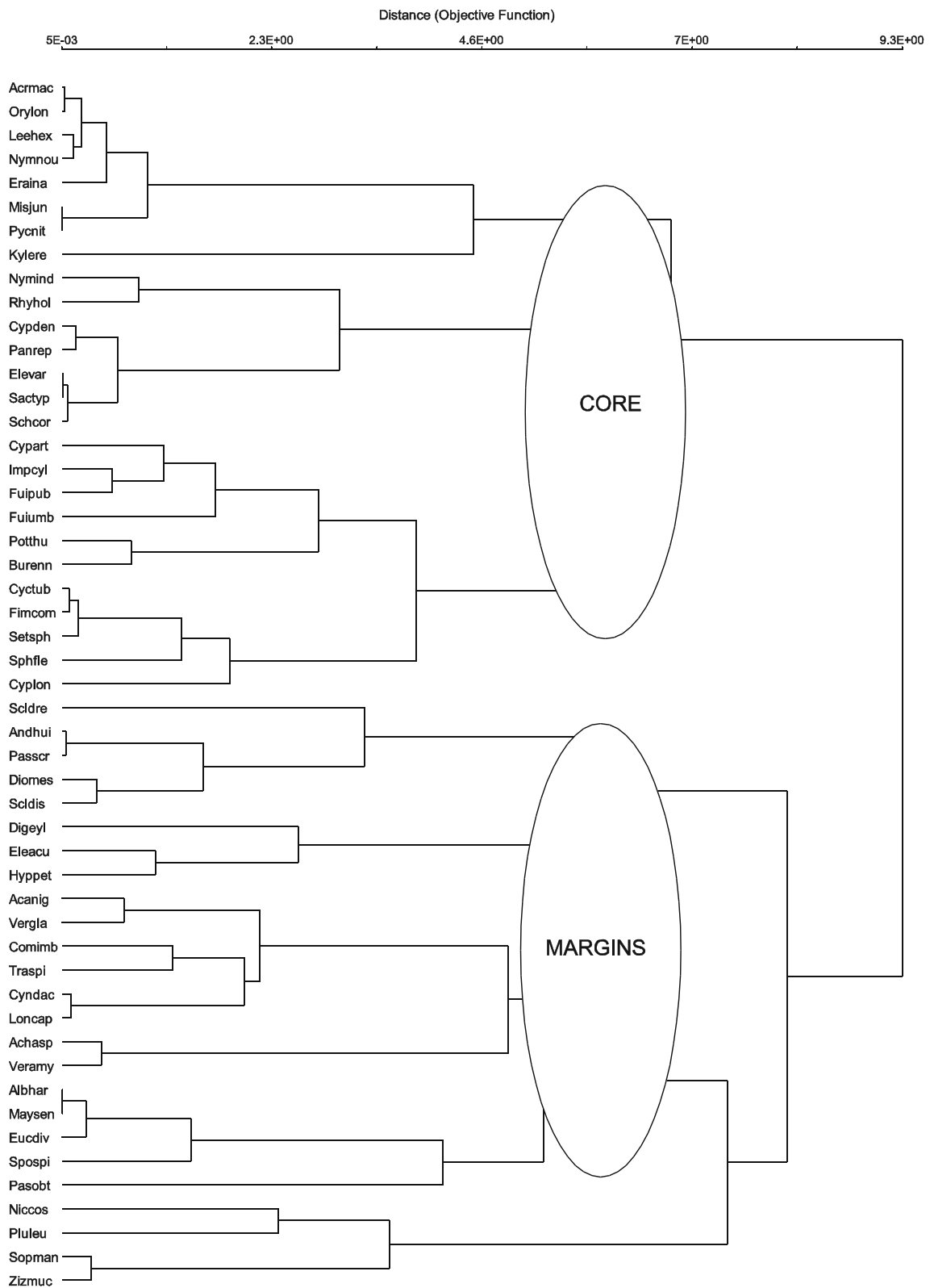


Fig. 5 Dendrogram showing species groupings from entire transects in seasonally flooded sedge floodplains (SFS - N=10). Core species are those that occur in the main body of the floodplain, >40 m from island

perimeters, and margin species are those that occur in the 40 m zone between island perimeters and the core

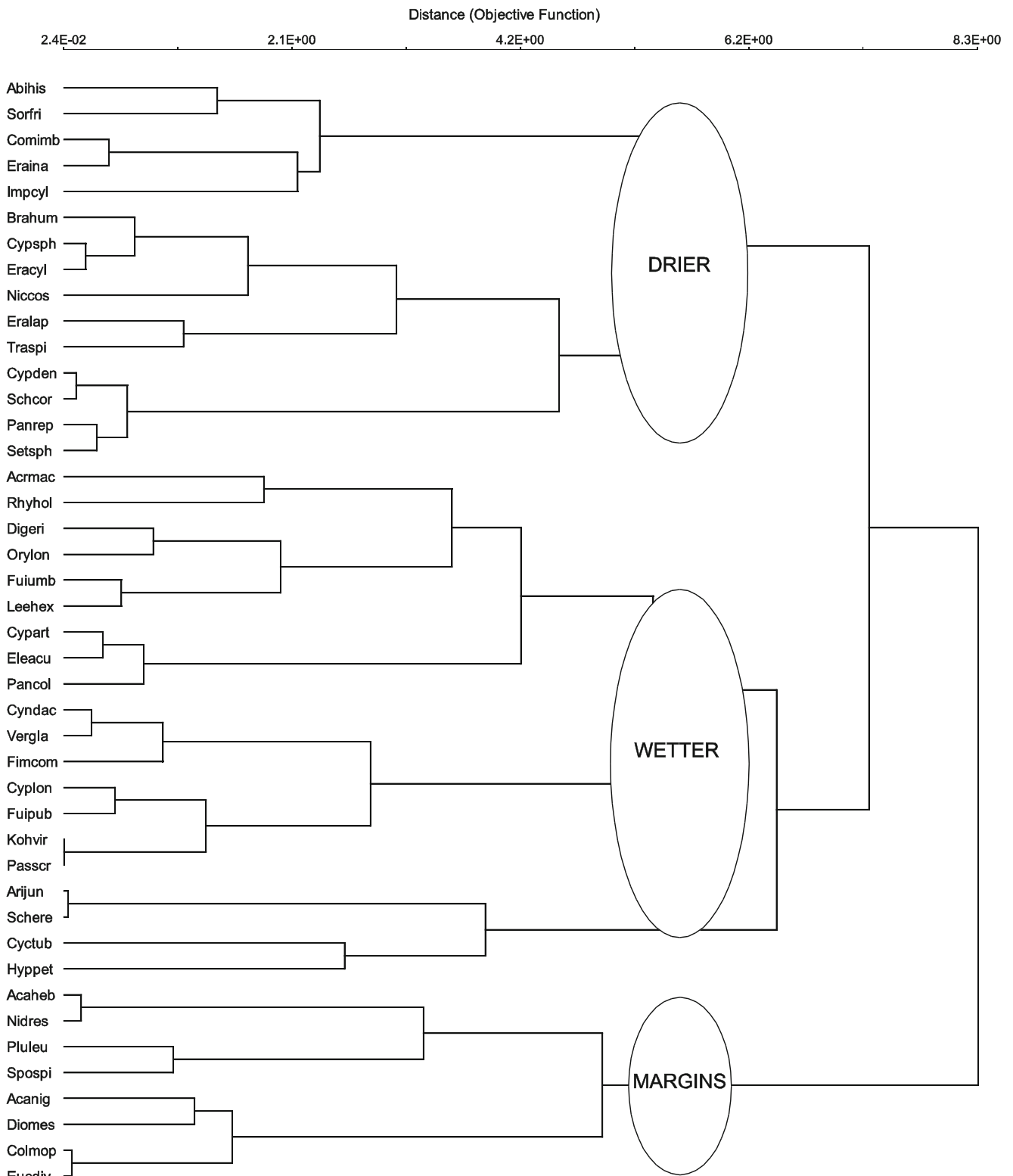


Fig. 6 Dendrogram showing species groupings from entire transects in seasonally flooded grass floodplains (SFG - N=9). Margin and core groups are separated at the first division, while there is a pronounced division between wetter and drier communities at the second level of division

the duration of 3 preceding years provided the best hydrological fit in the main regularly inundated floodplain classes

suggests that many species will be perennial, with some form of vegetative reproduction, and capable of reaching maximum

abundance in 3 years. The aquatic communities are also comprised of many species whose optima (probably) lie outside of the range sampled; that is, they are aquatic species capable of tolerating short draw-down periods.

In seasonally pulsed floodplains of the Amazon near Manaus, Junk and Piedade (1993) found that grasses (Poaceae) were the dominant family, followed by the sedges, Cyperaceae; in general the proportions of herbaceous species were very similar to those found in this study, although overall richness was lower in the Okavango. They noted that pulse-adapted floodplain species had characteristically short reproductive cycles and high reproductive rates. Such traits are common in communities in those Okavango floodplains where average flood duration is less than 4.8 months; that is, the flooded grassland communities (top main branch in Fig. 4). Here, grasses are annual or short-lived tuft-forming perennials. A critical difference between the two studies may be that the Amazon data were compiled over several years, and covered both high and low water stages. Our study was essentially a snapshot of floodplain vegetation during the rising stage only, and a mixture of low-water grown species (terrestrial) and wetland species was recorded. Junk and Piedade found many species which showed great morphological and physiological plasticity, noting the ability of many aquatic species to survive the terrestrial phase by reducing leaf size or water content, or by aestivating as rhizomes in the sediments. These characteristics are found particularly in the wetter communities (mean duration >4.7 months, lower main branch in Fig. 4) of the Boro-Xudum system. Here these communities are dominated by clonal perennials, and many of the sedges use rhizomes and corms as storage organs. This not only allows them to survive short drawdown periods, but also the frequent fires that occur on seasonal floodplains in the Delta (Heinl et al. 2007).

It is clear that better knowledge of the seed-bank, and responses to draw-down and lengths of dry period would provide great insight into the development and maintenance of communities in these floodplains. Unfortunately many studies of wetland seed-banks appear to have been based on hydroperiods which have either been artificially modified (Lenssen et al. 1999; Ter Heerdt and Drost 1994) or sporadic, with dry intervals spanning years (Alexander et al. 2008; Brock and Rogers 1998). ter Heerdt and Drost (1994) found that in multiple samples taken from each of two different zones in marshes in Holland (which had lost much of their emergent cover as a result of prolonged inundation) communities with different dominant species developed after a draw-down, from seed-banks which did not differ in species composition. Alexander et al. (2008) similarly found, in a series of wetlands isolated from the main river channel in the

Central Murray region of Australia, that individual wetlands developed distinct plant communities despite initial similarities. It appears that the floodplain soils of the Okavango (with the possible exception of those which are flooded in less than 11 % of years) are equipped with both a robust, diverse seed-bank, and the perennating organs (rhizomes, stolons, corms, bulbs) of clonal species, which results in compositionally similar communities developing under equivalent flood regimes. Both types of propagules must be capable of withstanding not only extended periods of draw-down (or conversely, inundation), but also relatively frequent fire. Heinl et al. (2007) found that no differences in species composition on seasonal Okavango floodplains could be ascribed to fire frequency. Clearly, the high degree of interconnection of floodplains in this system must play a role in ensuring a diverse seed-bank, probably as a result of rising flood waters carrying seeds with them each year. In this respect, too, the arrival of the flood at the end of the rainy season means that many flowering species have seed set and ready for dispersal.

Conclusions

The hydrological variables annual flood frequency, duration and depth vary co-linearly in the Okavango Delta seasonal floodplains. As the ordination and cluster analyses show, distributions of herbaceous plant species are strongly correlated with all three of these variables. At the scale of the distributary (based on all sites sampled), the strongest correlate is flood frequency, while duration and depth are more important for seasonally flooded grassland, seasonal aquatic, and seasonal sedge communities respectively. Elevation differences within individual floodplains give rise to distinct within-floodplain communities. The considerable compositional overlap between marginal communities in some floodplains and core communities in others suggests that species composition is strongly related to extant hydrological conditions at both the distributary scale and the scale of the individual floodplain. It seems likely that there are sufficient propagules either in the soil of existing floodplains, or produced by plants in neighboring floodplains to ensure that similar communities will develop under similar conditions anywhere in the distributary studied, but this aspect of community ecology needs further study in the Okavango.

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Appendix

Table 8 Vegetation survey site data

Locality name	Site code	Coordinates: UTM Zone 34 S Datum WGS 84		Date completed	Number of transects	Total number of quadrats	Number of core quadrats ¹	Annual frequency (years flooded of 18 year record)	Number of years since last flood	Mean monthly optimum duration (preceding 3 years)	Mean depth at time of survey (cm)
		Easting	Southing								
Bobo	BOB	724069	7825022	17-Apr-07	3	40	27	8	1	2.8	Dry
Bokoro	BOK	732931	7821944	16-May-07	2	35	25	17	1	8.6	55
Chao	CHA	703725	7851938	13-Jul-07	1	35	31	17	1	7.8	91
Horseback	HBK	672444	7841718	12-Apr-07	1	33	28	10	1	5.8	34
Ivory 2	IV2	725917	7825856	14-Mar-07	3	38	26	8	1	3.4	Dry
Kiri	KIR	708023	7829330	28-Mar-07	5	38	18	7	2	5.8	Dry
Kolobahatse A	KOA	728756	7821640	18-Apr-07	5	34	15	1	18	0.0	Dry
Kolobahatse B	KOB	726729	7820543	19-Apr-07	4	38	22	2	8	1.6	Dry
Kunoga	KUA	736725	7808128	20-Apr-07	4	37	21	12	1	7.4	Dry
Mamoxinxha	MAM	684705	7822605	24-Apr-07	3	35	23	7	1	7.0	5
Maxhanasesunda	MAX	736266	7811652	03-May-07	3	38	26	1	11	1.1	Dry
Mombo	MOM	688267	7871024	21-Mar-07	2	37	28	13	1	7.1	22
Mombo central	MOC	689481	7863255	23-Mar-07	3	33	22	17	1	8.3	44
Mombo south	MOS	689680	7870351	22-Mar-07	2	32	25	18	1	9.8	11
Moporota	MPO	732434	7829186	17-May-07	3	35	23	15	1	8.4	16
Ntswi	NTS	724322	7838584	24-May-07	3	39	27	17	1	8.8	29
Nxabega 1	NX1	689164	7841330	03-Apr-07	3	36	24	16	1	8.9	71
Nxabega 2	NX2	688060	7839986	04-Apr-07	3	36	24	18	1	8.1	70
Nxaraga 1	MIL	727828	7837924	25-May-07	3	30	28	18	1	7.7	46
Nxaraga 2	NXA	727489	7836509	18-May-07	3	40	28	17	1	6.8	35
Selby	SEL	678014	7835038	11-Apr-07	5	34	14	6	1	4.5	Dry
Tshwaramasepa	TSW	693444	7815862	25-Apr-07	3	34	22	1	1	0.3	20
Tsutsubega	TSU	737079	7802066	04-May-07	2	30	22	14	16	7.1	Dry
Xaa	XAA	731970	7830521	23-May-07	5	37	18	17	1	9.4	27
Xaxaba north	XAN	708319	7840463	16-Mar-07	2	39	31	8	2	3.7	Dry
Xaxaba south	XAS	708120	7837970	27-Mar-07	2	37	29	6	3	2.0	Dry
Khanyani	XHA	697992	7802480	26-Apr-07	3	35	23	2	1	3.4	Dry
Xudum	XUS	716610	7796727	10-May-07	2	34	26	10	1	7.3	24
Xwaapa north	XWN	718409	7805718	08-May-07	3	38	26	12	1	8.7	56
Xwaapa south	XWS	722345	7801062	09-May-07	3	35	23	7	1	4.2	Dry

¹ Excluding the 2 quadrats at the dryland ends of each transect

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