EFFECTS OF ANNUAL FLOODING ON DISSOLVED ORGANIC CARBON DYNAMICS WITHIN A PRISTINE WETLAND, THE OKAVANGO DELTA, BOTSWANA

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Abstract: In the Okavango Delta in Botswana, dissolved organic matter (DOM) transport is controlled by the slow movement of an annual flood 'pulse' across permanently and seasonally flooded wetlands, known respectively as the Permanent Swamp and Seasonal Swamp. We studied temporal and spatial variations in fluorescence index (FI) and specific UV absorbance (SUVA) of DOM to identify DOM sources and fate during the flood. Dissolved organic carbon (DOC) concentrations ranged from 2 to 25 mg C L^{-1} in channels of the Delta, with seasonal floodplains having consistently higher concentrations. Chemical indices, such as DOC concentrations, conductivity, specific UV absorbance (SUVA), fluorescence, total dissolved nitrogen, and chlorophyll *a*, were analyzed for channel and floodplain sites in the Seasonal Swamp. DOC concentrations increased during the rising limb of the flood in the Seasonal Swamp. SUVA of whole water samples and fluorescence index (FI) of fulvic acids isolated from channel and floodplain sites changed in a manner indicating the release of DOM by leaching of plant litter during the flood. After the flood receded, DOC concentrations and fulvic acid content decreased, and microbially-derived sources of organic matter dominated. Along two river reaches, measuring over 400 km each, variations in DOC concentrations were primarily due to geomorphology, with the effects of the annual flood overprinted atop the spatial controls. Increasing downstream DOC concentrations were found to be a product of inundation of DOC-rich seasonal floodplains and evaporation-enriched waters downstream. Increasing SUVA, dissolved nitrogen, and fulvic acid content, and decreasing FI downstream suggested microbial processing of terrestrial DOM and possible release of nutrients incorporated in the DOM.

Key Words: DOC, dissolved organic carbon, flood, swamp, wetland, flood-pulse, fluorescence, absorbance, conductivity, fulvic, nutrient

INTRODUCTION

An important aspect of the biogeochemistry of many wetlands is the high concentration of dissolved organic matter (DOM) (Mann and Wetzel 1995), including dissolved organic carbon (DOC) and dissolved organic nutrients. DOM influences the physical and chemical environment in wetlands through light attenuation (Zafiriou et al. 1984) and metal complexation (Kolka et al. 2001). DOM is also important in trophic dynamics (Hessen and Tranvik 1998) because DOM supports the growth of heterotrophic microorganisms (McKnight et al. 1993, Stone and Berman 1993). Further, the incorporation of nitrogen and phosphorus into the DOM pool can influence nutrient cycling in wetlands (McKnight et al. 1985, Qualls and Richardson 2002, Qiu et al. 2003).

In many landscape types, the mobilization of DOM has been attributed to the flushing of upper soil horizons during hydrologic events, such as snowmelt and storm runoff (e.g., Hornberger et al. 1994, Boyer et al. 1997, McClain et al. 1997, Villar and Bonetto 2000). Much of the research on DOM mobilization in wetlands has focused on seasonal DOM variations in rivers that drain wetlands. In the USA, Gergel et al. (1999) examined Wisconsin lakes and rivers influenced by wetlands and found that the proportion of wetlands in the watershed explained much of the variability of DOM in rivers. Qualls and Richardson (2002) found that canals draining the Everglades marshes of southern Florida contained DOC concentrations in the range of 20 to 40 mg C L^{-1}. Golladay and Battle (2002) found higher DOC concentrations during flood periods than during dry periods in a coastal plain stream draining a wetland in southwestern Georgia. In order to understand better the DOM contributions from wetlands to streams during flooding events, a better characterization of DOM mobilization within wetlands during flood events would be valuable.

The Okavango Delta is an extensive pristine and oligotrophic wetland in Botswana. Annually, a large flood travels uninterrupted downstream along the Okavango River and inundates the Okavango Delta from April to September. Cronberg et al. (1996) proposed that the annual flood causes a release of DOM, derived from carbon stores in seasonal floodplains of the Delta, such as soil and vegetative litter. O'Connell et al. (2000) showed that leaching of floodplain leaf litter released much larger quantities of DOC than leaching of soil. After leaching vegetative litter and floodplain soils from the Delta, Mladenov (2004) confirmed that the DOC released per gram of dry mass from senescent floodplain vegetation was over two orders of magnitude greater than for leached soils.

Once DOM has been mobilized from source areas in the Okavango Delta, the extent of downstream transport of DOM may be affected by biogeochemical and photochemical processes that occur within the wetland. For example, microbial consumption of DOM was identified as a key process by Cronberg et al. (1996), who suggested that more labile DOM components are preferentially processed by microbial communities and more recalcitrant fulvic acid fractions are left behind in the distal regions of the Delta. Another process that may affect the amount of DOM transported through the Delta is photodegradation, especially given the slow movement of water through floodplains, the long residence times (months) of water in the Delta, and the exposure to UV radiation. Photodegradation may contribute to transformations and losses of DOM (Chen et al. 1978, Graneli et al. 1996) and, in turn, may affect the downstream transport of DOM. Exposure of larger molecular weight, photoreactive DOM, such as that from lignocellulose compounds in vegetation, to sunlight has been shown to cause the transformation to more labile components (Moran and Zepp 1997, Vahatalo et al. 2003).

To understand how these processes affect DOM, it is important first to determine the sources and chemical quality of DOM. To differentiate between microbial and plant/soil precursor materials, specific UV absorbance (SUVA, the absorbance at 280 nm normalized to the DOC concentration) has been used (Weishaar et al. 2003). Aromatic groups, which are more abundant in humic substances, have a high SUVA, are derived from lignaceous materials, and tend to absorb UV radiation more strongly than aliphatic groups. Another method that provides information about the different sources of DOM is fluorescence spectroscopy. Fluorescence has been used to differentiate between fulvic acid derived from the degradation of lignin-containing organic material in plants and soils and fulvic acid derived from degradation of microbial organic material. These differences can be represented as a fluorescence index (FI) (McKnight et al. 2001). FI is a measure of the breadth of one of the two main fluorophores of fulvic acid (FA), most likely associated with quinone moieties in fulvic acid (Klapper et al. 2002). When microbial sources of DOM dominate, as they do in Antarctica, FI values are highest at around 1.74 for Lake Fryxell fulvic acid (Hood et al. 2003). When vegetative sources are dominant, as in the case of the Suwannee River, FI values are low, typically around 1.24 for Suwannee River reference fulvic acid (Hood et al. 2003). In the Okavango Delta, the FI in leachates from vegetative sources, such as grass, reeds, and papyrus leachates, were found to be no lower than 1.37 (Mladenov 2004). Combining spectroscopic data, such as SUVA or FI, with hydrologic data is useful for understanding seasonal changes in DOC sources. Hood et al. (2003) analyzed temporal and spatial patterns in the FI of fulvic acids to show that, in a mountain catchment, snowmelt caused a shift to more vegetation-derived sources of DOM and development of algal blooms in lakes in summer caused a shift to more microbial-derived sources of DOM.

In the study presented here, we explored the hypothesis put forward by Cronberg et al. (1996) that DOM in the water column has its source in carbon stores in the seasonal floodplains of the Okavango Delta during the annual flood. The Cronberg et al. study (1996) examined a suite of water chemistry parameters along the Boro River in the Delta during four individual sampling efforts in 1991 and 1992. Our study investigated DOC dynamics in the Delta with greater detail by 1) examining temporal and spatial variations

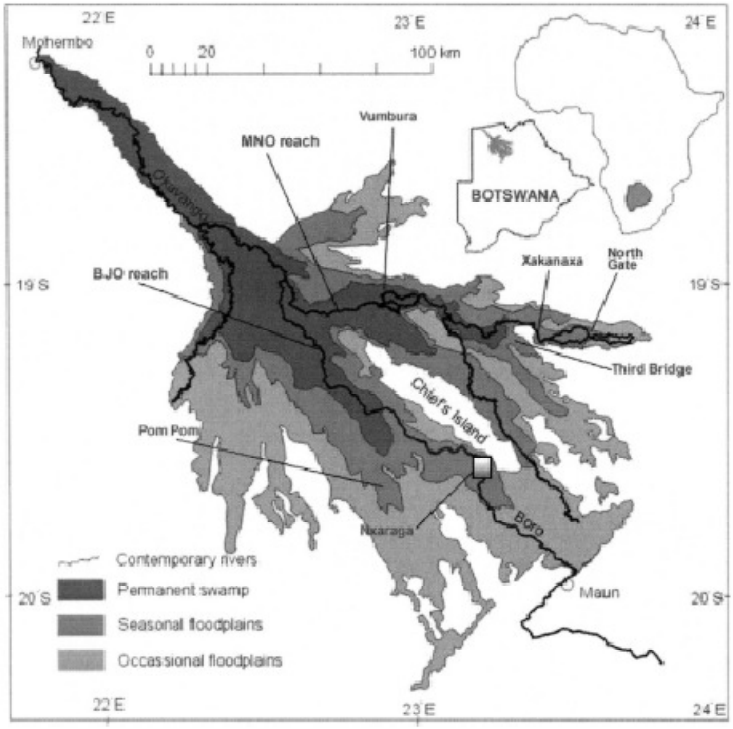

Figure 1. Map showing the Okavango Delta, the BJO and MNO reaches, and paired (channel-floodplain) sampling locations, including the Nxaraga site (shown with rectangles) in the Seasonal Swamp. The inset shows the location of the Okavango Delta in Botswana and Africa.

in DOC and other chemical indices at channel and floodplain sites in the Seasonal Swamp from January 2001 to November 2002, 2) comparing DOC and conductivity data at paired channel and floodplain sites throughout the Delta, and 3) examining spatial variations in DOC and other chemical indices along two of the major rivers in the Delta. Chemical indices measured included SUVA, FI, fulvic acid content, chlorophyll *a* concentrations, and total dissolved nitrogen concentrations. We also studied the potential importance of microbial and photochemical processes as sinks of DOM in the Delta. Our results showed that, beyond the dominant controls exerted on DOC by the permanent and seasonally-flooded regions, the annual flood overprinted controls on DOC quantity and chemical quality. The multiple lines of evidence we used provide support for the hypothesis that mobilization of DOM from floodplains of the Seasonal Swamp occurs during the annual flood and results suggest that subsequent microbial and photochemical transformations of DOM may be dominant biogeochemical processes in the Delta.

SITE DESCRIPTION

Unlike many large deltaic wetlands in arid zones, such as the Sudd, Niger, and Pantanal, the Okavango Delta has not been drained or exploited for water supply. Further, the rivers upstream from the Delta are unaffected by dams, diversions, or pollution, and the annual flood that supplies water and sediment to the Delta has not been directly altered (McCarthy and Ellery 1998). Thus, the Okavango Delta provides an opportunity to study biogeochemical aspects of an unaltered flood pulse (Junk et al. 1989) in a large pristine wetland.

The Okavango Delta is a low gradient (1:3400) wetland (McCarthy and Ellery 1998) with dry land masses, channels, lagoons, floodplains, and permanent and seasonal swamp areas (Figure 1). The Delta is bor-

dered by the Kalahari Desert and has an area of between 6,000 and 13,000 km² (Gieske 1997). The Delta has three distinct hydrotones (Figure 1). The Okavango River flows into the Panhandle hydrotone, where it meanders through a permanently-flooded, papyrus-dominated landscape. In the Permanent Swamp hydrotone, the Okavango River divides into three major distributary channels, the Thaoge in the west, the Jao-Boro immediately to the west of Chief's Island, and the Nqoga-Maunachira to the east of Chief's Island (Figure 1). The Permanent Swamp is permanently flooded and dominated by papyrus, with many distributary channels, lagoons, and lakes. Here, water moves slowly between partially-submerged papyrus and reeds found in the lagoons and channels. Because the only dry land in the Permanent Swamp consists of areas of peat accumulation and some islands, few large mammals venture into this region, and the only transportation is via canoe or motorboat. The Seasonal Swamp hydrotone is the most downstream and contains many dry land areas. In the Seasonal Swamp, flood waters flow mainly through channels, bordered by grasses and reeds, and overflow into grassy floodplains.

The hydrologic regime of the Delta is governed by precipitation during the summer rainy season and flood during the winter dry season from April to September. The flood pulse that inundates the Okavango Delta is a single flood event, occurring on the order of months (see Gumbricht et al. 2004). The flood waters that supply the Delta originate as precipitation in the Angolan highlands during the rainy season (from November to March). After several months (by February through April), this flood pulse reaches the inlet to the Delta at the town of Mohembo. It takes another four months for the flood pulse to travel through the entire wetland to the outlet of the Delta near Maun (approximately 400 river km downstream from the inlet). The first flood waters (the "flood front") often arrive at the outlet of the Boro River (Figure 1) in August, and the peak flood follows one to two months later. On average, the amount of water supplied to the Delta by the annual flood is twice the amount contributed by precipitation, yet precipitation can fill the local groundwater storage and affect the size of the next flood. For example, precipitation during the 2000/2001 rainy season was much greater than precipitation during 2001/2002 rainy season and may have contributed to the larger extent of the 2001 flood.

Water brought to the Delta by flood or rain is lost principally via evapotranspiration (ET), which accounts for the loss of over 95% of water input to the Delta (McCarthy and Ellery 1998). After peak flooding occurs, the input of water to the Delta decreases and the effects of evapotranspiration are most evident as the floodplains dry out. We refer to this period as "flood recession" even though the waters generally do not recede. Only 2–3% of the total inflow exits the Delta as surface water via the Boro River near Maun (Figure 1). During 2001 and 2002, there was no surface-water outflow from the Nqoga-Maunachira river system.

Cronberg et al. (1996) studied the water chemistry of the Delta during four sampling surveys (from 1990 to 1991) and found that DOC concentrations in the Seasonal Swamp had a much greater seasonal variance (standard deviations between 4.2 and 17.8 mg C L^{-1}) than those measured in the Permanent Swamp (standard deviations between 0.8 and 5.8 mg C L^{-1}). These surveys provided only DOC concentrations averaged for all Permanent and Seasonal Swamp samples, and values collected along the length of the Boro River were not presented.

From 1999 to 2002, we studied the temporal variation in DOM in the Seasonal Swamp by measuring DOC concentrations and other chemical indices at the Nxaraga site. The Nxaraga site is located along the Boro River, 306 km downstream from the inlet to the Delta (Figure 1), and is characteristic of terminal floodplains of the Seasonal Swamp, with a main distributary channel that overflows into adjacent floodplains. Three sites were continuously monitored at Nxaraga (Figure 2): one in the Boro channel ("channel" site), one at a flume marking the entrance to a floodplain ("flume" site), and one in the center of the 1.6×10^5 m² floodplain ("floodplain" site). The flume is located at a constriction between floodplains, approximately 1500 m from the channel (Figure 2), and receives water from the channel via lateral overland flow. Before the arrival of the flood, this floodplain is covered by thick layers of dry sedge stands and grassy detritus, produced after the previous flood season (Hoberg et al. 2002). This organic matter is resuspended when flood waters saturate the area. At the end of May 2002, the floodplain and channel sites at Nxaraga experienced a fire, which left behind charred detritus and ash layers.

Water samples were collected at mid-channel sites along the Boro-Jao-Okavango (BJO) and Maunachira-Nqoga-Okavango (MNO) river systems (Figure 1). These two river systems together receive up to 84% of the total inflow of the Okavango River (McCarthy and Ellery 1998). In 2002, samples were collected at 35 sites (Table 1) along 400 km of BJO, stretching from Mohembo to the outlet at Maun. The first 260 km flow through Panhandle and Permanent Swamp hydrotones and the remaining 140 km flow through the Seasonal Swamp (Figure 1). In 2002, samples were collected at 39 sites (Table 1) along the 380-km-long MNO reach. The first 360 km of the MNO reach flow through Panhandle and Permanent Swamp hydrotones,

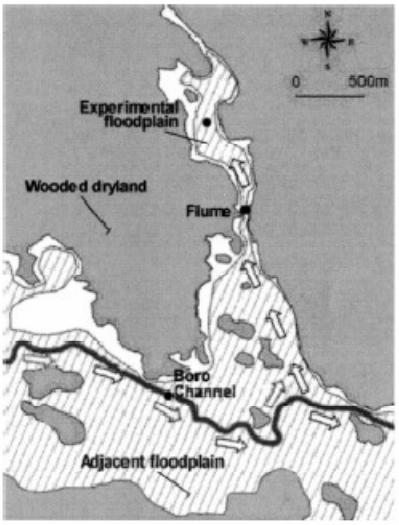

Figure 2. Detail of Nxaraga site, showing the channel, flume, and floodplain sampling sites (solid circles), Boro channel (solid line), adjacent floodplain (white), and the extent of flood (striped) for 1999 (survey data was not available for 2001 and 2002). Arrows show direction of flow during the annual flood.

stretching from Mohembo to Xakanaxa (Figure 1). The last 20 km of the MNO reach, from Xakanaxa at 360 km to North Gate at 380 km, flow through the Seasonal Swamp. The inlet to the Delta at Mohembo is considered the 0 km point, and all other sampling sites are given with reference to the inlet.

Over 85 samples were collected from five paired channel-floodplain sites (Table 1) throughout the Delta during the 2002 flood season. Third Bridge, North Gate, and Xakanaxa are paired sampling sites located near the MNO reach (Figure 1); Nxaraga sites are adjacent to the BJO reach (Figure 1); and Pom Pom sites are adjacent to the Xudum River (not shown).

METHODS

Sample Collection

Samples for chemical and spectroscopic analyses were collected in 300-mL opaque HDPE bottles, then immediately filtered in the field through pre-combusted GF/F glass fiber filters with nominal pore size of 0.7 µm, transferred into clean 300-mL opaque HDPE bottles, acidified to pH 2 with 1N HCl, and stored at 4 °C until analysis at the Harry Oppenheimer Okavango Research Center (HOORC) and the University of Colorado. The hydrologic data (flow and stage) for the Nxaraga sites were collected by researchers at the HOORC in Maun and prepared by Wolski (unpublished) and Krah (unpublished).

At the Nxaraga site, the monitoring program was conducted from 2001 to 2002 (Table 1). In 2001 and for most of 2002, surface-water samples from the three Nxaraga sites were collected weekly during the flood season and once or twice a month during the rainy season as grab samples. From May to July 2002, samples at the channel site were collected with a Kemmerer depth-integrated sampler and combined from 0.2 m, 0.6 m, 1m, and 1.5 m depths. Channel, flume, and floodplain samples were collected at the midpoint of the Boro River channel, at the midpoint of the flume opening, and in the center of the floodplain, respectively.

Table 1. Sampling program for temporal and spatial measurements.

Sampling type	Location	Date	# of samples	Analyses/measurements
Continuous temporal at Nxaraga site, 306 km downstream of inlet on BJO	Channel	Jan 2001-Nov 2002	38	DOC, conductivity, TDN, fulvic acid content, UV absorbance, fluorescence, chlorophyll a
	Flume	Jan 2001-Nov 2002	36	
	Floodplain*	Jan 2001-Nov 2002	36	
Synoptic along river reaches	BJO	29 May 2001	5	DOC, conductivity, TDN, fulvic acid content, UV absorbance, fluorescence, chlorophyll a
		4 Jul 2001	7	
		2-3 Aug 2001	6	
		9-10 Jul 2002	35**	
	MNO*	28-30 Jun 2002	39**	
Paired channel-floodplain sites	Xakanaxa	8 Jun 2002, 2 Jul 2002	5	DOC, conductivity
	Third Bridge	8–9 Jun 2002, 13 Jul 2002	4	
	North Gate	9-10 Jun 2002	4	
	Pom Pom	23 Jun 2002, 14 Jul 2002	7	
	Nxaraga	11 Jan 2001-21 Nov 2002	67	

* Chlorophyll *a* not measured at these sites
** One sample collected at every 5 to 10 km

Samples from paired channel-floodplain sites were collected in 2002 as grab samples (Table 1). Only DOC concentrations and conductivity were measured at these sites.

Along the BJO and MNO reaches, downstream sampling (Table 1) in 2001 and 2002 was conducted using a motorboat. In 2001, samples were collected every 10 to 15 km in the Seasonal Swamp but only 30 to 80 km apart in the Panhandle and Permanent Swamp along the BJO reach. For a higher resolution of sampling, the 2002 sampling was conducted at 5- to 10-km intervals along the BJO and MNO reaches. To facilitate safe and expeditious sample collection, surface-water samples were collected as grab samples. It was not possible to collect samples along the BJO reach from 310 km to 370 km in 2002 because low water levels made it difficult to access this stretch by motorboat or four-wheel drive vehicle.

Analyses

DOC concentrations were measured using a Shimadzu TOC-5050 Total Organic Carbon Analyzer within one to four months of sample collection and were replicated within runs and over time. The standard deviation of replicates was less than 5% for all samples. Conductivity was measured *in situ* using a YSI-30 Salinity-Conductivity-Temperature meter. Some conductivity measurements included in our data set were made by HOORC analysts using the same instrument.

Total dissolved nitrogen (TDN) concentrations were measured using an Antek 9000 Series Total Dissolved Nitrogen Analyzer. Nitrate was measured using a Dionex DX-500 Ion Chromatograph at the U.S. Geological Survey (in Boulder, Colorado), but nitrate concentrations were undetectable in all samples (detection limit 0.001). Ammonia concentrations were not measured. Instead, average June 1991 values for ammonia (0.146 mg L^{-1} as NH_4-N for the Seasonal Swamp and 0.051 mg L^{-1} as NH_4-N for the Permanent Swamp) from Cronberg et al. (1996) were used to estimate dissolved organic nitrogen (DON) concentrations.

Absorbance at 280 nm for all 2001 and 2002 samples was measured using an Agilent 8453 UV-VIS spectrophotometer with ChemStation software and a 1-cm path-length cell. Each sample was measured three times, and the standard deviation of replicates was less than 5% for all samples. Specific UV absorbance (SUVA) was calculated as the absorbance (measured at 280 nm) per mg C L^{-1} of DOC. For comparison, the SUVA of two end members for aquatic fulvic acids, Suwannee River fulvic acid (a standard of the International Humic Substances Society) and Lake Fryxell fulvic acid (McKnight et al. 2001) was measured to indicate plant/soil source and microbial DOC sources, respectively.

Hydrophobic acids were isolated from 150 mL of filtered and acidified water sample using small volume (10 mL) chromatographic columns filled with XAD-8 resin following the method of Thurmann and Malcolm (1981). For consistency with other studies (McKnight et al. 1997, Klapper et al. 2002, Hood et al. 2003), these hydrophobic acids will be referred to as fulvic acids (FA). Fulvic acid fractions analyzed for fluorescence were diluted to 5 mg C L^{-1} or to an absorbance below 0.02 (at 280 nm) in order to minimize the inner-filter effect (Puchalski et al. 1991) and were run in a JY-Horiba/Spex Fluoromax-2 spectrophotometer with DataMax data acquisition software. Because we found that pH influenced the fluorescence signal (e. g., raising the pH incrementally from pH 2 to pH 7 caused narrowing of the fluorescence curve at 450 nm emission and 370 nm excitation), a pH of 2 was maintained in all fulvic acid samples for consistency. Dilute fulvic acid fractions were scanned at an excitation wavelength of 370 nm and an emission range of 400–550 nm at 5-nm increments, and the wavelength at which peak intensities occurred was recorded. The instrument was calibrated and intensity values were corrected for lamp spectral properties according to Klapper et al. (2002). Blank subtraction to prevent the effects of Raman scattering was performed according to McKnight et al. (2001). Fluorescence index (FI) values were then calculated from the ratio of intensities emitted at 450 nm and 500 nm (McKnight et al. 2001). The daily recorded intensity of the water Raman scatter peak was used to normalize the intensity of the spectra to November 2001, when fluorescence analyses began, to account for the decay in lamp intensity over time. Fulvic acid from the Suwannee River (SR) in Georgia (a standard of the International Humic Substances Society) was employed as the terrestrial/vegetation end-member source (McKnight et al. 2001). Fulvic acid from Lake Fryxell (LF) in Antarctica was used as the microbial end-member source (McKnight et al. 2001) and has been used in other studies to represent the microbial end-member (Klapper et al. 2002, Hood et al. 2003, Fulton et al. 2004). FI was measured for SR and LF fulvic acids regularly for comparative purposes (measuring at 1.24 and 1.74, respectively) and, after correction for lamp spectral properties, the standard deviation of triplicates was less than 0.01. The average FI of 1.40 for plant leachate (PL) fulvic acids (Mladenov 2004) is also included for comparative purposes. Among samples, collected over time from the same system and analyzed with the same instrument with appropriate corrections, changes in FI of 0.05 have been found to indicate shifts in dominant source (Hood et al. 2003).

Using the method of Marker et al. (1980), suspended particles for chlorophyll *a* analysis were collected by filtration of water samples onto 47-mm Whatman glass-fiber filters (GF/F). Filters were frozen until analysis, then thawed and extracted for 24 hours in buffered acetone solution at room temperature. Chlorophyll *a* concentration was determined spectrophotometrically with an Agilent 8453 UV-VIS spectrophotometer and a 1-cm path-length cell. The absorbance of the extract at 665 nm was corrected for the background absorbance in the near infrared (750 nm), and absorbance values at both wavelengths were corrected for the presence of pheophytin after acidification of the sample. Absorbance values were converted to chlorophyll *a* concentration according to Steinman and Lamberti (1996).

RESULTS

Temporal Variations in DOC Concentrations and Chemical Quality

At the Nxaraga channel, flume, and floodplain sites, a peak in surface-water DOC concentrations occurred in June 2001 (Figure 3) and 2002 (Figure 4), approximately two to four weeks before peak flood. The peak DOC concentration in 2002 was up to 17 mg C L^{-1} higher than the peak DOC in 2001 (Figures 4d through 4f). In 2001, DOC concentrations decreased during peak flood and stabilized to average values of 9.5 mg C L^{-1}, 11.5 mg C L^{-1}, and 10.7 mg C L^{-1} at the channel, flume, and floodplain sites, respectively (Figure 3). In contrast to the channel and flume site, DOC concentrations at the floodplain site began to increase at the end of flood recession and throughout the summer rainy season from November 2001 through March of 2002 (Figure 4f).

For each flood event, the lowest conductivity was observed immediately after peak flood at all sites (Figures 4g through 4i) and during flood recession, conductivity increased to pre-flood levels.

Between peak flood times (during periods of low stage and stagnant water), generally, SUVA values were lowest (Figures 5a through 5c). During peak flood, high SUVA values were observed (Figures 5a through 5c), with highest SUVA values detected at the floodplain site. In all samples collected during the flood seasons of 2001 and 2002, linear regressions showed that DOC and UV absorbance at 280 nm were highly correlated (Table 2).

At all sites during 2001, a decrease in FI values, toward a more vegetation-derived fulvic acid, occurred during peak flood (Figures 5d through 5f). During August 2002, the lowest FI values were 1.41 at the channel, 1.44 at the flume, and 1.44 at the floodplain. During flood recession in 2001, FI values increased to 1.57 at the channel, 1.53 at the flume, and 1.51 at the floodplain. In 2002, FI values during flood recession increased only at the channel and flume sites (Figures 5d and 5e). FI values at the floodplain in 2002 continued to decrease to 1.40 on 24 October (Figure 5f), long after peak flood. In bivariate correlations, FI values showed a significant negative correlation (Table 2) with SUVA values for all samples collected during 2001 and 2002.

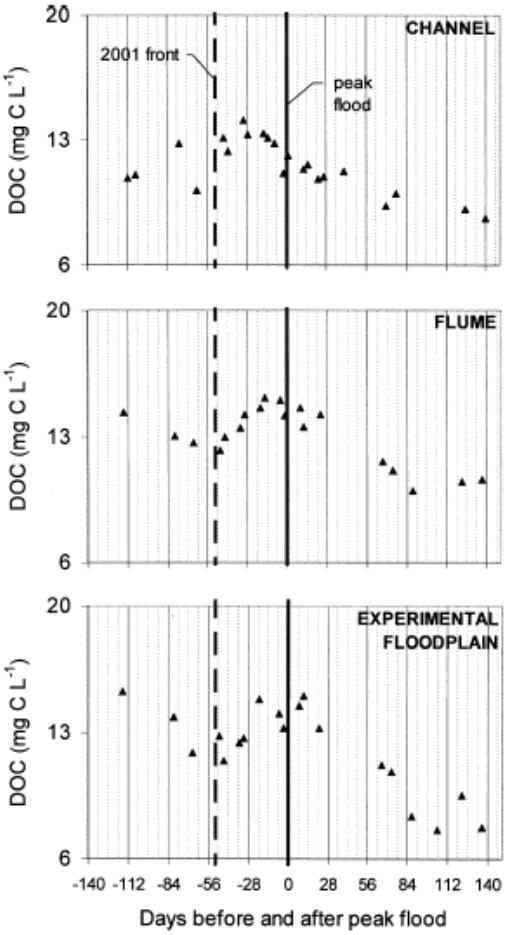

Figure 3. DOC concentrations on days before (negative) and after (positive) the peak flood for a) channel, b) flume, and c) floodplain sites at Nxaraga. Dates of the arrival of the flood front are shown for 2001.

Fulvic acid accounted for 60 to 75% of the DOC at the channel, flume, and floodplain sites (Figures 5g

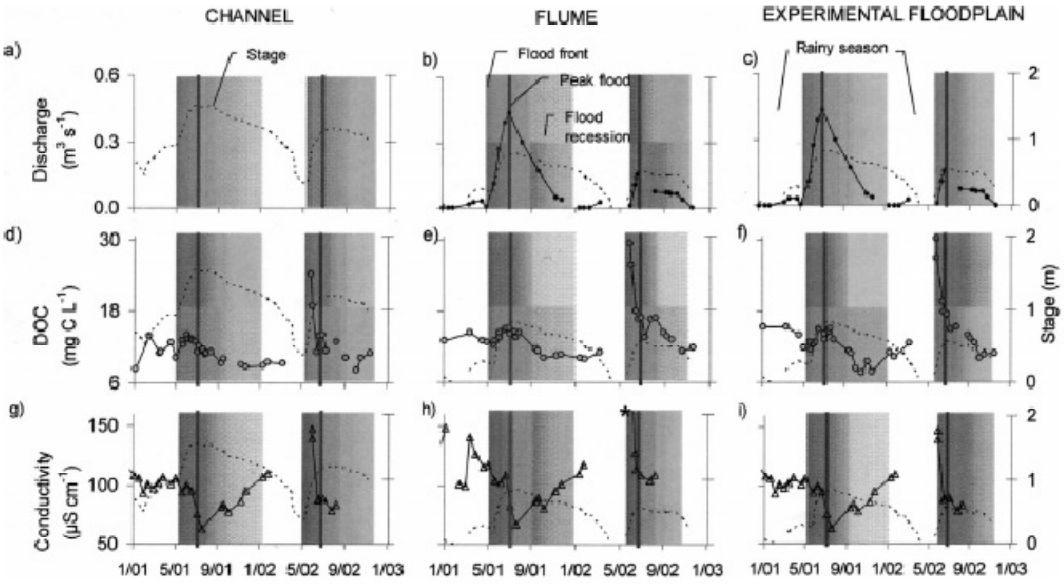

Figure 4. Temporal variations at Nxaraga in a-c) stage (dashed line) and discharge (solid line with filled diamonds), d-f) DOC concentration (solid line with shaded circles), and g-i) conductivity (solid line with triangles) in the Seasonal Swamp from 2001–2002. Left panels show data for the at the channel sampling site; middle panels show data for the flume site; and right panels show data for the floodplain site. The conductivity measurement at the flume on 4 June 2002 was 224 µS cm^{-1} (shown as an asterisk). Stage and discharge is shown for both flume and floodplain sites but was only measured at the flume. Approximate dates of the peak flood for 2001 and 2002 are shown with shaded vertical lines. The shaded region before the peak flood line represents the approximate time of the rising limb of the flood, initiated by the flood front. The shaded region after the peak flood line represents the approximate time of flood recession. The flood season is taken to be the time during which there is discharge through the flume. Note that a stagnant period exists during which there is no discharge through the flume.

through 5i). At all sites, a temporal pattern was observed of fulvic acid content increasing to about 75% during the flood. In 2002, a decrease in fulvic acid content occurred at all sites during flood recession.

At the channel site, an increase in chlorophyll *a* concentrations was observed during the 2001 flood recession, and a decrease occurred during the 2002 flood. At the flume site, chlorophyll *a* concentrations decreased during flood recession, increased during the 2001/2002 rainy season, peaked during the rising limb of the 2002 flood, and decreased during the 2002 flood (Figures 5j and 5k).

During the flood of 2002, the DOC concentrations at paired channel-floodplain sites throughout the Seasonal Swamp ranged from 5 to 15 mg C L^{-1}. On average, DOC concentrations were 2.3 mg C L^{-1} higher at the floodplain sites than at channel sites (Figure 6a). Average conductivity values were 21 µS cm^{-1} higher in floodplains than in channels (Figure 6b). DOC concentrations were highly correlated with conductivity values at all channel sites ($r^2 = 0.94$, $p < 0.001$, $n = 47$) and floodplain sites ($r^2 = 0.96$, $p < 0.001$, $n = 40$).

Spatial Variations in DOC Concentrations and Chemical Quality

The downstream sampling in the BJO reach on 29 May, 4 July, and 2 August 2001 (Figure 7a through 7f) showed a trend of increasing DOC concentrations and decreasing FI values with distance. At 251 and 282 km downstream, the DOC concentration decreased as the peak flood line moved downstream over time (Figure 7a, 7c, and 7e). Similarly, at 306 km downstream, DOC concentrations were highest in July, just after the flood front had passed but before the peak flood had arrived and lowest in August after the peak flood had passed (Table 3). As the peak flood "wave"

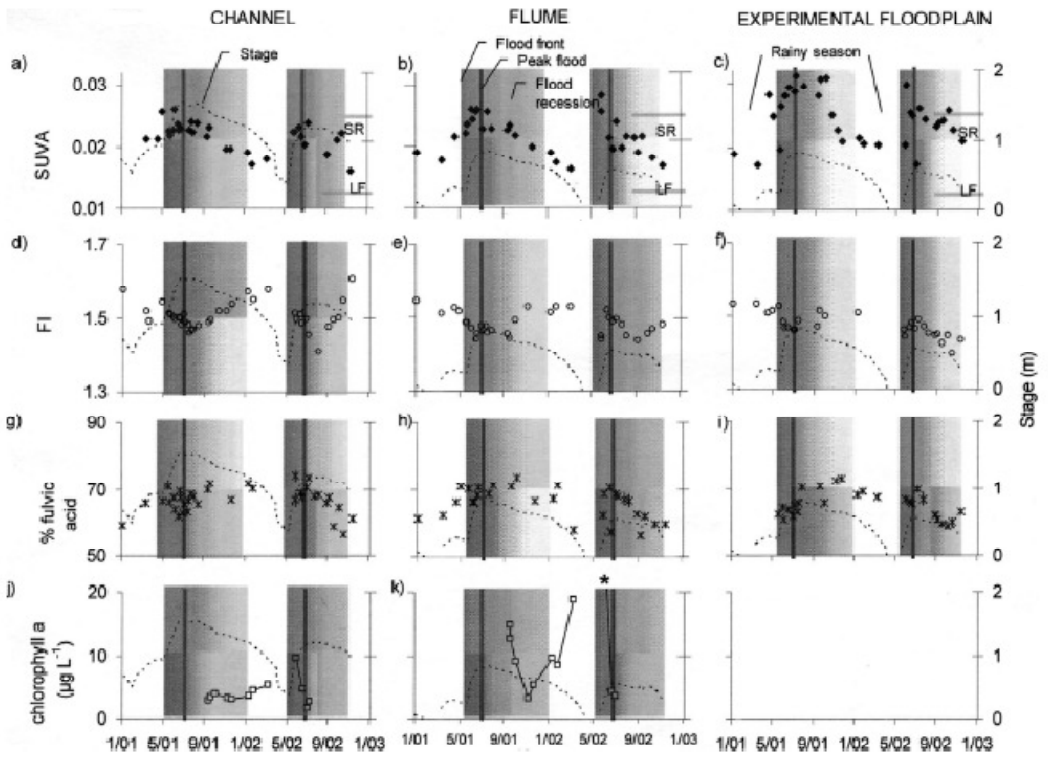

Figure 5. Temporal variations in a-c) SUVA at 280 nm (solid diamonds) of filtered water samples, d-f) fluorescence index (circles) of fulvic acid samples, g-i) % fulvic acid (stars), and j-k) chlorophyll *a* concentration (squares), at the channel sampling site at Nxaraga in the Seasonal Swamp from 2001–2002. Left panels show data for the channel sampling site; middle panels show data for the flume site; and right panels show data for the floodplain site. The chlorophyll *a* concentration at the flume on 4 June 2002 was 30 µg L^{-1} (shown as an asterisk). Chlorophyll *a* concentrations were not measured at the floodplain site. Lake Fryxell fulvic acid (LF) and Suwannee River fulvic acid (SR) mark the microbial and terrestrial end-members, respectively, for SUVA. The FI values of LF, SR, and plant leachate (PL) fulvic acids were 1.74, 1.24, and 1.40, respectively. Approximate dates of the peak flood for 2001 and 2002 are shown with vertical lines. The shaded region before the peak flood line represents the approximate time of the rising limb of the flood, initiated by the flood front. The shaded region after the peak flood line represents the approximate time of flood recession. The flood season is taken to be the time during which there is discharge through the flume.

moved downstream (Figure 7b), FI values during peak flood (at 251 km, for example) were lower than prior to flood arrival. Although the temporal variations in FI values shown in Table 3 are greater than the error associated with the measurements, the differences are less than 0.05 and should be interpreted cautiously.

The downstream sampling in the BJO reach on 9–10 July 2002 was conducted when the flood front was at 390 km and the flood peak was at 285 km, similar to the conditions on 4 July 2001. This downstream sampling included several additional measurements of DOM composition to gain more insight into the processes controlling DOM during the flood in the Delta. Similar to the 4 July 2001 sampling, there were sharp increases in most profiles (except fulvic acid content and chlorophyll *a*) near the start of the Seasonal Swamp (after the 262-km point along the BJO reach and after the 330-km point along the MNO reach).

Results showed an increase in DOC concentrations from 1.9 mg C L^{-1} at Mohembo in the Panhandle to 22.3 mg C L^{-1} at Maun near the outlet of the BJO reach (Figure 8a). Conductivity profiles (Figures 8c and 8d) increased with distance from the inlet along the BJO reach. There was a similar increase along the

Table 2. Bivariate correlations for dissolved organic carbon (DOC), conductivity (Cond), UV absorbance at 280 nm (UV280), specific UV absorbance (SUVA), fluorescence index (FI), fulvic acid content (FA), and chlorophyll *a* (Chl a) for temporal samples collected at Nxaraga (only significant correlations are shown). N indicates number of samples.

		DOC	Cond	UV280	SUVA	FI	FA	Chl a
DOC	Pearson Corr.		0.814**	0.898**				0.589**
	Sig. (2-tailed)		<0.001	<0.001				0.004
	N		67	108				22
Cond	Pearson Corr.	0.814**		0.754**				0.847**
	Sig. (2-tailed)	<0.001		<0.001				<0.001
	N	67		67				18
UV280	Pearson Corr.	0.898**	0.754**		0.574**	−0.251*		0.626**
	Sig. (2-tailed)	<0.001	<0.001		<0.001	0.016		0.002
	N	108	67		98	92		22
SUVA	Pearson Corr.			0.574**		−0.264*		
	Sig. (2-tailed)			<0.001		0.017		
	N			98		82		
FI	Pearson Corr.			−0.251*	−0.264*			
	Sig. (2-tailed)			0.016	0.017			
	N			92	82			
FA	Pearson Corr.							
	Sig. (2-tailed)							
	N							
Chl a	Pearson Corr.	0.589**	0.847**	0.626**				
	Sig. (2-tailed)	0.004	<0.001	0.002				
	N	22	18	22				

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

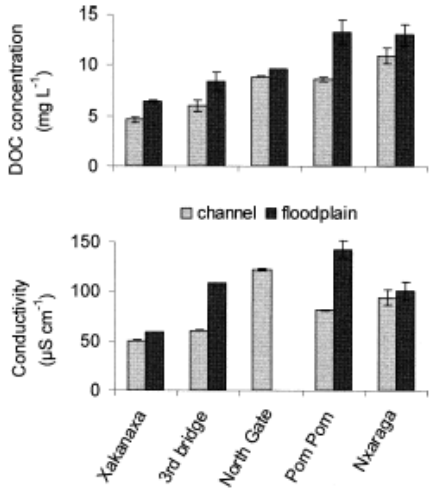

Figure 6. a) DOC concentrations (mg C L^{-1}) and b) conductivity (µS cm^{-1}) in paired channel-floodplain sites in the Okavango Delta in 2002. Conductivity values at the North Gate floodplain were not recorded.

MNO reach, and in general, conductivity correlated well with DOC concentrations for both reaches (Tables 4 and 5). Shifts in DOC properties or conductivity do not appear to correlate with the locations of the flood peaks on the BJO reach (285 km) and the MNO reach (260 km).

Given the low average NH_4 concentrations previously observed along the Boro River (Cronberg et al. 1996) and the undetectable NO_3^- concentrations we determined, we estimated that over 90% of the TDN in samples collected along the length of the BJO and MNO reaches was in the organic form. TDN concentrations along the BJO reach increased exponentially ($r^2 = 0.67$) in the Permanent and Seasonal Swamps (Figure 8e). In contrast, TDN concentrations along the MNO reach showed a minor increase in the Panhandle and Permanent Swamp (Figure 8f) but increased exponentially ($r^2 = 0.77$) in the Seasonal Swamp.

Increases in SUVA concentrations and decreases in FI occurred with distance downstream of the inlet along the BJO and MNO reaches (Figures 8g through 8j). In bivariate correlations, SUVA and FI were inversely related and significantly correlated for both reaches (Tables 4 and 5). Linear regressions showed that SUVA and TDN concentrations were significantly correlated along both reaches (Tables 4 and 5). A significant rise in fulvic acid content (from less than 40%

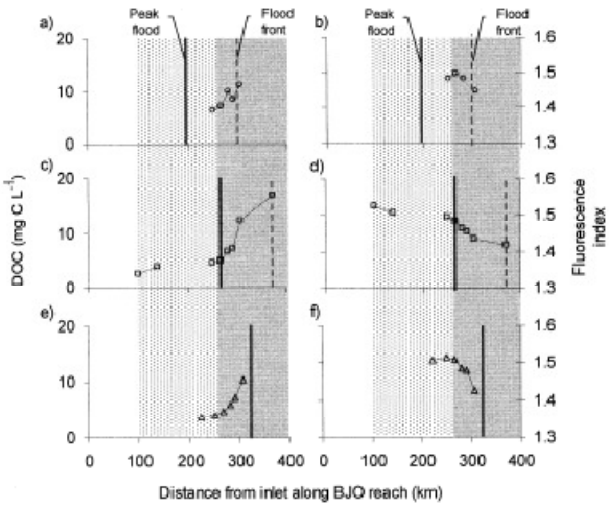

Figure 7. Spatial variations along the BJO reach in DOC concentrations and FI values for 29 May 2001 (a-b), 4 July 2001 (c-d), and 2 August 2001 (e-f). Peak flood (solid line) and flood front (dashed line) locations are shown. The August 2001 flood front is not shown, as it was located downstream of the Delta outlet. Approximate regions of Panhandle (no shading), Permanent Swamp (light shading), and Seasonal Swamp (dark shading) hydrotones are shown.

fulvic acid to greater than 70% fulvic acid) also occurred with distance downstream (Figures 8k and 8l).

Correlations in our spatial data set between chlorophyll *a* and TDN were significant (Tables 4 and 5). Chlorophyll *a* concentrations showed a general increase with distance from the inlet (Figure 8m).

DISCUSSION

DOC Mobilization by Annual Flood

Our results demonstrate that the annual flood is an important pathway for the transport of organic matter in the Okavango Delta, as proposed by Cronberg et al. (1996). Our monitoring of DOC concentrations at the Nxaraga channel-flume-floodplain sites revealed a pattern of DOM flushing during the rising limb of the flood, followed by a decrease in DOM after the peak flood (Figure 3). Furthermore, spectroscopic analyses (SUVA and FI) at all three Nxaraga sites demonstrated that the "pulsed" DOM had vascular plant origins. Mobilization of terrestrial DOC by flood in the Okavango Delta is consistent, to some extent, with discharge-DOM relationships observed in the Orinoco River (Paolini 1995, Battin 1998) and other tropical montane watersheds (McDowell and Asbury 1994). The increase in DOC concentrations with the ascending limb of the hydrograph in the Delta is also consistent with observations in temperate watersheds (Grieve 1991, Hornberger 1994, Bishop 1996, Boyer et al. 2000, Hood et al. 2003). However, with the exception of observations of higher molecular weight DOC during the wet period in the northern Everglades (Wang et al. 2002), the mobilization of vegetation-derived OM by a major hydrologic event has not been widely studied within wetlands.

Mobilization of terrestrial DOC by the flood is also suggested by the spike in DOC concentrations in 2002 (up to 17 mg C L^{-1} higher than observed in 2001 (Fig-

Table 3. DOC concentrations and FI values at three location along the BJO reach during the 2001 downstream sampling campaigns.

	251 km		282 km		306 km		Location of	
Date sampled	DOC	FI	DOC	FI	DOC	FI	peak flood (km)	flood front (km)
29-May-01	6.3	1.48	10.0	1.48	11.2	1.44	196	301
4-Jul-01	4.6	1.49	6.5	1.46	12.3	1.43	266	371
2-Aug-01	3.9	1.52	6.0	1.49	10.3	1.43	323	—

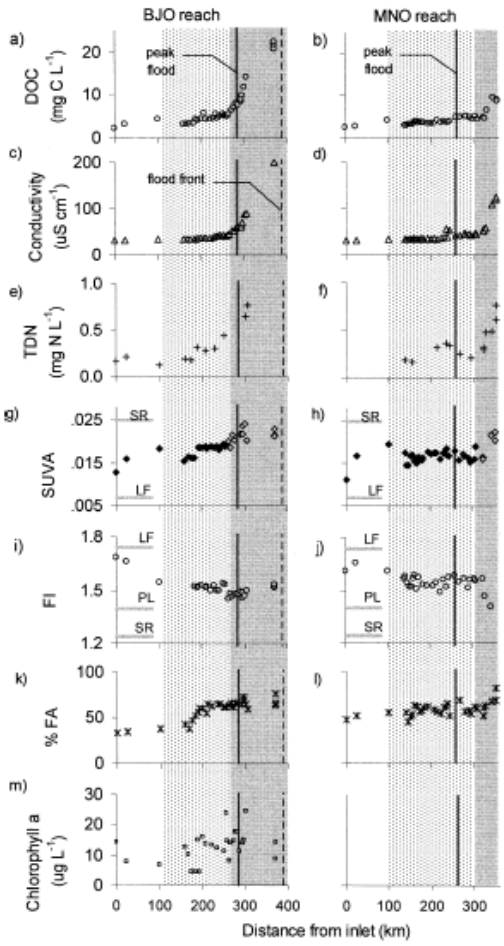

Figure 8. Longitudinal profiles of a) DOC concentration, c) conductivity, e) total dissolved nitrogen, g) specific UV absorbance of filtered water samples, i) fluorescence index of fulvic acid samples, k) % fulvic acid, and m) chlorophyll *a* concentrations along the BJO reach, collected on 9–10 July 2002. Right panels show the same longitudinal data for the MNO reach, collected on 28–30 June 2002, respectively. Chlorophyll *a* concentrations were not measured for the MNO reach. The approximate locations of peak flood (vertical dashed lines) and flood front (solid vertical line) are shown for the BJO and MNO reaches. Approximate regions of Panhandle (no shading), Permanent Swamp (light shading), and Seasonal Swamp (dark shading) hydrotones are shown. Lake Fryxell fulvic acid (LF) and Suwannee River fulvic acid (SR) mark the microbial and terrestrial end-members, respectively, for SUVA and FI. The FI of plant leachate (PL) is also shown for reference.

ures 4d through 4f)) occurring immediately upon the arrival of the flood. The entire Nxaraga site burned in May of 2002, just before the flood front arrived, and partially burned detritus was observed in the water column on 4–6 June 2002. Incomplete burning may have produced more detritus available for conversion to DOC. Inundation of burned areas can result in large organic matter inputs to the water column compared to unburned areas (Battle and Golladay 2003, Mladenov 2004).

From our paired channel-floodplain data, greater DOC concentrations in floodplains of the Seasonal Swamp compared to nearby channels support the idea that floodplains are potential DOM sources during the annual flood. Further, the rapid release of large amounts of DOC from vegetation (O'Connell et al. 2000, Mladenov 2004) suggests that the wetting of dried vegetation during the flood causes fresh DOM to be mobilized. Evidence of vegetation-derived DOC from SUVA and FI values in the floodplain at Nxaraga further indicate that floodplains may be important contributors to DOC in the Seasonal Swamp. FI values in vegetation leachates (from 1.37 to 1.53, Mladenov 2004) that are in the range of FI values observed during peak flood corroborate the interpretation of vegetation-derived sources during flood.

DOC Transformations After Peak Flood

The amount of DOC present in the water column after peak flood may be influenced by hydrologic processes, such as dilution, evapoconcentration, depletion of source areas, and contraction of flooded areas, and biogeochemical processes, such as microbial degradation and photobleaching. The relative contributions of hydrologic processes to the changes in DOC concentration can be determined, in part, from the temporal variation in conductivity, which gives an indication of inorganic solute concentrations. Decreased conductivity during peak flood, described as a dilution effect on inorganic solutes (Cronberg et al. 1996), suggests that dilution contributes to the decrease in DOC concentrations, which begins just before peak flood. Immediately after peak flood and during flood recession, increasing conductivity suggests that inorganic solutes were concentrated by evaporation (Cronberg et al. 1996). In contrast, DOC concentrations in our study did not increase immediately after peak flood or during flood recession (Figure 4d through 4f), even though evapoconcentration was occurring in the floodplain. Instead, DOC concentrations remained relatively stable after peak flood, suggesting that degradation of DOM by microbial and photolytic processes could be significant at this time. At the floodplain site, DOC concentrations did increase during flood recession

Table 4. Bivariate correlations for dissolved organic carbon (DOC), conductivity (Cond), UV absorbance at 280 nm (UV280), specific UV absorbance (SUVA), fluorescence index (FI), fulvic acid content (FA), and chlorophyll *a* (Chl a) for downstream samples collected along the BJO reach (only significant correlations are shown). N indicates number of samples.

		DOC	Cond	UV280	SUVA	FI	FA	TDN	Chl a
DOC	Pearson Corr.		0.975**	0.984**	0.678**		0.526**	0.947**	
	Sig. (2-tailed)		<0.001	<0.001	<0.001		0.003	<0.001	
	N		35	35	31		30	11	
Cond	Pearson Corr.	0.975**		0.949**	0.566**		0.444*	0.940**	
	Sig. (2-tailed)	<0.001		<0.001	0.001		0.014	<0.001	
	N	35		35	31		30	11	
UV280	Pearson Corr.	0.984**	0.949**		0.718**		0.558**	0.932**	
	Sig. (2-tailed)	<0.001	<0.001		<0.001		0.001	<0.001	
	N	35	35		31		30	11	
SUVA	Pearson Corr.	0.678**	0.566**	0.718**		−0.711**	0.805**	0.760*	
	Sig. (2-tailed)	<0.001	0.001	<0.001		<0.001	<0.001	0.011	
	N	31	31	31		26	28	10	
FI	Pearson Corr.				−0.711**		−0.788**		
	Sig. (2-tailed)				<0.001		<0.001		
	N				26		27		
FA	Pearson Corr.	0.526**	0.444*	0.558**	0.805**	−0.788**		0.795**	
	Sig. (2-tailed)	0.003	0.014	0.001	<0.001	<0.001		0.006	
	N	30	30	30	28	27		10	
TDN	Pearson Corr.	0.947**	0.940**	0.932**	0.760*		0.795**		0.775*
	Sig. (2-tailed)	<0.001	<0.001	<0.001	0.011		0.006		0.014
	N	11	11	11	10		10		9
Chl a	Pearson Corr.							0.775*	
	Sig. (2-tailed)							0.014	
	N							9	

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

(Figure 4f), and this behavior may be due to evapoconcentration exceeding the effects of DOC degradation.

Microbial consumption of DOM during the flood and the dominance of heterotrophic processes over primary production in floodplains at Nxaraga were previously proposed by Hoberg et al. (2002). The return to more microbial FI after peak flood suggests that concomitant microbial degradation of DOM and depletion of terrestrial source areas balanced some of the effects of evapoconcentration, leading to the observed decrease and stabilization in DOC concentrations after peak flood (Figures 3 and 4). Bacterial consumption of vegetation-derived DOM in floodplains may also be stimulated by UV light because photobleaching can rapidly transform plant-derived DOM into more labile, lower molecular weight photoproducts with diminished UV absorbance (Moran and Zepp 1997, Vahatalo et al. 2003). Qualls and Richardson (2003) found that the degradation of organic matter by UV light was more significant than bacterial degradation in the Everglades. In our results for the Nxaraga sites, microbial degradation and photodegradation are both suggested by a shift to lower SUVA between peak floods (typically August to March for the channel site). The relative contribution of both processes to DOC decay in the Delta warrants further research.

During the rainy season, chlorophyll *a* concentrations increased and may have contributed more to the microbial FI and SUVA values measured. Hoberg and Lindholm (2000) also found that chlorophyll *a* concentrations correlated significantly ($r^2 = 0.64$) with total nitrogen concentrations from samples they collected at the same experimental floodplain site. Although our study does not provide a record of TDN concentrations for any temporal monitoring sites, our spatial data show a strong correlation between TDN and chlorophyll *a* (Table 4). Temporal monitoring of organic and inorganic forms of nitrate is needed to determine whether algal productivity in the floodplain is a result of nutrient release during the degradation of organic matter.

DOC Transformations Along Spatial Gradients

Consistent with the findings of Cronberg et al. (1996), who showed the greatest seasonal variations in DOC concentrations in the Seasonal Swamp, we observed variations of 2 to 4 mg C L^{-1} from May to August 2001 at several sites in the Seasonal Swamp.

Table 5. Bivariate correlations for dissolved organic carbon (DOC), conductivity (Cond), UV absorbance at 280 nm (UV280), specific UV absorbance (SUVA), fluorescence index (FI), fulvic acid content (FA) for downstream samples collected along the MNO reach (only significant correlations are shown). N indicates number of samples.

		DOC	Cond	UV280	SUVA	FI	FA	TDN
DOC	Pearson Corr.		0.934**	0.984**	0.700**	−0.617**	0.706**	0.870**
	Sig. (2-tailed)		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	N		38	39	39	32	34	13
Cond	Pearson Corr.	0.934**		0.940**	0.662**	−0.591**	0.690**	0.915**
	Sig. (2-tailed)	<0.001		<0.001	<0.001	<0.001	<0.001	<0.001
	N	38		38	38	31	33	13
UV280	Pearson Corr.	0.984**	0.940**		0.792**	−0.626**	0.694**	0.892**
	Sig. (2-tailed)	<0.001	<0.001		<0.001	<0.001	<0.001	<0.001
	N	39	38		39	32	34	13
SUVA	Pearson Corr.	0.700**	0.662**	0.792**		−0.396*	0.589**	0.874**
	Sig. (2-tailed)	<0.001	<0.001	<0.001		0.025	<0.001	<0.001
	N	39	38	39		32	34	13
FI	Pearson Corr.	−0.617**	−0.591**	−0.626**	−0.396*		−0.489**	−0.726*
	Sig. (2-tailed)	<0.001	<0.001	<0.001	0.025		0.007	0.027
	N	32	31	32	32		29	9
FA	Pearson Corr.	0.706**	0.690**	0.694**	0.589**	−0.489**		0.693*
	Sig. (2-tailed)	<0.001	<0.001	<0.001	<0.001	0.007		0.012
	N	34	33	34	34	29		12
TDN	Pearson Corr.	0.870**	0.915**	0.892**	0.874**	−0.726*	0.693*	
	Sig. (2-tailed)	<0.001	<0.001	<0.001	<0.001	0.027	0.012	
	N	13	13	13	13	9	12	

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

The higher DOC concentrations observed on 29 May 2001 at 251 and 282 km, when both sites were experiencing expanding flow, were consistent with the findings of Cronberg et al. (1996) that DOC concentrations in Seasonal Swamp samples were highest during the period of ''baseflow to expanding flow.'' It is important also to highlight that more senescent litter is available in the floodplains during this period of expanding flow (which coincides with the dry winter) than during the summer rainy season. This may enhance the amount and availability of detritus for leaching.

Spatial variations in chemical properties of DOM also indicate likely sources and transformations of DOC. There is evidence that microbial degradation has an important effect on DOC quality along spatial gradients. Microbial processing of DOM can cause recalcitrant DOM to remain in solution, while more labile fractions are consumed. A measure of the biologically recalcitrant DOM can be seen in the fulvic acid content. In the Okavango Delta, the downstream increase in fulvic acid content with distance from the inlet (from 33% to 76% along the BJO reach and 46% to 82% along the MNO reach) suggests significant microbial processing of DOM. This is consistent with the findings of Cronberg et al. (1996) that ''the proportion of humics plus hydrophobic acids and neutrals increased from the Panhandle (about 66%) to the outlet of the Delta (about 82%).'' However, insufficient evidence exists to show how far the mobilized DOC is carried because the turnover of DOC in the Delta remains unknown.

The contribution of different landscape components of the wetland to DOC quality is evidenced by steeper DOC, conductivity, TDN, SUVA, and FI gradients (Figure 8) in the Seasonal Swamp, where floodwaters move laterally across detritus-rich floodplains. This shift in profile slopes for most parameters at the start of the Seasonal Swamp hydrotone was observed along the BJO reach in 2001 and 2002. The importance of landscape contributions to DOC quality is further supported by similar observations of steeper profile slopes along the MNO reach at approximately 300 km, which is the start of the Seasonal Swamp hydrotone for that reach. The steeper profiles do not seem to be related to the location of the peak flood at either the BJO or MNO reaches, and this suggests that the large-scale variability in DOC is governed by the geomorphology of the Delta.

In comparison to the effects of the geomorphology of the system, represented by the deeper Permanent Swamp and the shallow Seasonal Swamp hydrotones, the effects of flood suggested in Figure 7 are small but nonetheless measurable. From downstream sampling of major ions along the BJO reach, Sawula and Mar-

tins (1991) suggested that, "in addition to spatial variation in the concentration of main elements [ions], a seasonal variation also seems to exist." Similarly, a seasonal variation in DOC overprinted on the spatial variation is most evident in the Seasonal Swamp, as seen for the 2001 surveys (Table 2) along the BJO and for the Nxaraga sites (Figure 4). During the time between flood front and flood peak, DOC concentrations at any one point may be at the highest because of the flushing effect. Meanwhile, after the flood peak has passed that point, DOC concentrations decrease, potentially due to dilution and depletion of source areas. Because we did not perform temporal sampling in the Panhandle or Permanent Swamp, we do not know how those areas respond to the passing of the flood. The results of Cronberg et al. (1996) suggest that seasonal variations could be less than 1 mg C L-1 in permanent channels, and temporal variations could be measured in the future in the permanently-flooded hydrotones. Further, higher resolution downstream sampling efforts (such as the 2002 BJO survey) carried out at several times during the flood progression (such as in 2001) would help to resolve the extent to which new organic material is flushed into the water column and transported downstream as the peak flood moves downstream.

Despite an indication of greater algal growth with distance downstream (from increasing chlorophyll *a* concentrations), the longitudinal increase in SUVA and concomitant decrease of FI values in the 2002 BJO and MNO surveys show that vegetation-derived sources of DOC are progressively more dominant than algal sources with distance downstream. A strong spatial correlation between SUVA and FI (Tables 4 and 5) is expected because, generally, higher SUVA values and lower FI values both support terrestrially-derived DOM. The strong spatial correlation between SUVA and TDN (Tables 4 and 5) is important because it shows that where there were more terrestrial sources of OM (i.e., downstream), more nitrogen was available in the water column. Although some amount of evaporative concentration of nutrients is likely in shallow areas downstream, these results suggest that the release of nutrients incorporated in the DOM (through degradation by bacteria or UV light) is an important pathway for nutrient availability in the channels of the Okavango Delta. This has also been suggested by Cronberg et al. (1996), who found that a high proportion (65 to 75%) of nitrogen was bound to organic forms.

Our results also showed that source areas for inorganic solutes may be similar to those for organic solutes, even though source materials may be different. For example, both OM contained in dead standing stock and salts deposited on floodplains (after evaporation of the previous year's flood waters) can be flushed into the water column when floodplains are inundated by the flood. Further, due to complex vegetation-driven ground-water recharge from channels toward the center of islands (Gieske 1996), highly saline pools occasionally form in the centers of islands, which may contribute to increased conductivity upon inundation by flood. The hypothesis of similar source areas for DOC and inorganic ions is supported by the significant correlation observed between DOC and conductivity (Table 4) along the BJO reach, both of which increased with distance downstream. The observation of increasing conductivity was consistent with the downstream increase in anion concentrations reported by Sawula and Martins (1991) along the Boro River. Although they attributed this increase mainly to evaporative concentration, Sawula and Martins (1991) also described high silica (the most abundant element in the water column of the Delta) concentrations in the middle section of the Boro River, which they attributed to the mixing [of Boro water] with waters draining the swamps or floodplains. The correlation between DOC and conductivity in our study also suggests that an evaporative enrichment of DOC in these shallow seasonal floodplains contributes to the steep DOC increase in the Seasonal Swamp. Nevertheless, the relative contributions of flushing, evaporation, and degradation processes remain difficult to quantify, demonstrating the need for a time-variable DOC model.

CONCLUSIONS

The relevant findings of this study were that 1) DOC concentrations increased during the rising limb of the flood at Seasonal Swamp sites, and this increase is attributed to the inundation of vegetative sources, namely detritus on the floodplains; 2) higher DOC concentrations and conductivities in floodplains compared to channels suggests that floodplains may be source areas for DOC and, possibly, inorganic ions; 3) a downstream increase in vegetation-derived DOC may be attributed to both increasing inundation of DOC source areas and the effects of evaporative concentration; and 4) highly correlated downstream increases in fulvic acid content, SUVA, FI, and TDN may suggest that the bacterial processing of vegetative organic matter releases nutrients that were previously incorporated in the organic matter.

Given that more than 70% of the inflowing DOC mass accumulates in the Delta (Cronberg et al. 1996) and that an additional flux of DOC originates from the leaching of vegetation within the Delta, a better understanding of the fate of this large pool of DOC is needed. In this study, we found several lines of evidence suggesting that the consumption of DOC by

bacterial communities may be significant. Furthermore, the shift from vegetation-derived to microbially-derived DOC sources, demonstrated by changes in SUVA and FI measurements, was interpreted as showing that microbial degradation contributes to the removal of DOC with time. The observed changes in SUVA also suggested that degradation by UV light could be an important process that affects the fate of DOC. Photodegradation and consumption may be very important at the Delta-scale because, in addition to fueling the basic trophic compartments, these processes could potentially produce a large efflux of inorganic C, which may represent a significant quantity for regional and global C budgets.

Another process that warrants further study is the liberation of nutrients incorporated in vegetation-derived OM during DOC consumption. As a result of greater leaching of plant litter in the Seasonal Swamp than in the Permanent Swamp (Murray-Hudson, personal communication 2004) and subsequent microbial degradation of this fresh OM, there may be a greater availability of nutrients in the Seasonal Swamp than in the Permanent Swamp. This scenario is supported by increasing gradients of SUVA and TDN (most of which is dissolved organic nitrogen) with distance downstream and the significant correlation between SUVA and TDN concentrations along the BJO and MNO reaches, observed during the 2002 downstream sampling. The release of nutrients incorporated in DOM may stimulate algal productivity, as shown by the increase in chlorophyll *a* with distance downstream. Thus, the biogeochemical processes stimulating DOC transformations may greatly influence productivity in the oligotrophic Okavango Delta and other large wetlands.

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