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Organic carbon composition and oxygen metabolism across a gradient of seasonally inundated limesink and riparian wetlands in the southeast Coastal Plain, USA

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Abstract. A set of three relatively pristine seasonally inundated limesink wetlands and one riparian wetland was studied over a 4–6 month long inundation period in 2001. Patterns in organic matter properties and oxygen consumption in the water column followed a previously documented ecological gradient based on soil composition, vegetation type, and canopy cover. The full canopy, cypress-gum swamp had the highest mean concentrations of dissolved organic carbon (DOC; 26.2 mg/l) and dissolved lignin (sum 6; 299 μg/l) with lower concentrations observed in the partial canopy, cypress savanna (22.0 mg/l DOC; 252 μg/l sum 6) and the open marsh savanna (20.6 mg/l DOC; 135 μg/l sum 6), respectively. During the inundation period, DOC increased in concentration, dissolved lignin decreased, and δ^{13}C shifted to more positive values which collectively indicate a large reduction in the percentage of aromatic carbon during the inundation period. All wetlands had very high concentrations of organic matter, yet microbial oxygen consumption was almost always stimulated by the addition of glucose rather than inorganic nutrients. Stimulation by glucose suggests that there were very small pools of highly bioavailable forms of DOC in the wetlands. A larger pool of moderately bioavailable organic matter had the capacity to sustain microbial oxygen consumption rates under dark conditions for at least 15 d. During the inundation period, the cypress-gum swamp had the lowest average rates of whole water oxygen consumption (1.0 μM/h) with increasing rates observed in the cypress savanna (1.3 μM/h), marsh savanna (1.6 μM/h), and riparian wetland (1.9 μM/h), respectively. The lignin compositional fingerprint varied across the gradient of limesink wetlands, and was useful for identifying different sources of vascular plant-derived DOM. Vascular plant production, algal production, microbial respiration, and UV degradation are all important drivers of DOM cycling, and the consistencies observed in this initial assessment of seasonally inundated limesink wetlands suggest they vary in predictable ways across the ecological gradient.

Introduction

Seasonally inundated limesink wetlands (herein referred to as limesink wetlands) are abundant and unique aquatic ecosystems of the southeast Coastal Plain (Hendricks and Goodwin 1952). The overland hydrologic connectivity between limesink wetlands and adjacent streams is temporally discontinuous. The only exceptions occur during major flood events when overland flooding permits exchange of materials with adjacent forests, streams, and other wetlands (Michener et al. 1998). Furthermore, most limesink wetlands do not represent an important source of material to streams through groundwater flow because they are confined by impermeable clay lenses (Hendricks and Godwin 1952; Lide et al. 1995). Although fire represents an important control on ecosystem processes during the dry season (Kirkman and Sharitz 1994), limesink wetland biogeochemistry is primarily internal and limited to water column and soil processes during the inundation period. In contrast, riparian wetlands along stream corridors have natural hydrologic connections that allow for large contributions of dissolved organic carbon (DOC) from wetland soils to blackwater streams (Mulholland and Kuenzler 1979; Dosskey and Bertsch 1994). Many riparian wetlands in the US southeast Coastal Plain exhibit a hydrologic cycle that is similar to limesink wetlands in which spring flooding is followed by gradual dry down during summer and fall.

To date, most studies of limesink wetlands have focused on the ecology of these systems with particular emphasis on their high degree of plant and animal biodiversity (Dodd 1992; Sutter and Kral 1994; Kirkman et al. 1998). Primary productivity in limesink wetlands has not been comprehensively studied across the southeastern US landscape. Watt and Golladay (1999) found that litterfall productivity in forested limesink wetlands in south Georgia was among the highest reported for wetland systems, however, corresponding rates from adjacent marsh and cypress savanna wetlands were not determined. In a separate study, primary productivity in a cypress savanna in south Georgia was found to be primarily P-limited (Craft and Chiang 2002). No studies have yet examined the relative importance of algal production in limesink wetlands, but studies of other wetland types vary widely in their estimates of algal contributions to total productivity (Schalles and Shure 1989; Cronk and Mitsch 1994; Robinson et al. 1997; Stanley et al. 2003).

One strategy for resolving contributions of organic matter from vascular plants and algae to aquatic systems has been to look at biomarkers that are unique to different categories of producers. Dissolved lignin, a compound produced exclusively from leaching and degradation of vascular plants, represents one such component of freshwater dissolved organic matter (DOM) (Ertel and Hedges 1984). Dissolved lignin has proven to be a useful tracer for biologically recalcitrant aromatic organic matter derived from vascular plants, particularly when complemented with stable carbon isotope ($\delta^{13}C$) measurements (Opsahl and Benner 1997; Opsahl et al. 1999). Dissolved lignin also provides a molecular fingerprint, which can provide information regarding organic matter contributions to aquatic systems from different types of vascular plants (Opsahl et al. 1999).

Regardless of source, accumulations of organic matter as peat in limesink wetlands are small, indicating that efficient mechanisms of organic matter degradation are in place. Microbial metabolism of organic matter in southern wetlands is generally recognized for its importance in remineralization of organic matter as well as to trophic transfer through a microbial loop (Mann and Wetzel 1996). For example, DOM from wetland plants constitutes an important source of energy for microbial respiration (Johnson and Ward 1996; Mann and Wetzel 1996). DOM can also contribute to microbial food webs, although a strong linkage between microbial productivity and grazing has not been established (Johnson and Ward 1996). The roles of microbial metabolism in DOM cycling in limesink wetlands, as generally enclosed ecosystems with a regular wet/dry cycle, may be distinct from other wetlands.

The role of photochemical degradation of DOM has been recognized as a mechanism for direct remineralization of DOM in aquatic systems (Valentine and Zepp 1993; Miller and Zepp 1995). Dissolved lignin represents one specific compound that is biologically refractory but highly susceptible to photochemical degradation (Opsahl and Benner 1998; Opsahl and Zepp 2001). Photochemical processes are also known to convert biologically refractory DOM into bioavailable compounds that can elevate microbial respiration rates (Moran and Zepp 1997; Bano et al. 1998). However, direct exposure of bacteria to UV radiation, a process controlled in part by the form and amount of DOM, can inhibit overall microbial growth (Kahn and Wetzel 1999).

Oxygen consumption has been used in a variety of ways to examine microbial respiration and utilization of organic matter (Biddanda et al. 1994; Benner et al. 1995; Moran et al. 1999). Whole water experiments can provide an integrative measure of microbial respiration that can be used to make comparisons across gradients. Oxygen consumption measurements also offer the possibility of making determinations about whether organic matter or an inorganic nutrient is limiting growth of microbial communities (Benner et al. 1995).

Studies of limesink and riparian wetlands in the southeast Coastal Plain are needed because they are largely understudied relative to wetlands in other regions, yet they are prominent features of the landscape and are being altered or removed at an alarming rate. Indices for healthy systems should be developed for comparison to impaired systems to help set restoration goals. For example, if deforestation occurs within, or in close proximity to a wetland, the flux of organic matter to the wetland may decrease and its bioavailability may change. This would change patterns and rates of microbial metabolism which, in turn, would affect other biogeochemical processes such as nutrient cycling. In other instances, large nutrient pulses from runoff may lead to alterations in plant community structures which would have feedback effects on oxygen availability, the composition of organic matter, patterns of organic matter degradation, and microbial contributions to detritus-based food webs. New approaches should be developed to complement strategies of wetland protection that are based on traditional measurements of biological diversity of plant and animal communities.

The objectives of this study were to examine temporal patterns in organic carbon concentration and composition, and factors influencing oxygen consumption rates to see if these properties varied consistently across an ecological gradient. One riparian wetland was included for comparison. These studies represent initial efforts to gather biogeochemical data for comparison with other aquatic systems and to discuss possible relationships between several critical drivers of wetland ecosystem function.

Materials and methods

Study area

The general study area was the Dougherty Plain physiographic province of the southeast Coastal Plain in Georgia, USA (Figure 1). The wetlands in this study were located on the Ichauway Ecological Reserve, an 11,500 hectare tract with extensive uplands consisting of about 6500 hectares of longleaf pine and wiregrass, and about 1200 hectares of limesink wetlands. Allard (1990) derived a general classification scheme consisting of 18 nonalluvial wetland communities across the southeast Coastal Plain. Selection criteria for three limesink wetlands from the Ichauway Ecological Reserve came from an extensive classification of the landscape based on geomorphology, soils, and vegetation (Goebel et al. 1997).

The representatives of limesink wetlands follow an ecological gradient based on the extent and type of vegetation cover over each wetland. A cypress-gum swamp was selected as a representative of ecosystem type W18 which has a full overstory canopy consisting primarily of cypress (*Taxodium ascendens*) and black gum (*Nyssa sylvatica*). A cypress savanna was selected as a representative of ecosystem type W19 which has a partial overstory canopy consisting of

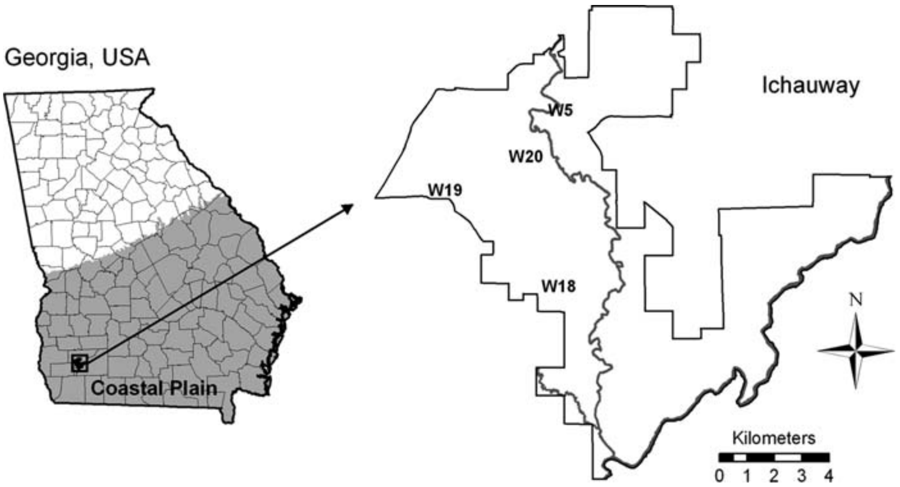

Figure 1. Location of the Coastal Plain physiographic province (shaded left) in Georgia, USA, and the Ichauway Ecological Reserve (right). The approximate locations of the four wetland study sites are indicated (see text for abbreviations). The exact coordinates are provided in Table 1.

cypress (*Taxodium ascendens*) and loblolly pine (*Pinus elliotii*), and a ground flora of grasses (*Panicum-Andropogon*). A grass-sedge marsh was selected as a representative of ecosystem type W20 which has a ground flora of grasses (*Panicum-Leersia*) and no overstory. A streamside riparian wetland was selected as a representative of ecosystem type W5, which is vegetated primarily by full overstory, old-growth cypress (*Taxodium ascendens*).

The ecological gradient followed by these wetlands also corresponds to the relative amount of direct sunlight reaching the water in each system. Although quantitative data are limited, an estimate of 6% sunlight transmittance at noon during the growing season was reported for the cypress-gum swamp (Aleric and Kirkman, in press). With only sparse emergent grass to attenuate light reaching the water, light transmittance in the marsh probably approaches 100%. The cypress savanna is between these extremes. A recent survey indicated that many of these wetlands showed little impact from human activities, and are, therefore, relatively pristine (Lynch et al. 1986).

Oxygen consumption and substrate limitation experiments

During each sampling event, a 12–20 l carboy was filled with water from about 10 cm underneath the surface microlayer. The carboy was filled completely to the top and capped to minimize any oxygen exchange with the atmosphere. The sample was then taken to a field vehicle so that incubation bottles could be filled with minimal delay. For each water sample, oxygen consumption experiments were set up as depicted in Figure 2. The BOD bottles were filled by siphoning water through silicone tubing. The end of the tubing was placed at the bottom of the bottles and approximately 3 times the bottle volume was allowed to overflow prior to slowly removing the tubing. The bottles were capped using ground glass stoppers.

For whole water oxygen consumption rates, four bottles were immediately fixed for determination of initial oxygen concentration. After 5–8 h, a second set of four bottles was fixed. A 5–8 h incubation period was chosen because this time interval was adequate time to measure changes in oxygen concentration while minimizing bottle effects (Benner et al. 1995; this study). For substrate amendment studies, the remaining eight bottles were treated as follows. Duplicate bottles were spiked with a solution of one of the following: $Na_2HPO_4 \cdot 7H_2O$, $NaNO_3$, NH_4Cl, $C_6H_{12}O_6$ to yield final concentrations of 300, 140, 140, and 700 μg/l, respectively. These additions ensured that final nutrient concentrations were well in excess of background values. The bottles were amended with substrate and incubated for 24 h before fixing. All bottles were incubated under dark conditions to prevent any photosynthetic activity from adding oxygen to the incubations. Incubations were carried out at the same temperatures for the different wetlands in order to allow for comparison of rates under similar conditions.

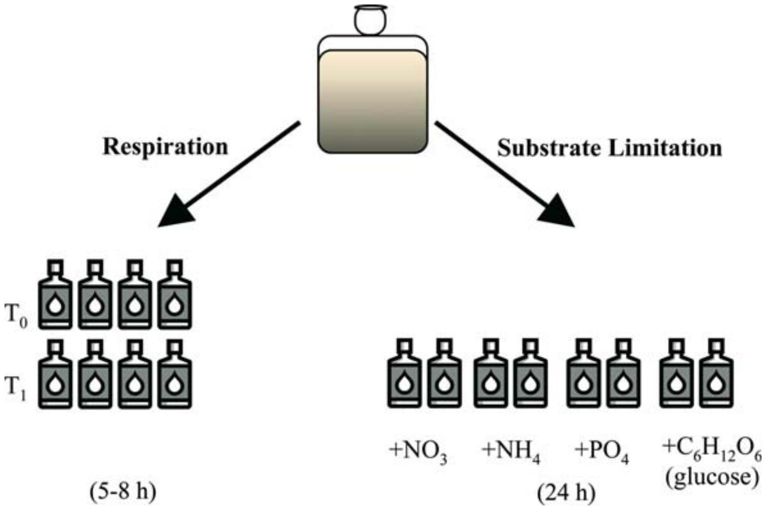

Figure 2. Experimental design used for measuring whole water oxygen consumption rates and growth limiting substrate of microbial communities.

A similar experimental design was used to look at longer-term, whole water oxygen consumption during 15 d incubations. In these experiments, water was aerated to near saturation prior to filling the BOD bottles. Aeration was necessary because ambient oxygen concentrations in some wetlands were at times below 100 μM and the available oxygen would be used up over a relatively short period of time. In each experiment, 24 BOD bottles were filled, and four samples were preserved at 0, 3, 6, 9, 12, and 15 d intervals.

The technique for measuring dissolved oxygen was based on a modified Winkler method (Carpenter 1965). Briefly, samples in BOD bottles were fixed immediately with 0.5 ml of a 1.2 M $MnSO_4 \cdot 5H_2O$ solution followed by 0.5 ml of a NaI/NaOH solution (12.5 M NaOH, 0.9 M NaI), and then shaken vigorously. After all samples were fixed, a 1.0 ml aliquot of 50% (v/v) of H_2SO_4 was added. A 50 ml aliquot was transferred to a sample cup using a volumetric pipette and immediately titrated using a 4.2 mM solution of $Na_2S_2O_3 \cdot 5H_20$. Titrations were made by a Mettler DL50 Graphix titrator using a platinum electrode which provides a potentiometric endpoint determination (Oudot et al. 1994; Graneli and Graneli 1991).

Inorganic and organic chemistry

Prior to water sample collection, all glassware and plasticware were washed with detergent, rinsed in hot water, soaked in 10% HCl, and rinsed with high purity water. A 2 l water sample was collected from study sites at the same time that the oxygen consumption experiments were set up. Water samples were put on ice and transported to the lab. Samples were filtered through glass fiber filters (GFF). Subsamples for NO_3/NO_2 and PO_4 analyses were stored frozen until analysis. Subsamples for NH_4 were treated with sodium phenolate and stored at 2 °C until analysis. All nutrient analyses were carried out using a Latchet autoanalyzer according to manufacturer's guidelines. Phosphate determinations are considered to represent soluble reactive phosphorous (SRP). DOC measurements were made according to the method of Benner and Strom (1993) using a Shimadzu TOC-V series total carbon analyzer.

A 1 l aliquot of each filtered water sample was lyophilized. The dried powder was collected and homogenized. A subsample was treated by vapor phase acidification to remove any inorganic carbon and analyzed for its organic carbon content using a Carlo Erba elemental analyzer (Hedges and Stern 1985). The dried powder was also analyzed for its lignin phenol composition based on the method of Hedges and Ertel (1982). A subsample was subjected to CuO oxidation and the resulting oxidation products were separated on an Agilent GC/MS 6890 system for both positive identification and quantification of the 6 major phenols derived exclusively from lignin (vanillin, acetovanillone, vanillic acid, syringaldehyde, acetosyringone, syringic acid). Sum 6 is used to represent to concentration of all 6 phenols in ng/l. Lambda 6 represents the amount of the 6 phenols normalized to organic carbon (expressed as mg phenol/100 mg OC). S/V is calculated from the sum of the three syringyl divided by the sum of the three vanillyl phenols. Cinnamic acid and ferulic acid were also measured to calculate C/V ratios, which is the sum of the two cinnamyl phenols divided by the sum of the three vanillyl phenols. Acid to aldehyde ratios, Ad/Alv and Ad/Als, were calculated from vanillin/vanillic acid and syringaldehyde/syringic acid, respectively. A second subsample was treated by vapor phase acidification and analyzed for its $\delta^{13}C$ composition. These analyses were carried out at the UC-Davis stable isotope facility, and are expressed relative to the PDB standard.

Results

Hydroperiods

The year 2000 represented one of the most extreme drought years on record with many stream and groundwater levels reaching record lows (Alhadeff and McCallum 2001). At the onset of 2001, W19 and W5 were completely dry, and W18 and W20 had measurable water at their deepest points (Figure 3). However, the vast majority of the surface areas of W18 and W20 were dry. Winter rains in 2001 were sparse in January and February. Between March and mid-April frequent strong storms resulted in approximately 45 cm of rainfall. The limesink wetlands remained flooded into the summer and all wetlands showed an increase in water levels during the June/July rains. Water persisted for about three months in W5, but as a riparian wetland, it became separated

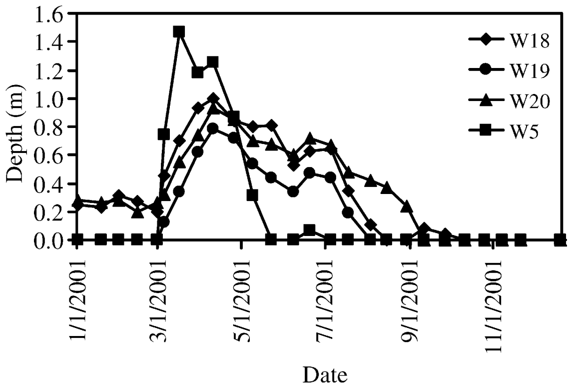

Figure 3. 2001 hydrographs for W18, W19, W20, and W5.

from its parent stream and was the fastest among all wetlands to dry. Irregular rainfall occurred throughout the remainder of the year, including one strong system in early September that produced heavy rainfall. Only W18 increased in volume from the heavy September rainfall.

Temperature and water chemistry

Temperature and water chemistry was assessed for all wetlands during each sampling event (Table 1). W20 had the highest average temperature which is consistent with a lack of canopy cover in a marsh wetland. W5 had the lowest average temperature, which is a function of well shaded, streamside habitat rather than upland habitat in which limesink wetlands exist. Ambient oxygen concentrations ranged from 0.9 to 6.3 mg/l with mean values from all wetlands showing that oxygen saturation is typically below 50%. Mean nutrient chemistry values and ranges indicated that water chemistry was generally similar in the three limesink wetlands, although average ammonium concentrations in W20 were substantially higher due to a single high value measured on May 21, 2001. Similarly, W5 had a single high NH_4 value which substantially elevated its average concentration. W5 also had higher average nitrate concentrations. In this instance, higher nitrate was caused by overbank flooding from the adjacent stream which had relatively high average nitrate concentrations. These results are generally consistent with those of Battle and Golladay (2001) that were made during the flooded periods of 1997–1998. Notably, each limesink wetland had a single sampling date in which phosphate was unmeasurable. With the occasional exception of PO_4 depletion, all wetlands appeared to consistently have measurable pools of dissolved nutrients (NH_4, NO_3 and PO_4).

DOC concentrations were high, ranging from 10 to 40 mg/l among all wetlands during the study period (Figure 4). DOC was relatively low in the

Table 1. Coordinates, mean temperature, and water chemistry measured during the inundation period of three limesink wetlands (W18, W19, W20) and one riparian wetland (W5) during 2001.

	W18	W19	W20	W5
Latitude (N)	31°13′38.74″	31°15′33.29″	31°16′15.30″	31°17′3.99″
Longitude (W)	84°29′8.28″	84°31′45.33″	84°30′27.54″	84°29′3.75″
Temp. (°C)	20.3 (12.0–26.0)	20.4 (10.0–24.5)	22.0 (13.0–27.5)	19.5 (12.0–23.0)
DO (mg/l)	2.6 (0.9–5.1)	3.7 (2.4–4.6)	3.9 (2.0–6.3)	3.5 (1.7–5.3)
NH_4-N (μg/l)	22.4 (13.5–30.1)	20.8 (0.0–54.7)	132 (5.0–273)	459 (39.4–1177)
NO_3-N (μg/l)	8.3 (2.7–20.2)	6.9 (2.4–14.0)	6.4 (2.1–19.3)	72.3 (6.6–146.4)
PO_4-P (μg/l)	8.2 (0.0–30.4)	3.1 (0–4.4)	3.0 (0.0–5.6)	24.8 (8.8–65.1)

Ranges are provided in parenthesis.
DO – dissolved oxygen.

early spring subsequent to flooding. Initial DOC concentrations varied consistently across the ecological gradient documented for limesink wetlands with highest mean DOC concentrations found in W18, somewhat lower concentration in W19, and the lowest in W20. All wetlands showed increasing DOC concentrations as the season progressed, but changes towards the end of the flooded cycle varied among wetlands. Similar to Johnson and Ward (1996), DOC concentrations corresponded to temperature with lower values (15.1 ± 5.2 mg/l) occurring at temperatures < 20 °C and higher values (24.8 ± 8.2 mg/l) at temperatures > 20 °C. Although changes in DOC concentrations were observed during the study, relative differences in DOC concentration continued to follow the ecological gradient.

In March 2001, dissolved lignin phenols (sum 6) concentrations ranged from 250 μg/l in W20 to 411 μg/l in W18 (Table 2). Similar to bulk DOC, early sum 6 concentrations varied consistently across the ecological gradient of

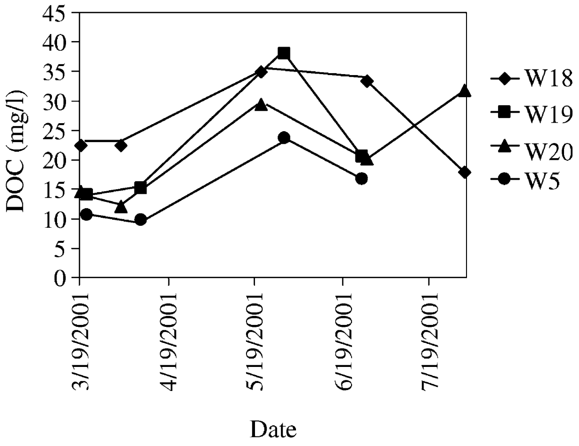

Figure 4. Wetland dissolved organic carbon (DOC) concentrations measured during the 2001 hydrograph.

Table 2. Lignin phenol parameters and stable carbon isotope ($\delta^{13}C$) composition of DOM during the inundation period of three limesink wetlands and one riparian wetland in 2001.

		3/19/2001	3/21/2001	5/29/2001	6/25/2001	6/27/2001	7/31/2001	Mean ± SD
Sum 6(μg/l)	W18	411				295	190	299 ± 110
	W19		323	311	123			252 ± 112
	W20	250				99	57	135 ± 101
	W5		280	183	136			200 ± 73
Lambda 6(mg phenols/100 mg OC)	W18	2.02				2.86	1.06	1.98 ± 0.98
	W19		2.71	0.82	0.60			1.37 ± 1.16
	W20	2.42				0.49	0.18	0.97 ± 1.11
	W5		2.75	0.77	0.81			1.44 ± 1.13
S/V	W18	0.49				0.60	0.61	0.57 ± 0.07
	W19		0.31	0.06	0.42			0.27 ± 0.18
	W20	0.86				0.90	1.25	1.00 ± 0.21
	W5		0.90	0.48	0.38			0.59 ± 0.28
C/V	W18	0.09				0.16	0.22	0.16 ± 0.07
	W19		0.15	0.10	0.19			0.15 ± 0.05
	W20	0.21				0.28	0.42	0.30 ± 0.11
	W5		0.08	0.12	0.11			0.10 ± 0.02
V(ad/al)	W18	0.92				0.86	0.87	0.88 ± 0.03
	W19		0.77	0.94	0.85			0.85 ± 0.09
	W20	0.96				1.06	1.09	1.04 ± 0.07
	W5		0.90	0.90	0.97			0.92 ± 0.04
S(ad/al)	W18	0.61				0.73	0.69	0.68 ± 0.06
	W19		0.72	0.64	0.62			0.66 ± 0.05
	W20	0.82				0.72	0.71	0.75 ± 0.06
	W5		0.77	0.82	0.68			0.76 ± 0.07
$\delta^{13}C$(‰)	W18	−28.41				−26.83	−28.82	−28.0 ± 1.1
	W19		−28.08	−27.45	−27.28			−27.6 ± 0.4
	W20	−27.01				−26.66	−26.80	−26.8 ± 0.2
	W5		−28.25	−27.69	−26.63			−27.5 ± 0.8

See methods section in text for abbreviations. $\delta^{13}C$ expressed relative to PDB standard.

vegetation cover with W18 having the highest dissolved lignin concentrations followed by W19, and then W20. In contrast to DOC, sum 6 concentrations decreased dramatically in all wetlands during the inundation period. The magnitude of change ranged from a 49% reduction in W5 to a 77% reduction in W20. Although large decreases in sum 6 were observed throughout the study, the relative distribution of sum 6 concentrations still followed the ecological gradient.

Lambda 6 differs from sum 6 because it represents the fraction of lignin in DOC (mg lignin phenol/100 mg OC) rather than lignin concentration. In March 2001, lambda 6 values were similar among wetlands, ranging from 2.0 to 2.8 mg/100 mg OC (Table 2). In all wetlands, lambda 6 values were much lower at the end of the study, with an extremely low value of 0.18 reported for W20. In contrast to the other wetlands, W18 showed an increase in June relative to March, but decreased thereafter. Reductions in lambda 6 indicate that the fraction of dissolved lignin in DOC decreased over the inundation period.

The ratios derived from dissolved lignin phenol analysis can provide useful information for distinguishing organic matter in different aquatic systems. In March, S/V ratios (Table 2) ranged from 0.31 to 0.90, with the highest value reported for W5. Among the limesink wetlands, W20 had a much higher mean S/V value than W19 and W18. The C/V ratios did not show any consistent temporal trends. The mean C/V value was about two fold higher at W20 than W19 and W18, while W5 had the lowest C/V. The Vad/al and Sad/al ratios were relatively constant over time. Among the limesink wetlands, all Vad/al ratios differed considerably, but Sad/al ratios did not. The Ad/Al ratios in W5 fell within the range of those in the limesink wetlands.

The $\delta^{13}C$ values of DOM ranged from -26.6 to -28.8 ppm during the study period (Table 2). The initial $\delta^{13}C$ value for W20 was enriched relative to the other wetlands. W20, W19 and W5 showed a net enrichment in ^{13}C ($\delta^{13}C$ became more positive), while $\delta^{13}C$ in W18 varied.

Oxygen metabolism

Oxygen consumption rates ranged from 0.0 to 2.7 μM/h among all the wetlands over the entire study period (Figure 5). In all wetlands, oxygen consumption rates were lowest during March, shortly after flooding. Oxygen consumption rates were higher in April and continued to increase in May. In June, oxygen consumption rates in W18, W19, and W20 were even higher, whereas the W5 oxygen consumption rate dropped. Overall, W5 had the highest mean oxygen consumption rates (1.9 μM/h), followed by W20 (1.6 μM/h), W19 (1.3 μM/h), and W18 (1.0 μM/h). Among the limesink wetlands, comparative rates followed the ecological gradient.

Continued oxygen metabolism was evident throughout the long-term incubations for all wetlands (Figure 6a–d). Oxygen consumption for W18, W19,

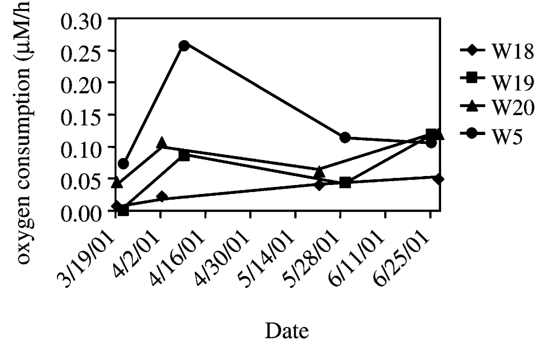

Figure 5. Wetland whole water oxygen consumption rates measured during the 2001 hydrograph.

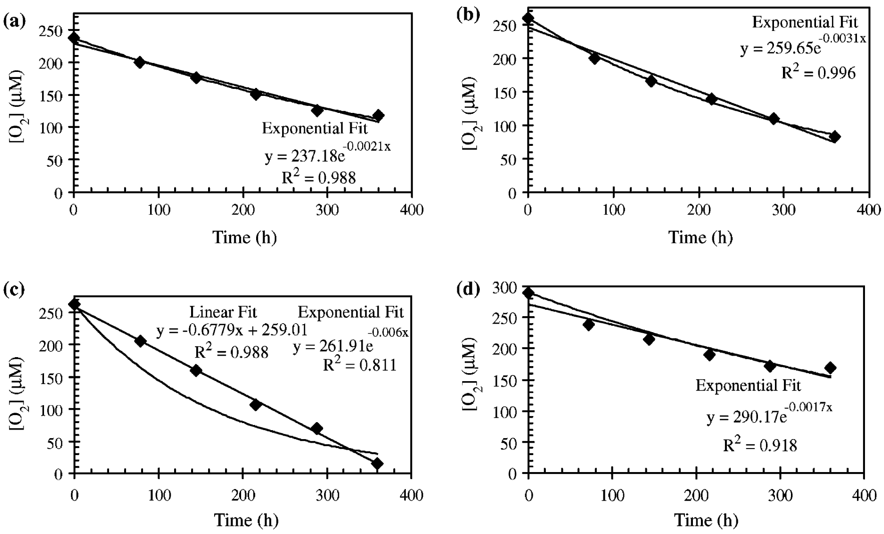

Figure 6. Long-term (15 d) whole water oxygen consumption in W18 (a), W19 (b), W20 (c), and W5 (d).

and W5 fit both linear and exponential models well. With the exception of W20, there was a small, but progressive, decrease in oxygen consumption rates over time. Slightly higher oxygen consumption rates between the first two time intervals of these experiments provide support for using relatively short incubations for comparing water column oxygen consumption rates among systems. Oxygen utilization for W20 was linear and almost all oxygen was consumed by the end of the 15 d incubation. Using the slope of the linear regressions for limesink wetlands, the highest oxygen consumption rate was observed at W20 (0.68 μM/h) followed by W19 (0.48 μM/h), and W18 (0.34 μM/h). The long-term patterns of oxygen consumption rates among the limesink wetlands were similar to those observed during the short term incubations and were consistent across the ecological gradient.

Growth limiting substrate determinations were made with each oxygen consumption experiment. In all but three incubations, the addition of glucose stimulated oxygen consumption, whereas the addition of individual inorganic nutrients had little effect (Table 3). This is consistent with the water chemistry data which indicate that inorganic P and N are usually present and available to the microbial communities (Table 1). P limitation was clearly evident in the cypress-gum swamp on one occasion and coincided with a date on which PO_4 was below the detection limit. In the cypress-savanna P was below the detection limit on one occasion, but OC was found to limit growth. Stimulation by OC was not expected when ambient P concentrations were low. It is possible that remineralization of organic P could meet the P demand under these conditions. Organic P would not be detected in the analysis for SRP. In two other experiments, substrate limitation could not be determined because all amendments completely depleted available oxygen.

Discussion

Comparisons with other systems

DOC concentrations ranged from 10 to 40 mg/l (Figure 4) and were comparable to those measured in other wetland types such as cypress deepwater swamps, freshwater marshes, and bogs (Thurman 1985). These values fell within the range of those reported in a survey of forty nine Carolina bays (Newman and Schalles 1990), which are another form of shallow, isolated wetlands that are common within the coastal plain provinces of North and South Carolina. These values are also similar to those reported for blackwater streams of the southeast Coastal Plain (e.g. Meyer 1986), including those

Table 3. Substrates limiting oxygen consumption by microbial communities based on enhanced oxygen consumption following amendment with an inorganic nutrient or glucose.

	W18	W19	W20	W5
3/19/2001	ND		OC	
3/21/2001		OC		OC
4/02/2001	P*		OC	
4/09/2001		OC*		OC
5/21/2001	OC		OC	
5/29/2001		OC		OC
6/25/2001		OC		OC
6/27/2001	OC		OC	
7/31/2001	ND*		ND*	
9/05/2001	OC		OC	

OC – organic carbon limitation; P – phosphate limitation; ND – not determined because all incubations caused complete oxygen depletion; * – PO_4 concentration ~ 0.

within the study area. However, blackwater stream DOC is primarily allochthonous whereas limesink wetland DOC is primarily autochthonous. Relatively high DOC concentrations are consistent with high rates of litterfall that have been reported for forested limesink wetlands in this study area (Watt and Golladay 1999).

Initial dissolved lignin concentrations (250–411 μg/l) in these wetlands were among the highest that have been reported in any aquatic ecosystem, although none have been previously published for wetlands (Table 2). Concentrations reported for larger rivers including the Mississippi River, the Amazon River, and several Arctic rivers are lower, ranging from 10–35 μg/l (Opsahl and Benner 1997, 1998; Opsahl et al. 1999). More comparatively, a concentration 138 μg/l was reported for the Satilla River, a blackwater Coastal Plain stream in south Georgia (Opsahl and Zepp 2001). Early lambda 6 values ranging from 2 to 2.8 mg/100 mg OC, were high relative to other systems. For comparison, the lambda 6 values of the above-mentioned rivers ranged from 0.5 to 1.5, indicating that the fraction of dissolved lignin in DOC present early in the hydroperiod of limesink wetlands is higher than in most other aquatic ecosystems. The δ^{13}C values are all similar to those reported for DOM in streams, and similar to average values of most C-3 vegetation (Trumbore and Druffel 1995).

Drivers of changes in substrate quality

DOC in limesink wetlands likely represents a combination of several sources including carryover that is stored in underlying soils, additional leaching of the previous year's litter fall after resaturation, and further degradation of the large layer of benthic leaf litter. Increases in DOC concentrations over the inundation period were observed in all wetlands. Increases through the growing season can result from several processes. Primary productivity by vascular plants and algae is evident during the growing season. Plant growth provides pathways by which fresh soluble DOM can enter the system relatively rapidly through leaching and excretion. However, high rates of litterfall associated with new productivity do not occur until the fall and winter, usually after the wetlands dry out. Another factor that can contribute to the observed increases in DOC concentration is evaporative concentration. Regardless of the interaction of these factors, all systems showed a consistent pattern of increase between the early and mid phases of the inundation period that largely follow the ecological gradient.

Although large changes in DOC were evident, bulk DOC measurements carry no compositional information about the DOM pool. Dissolved lignin is a specific component of DOC that is often used as a proxy for the biologically refractory aromatic component of DOM. Sum 6 showed 49–77% decreases over time providing evidence for a reduction in the aromatic content of the DOM pool (Table 2). The compositional changes were even more pronounced when dissolved lignin was normalized to the amount of DOC, with lambda 6 values decreasing 48–92%. The general trend of $\delta^{13}C$ values becoming more positive is consistent with the lignin phenol data, with the exception of one $\delta^{13}C$ value in W18. Aromatic compounds including lignin are generally more depleted in ^{13}C and reductions in aromatic compound will cause $\delta^{13}C$ values to become heavier (more positive). Therefore, the $\delta^{13}C$ trends provide supportive evidence that the larger pool of aromatic compounds behaves similarly to the dissolved lignin component. It appears as though aromatic DOM represents a progressively smaller fraction of the DOM pools in these wetlands over the inundation period.

Photochemical oxidation should be important in these wetlands given the high concentrations of aromatic carbon and seasonally high levels of solar UV radiation at these latitudes. S/V ratios have been shown experimentally to decrease as a function of photochemical degradation and can provide a useful indicator of prior photochemical degradation of DOM *in situ* (Benner and Opsahl 2001; Opsahl and Zepp 2001). However, with the exception of W5, S/V ratios in all wetlands showed small net increases during the inundation period. While this does not rule out the possibility of substantial photochemical degradation in these systems, it appears as though the mechanisms which can increase S/V ratios are more than enough to offset any change caused by photochemical degradation. Selective microbial degradation of V phenols and inputs of vascular plant debris with higher S/V values are two possibilities that could have contributed to the small increases in S/V.

Microbiological degradation of aromatic carbon is much slower than photochemical degradation of aromatic carbon (Opsahl and Zepp 2001) and not likely to explain the 2–5 fold decreases in dissolved lignin in the wetlands (Table 2). An influx of DOM from algal production could contribute to the observed decrease in lignin concentrations because algae are not vascular plants and, therefore, produce lignin-free DOM. Light availability varies across the ecological gradient and may control algal productivity with less algal production in the full canopy swamp (W18) and more in the marsh savanna (W20). A light-driven gradient in algal productivity may be consistent with the gradient of change observed in dissolved lignin concentrations. What is confounding in this study is that two of the important controls on DOM composition, algal productivity and photochemical degradation, yield similar changes in lignin composition, so the predominance of one process over the other can not be inferred from the available data.

Distinguishing vascular plant sources of DOM

The S/V ratio is often used to express the relative contributions of gymnosperm vs. angiosperm vegetation because gymnosperms have no syringyl phenols ($S/V \sim 0$), whereas angiosperms, including flowering plants and grasses, have abundant syringyl phenols ($S/V \sim 0.5$–2.0). Mean S/V values among limesink

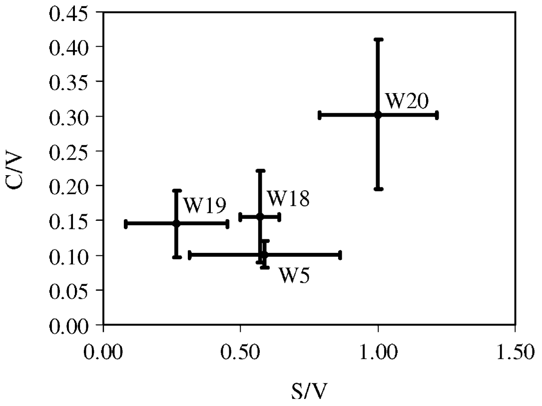

Figure 7. Property–property plot of C/V vs. S/V lignin compositional parameters.

wetlands were all considerably different (Table 2). The gradient of S/V values is consistent with the predominance of cypress (S/V ~ 0) within these systems. Tree cover in W19 is dominated by cypress and had the lowest average S/V, W18 is mixed cypress/gum and was intermediate, and W20 has no cypress and had the highest average S/V. Mean C/V values were slightly higher in W20 than W19 and W18. A property–property plot of C/V vs. S/V draws out these differences in the lignin molecular fingerprint (Figure 7). The higher S/V and C/V in W20 is consistent with the dominance of grass productivity in marshes which has high S/V and C/V relative to most other leaf litter (Hedges and Mann 1979).

In the riparian wetland (W5), S/V decreased substantially over the inundation period. The initially high S/V may be more reflective of inputs of riverine dissolved lignin brought in as this wetland was filled by the adjacent stream during the spring flood. Stream S/V signatures of ~1.0 are characteristic of temperate and tropical streams that have a significant contribution of angiosperm vegetation within their drainage basin (Opsahl and Benner 1997). Lower riverine values of S/V (0.2–0.4) have only been reported in Arctic rivers in which coniferous (gymnosperm) dominated forests predominate (Opsahl et al. 1999). Subsequent declines in S/V in W5 may have resulted from inputs of cypress litter (which dominates the canopy) through leaching and decomposition of material with an S/V of ~0.

Oxygen metabolism and organic matter bioavailability

Nitrification in wetland soils (White and Reddy 2003) and on macrophyte detritus (Eriksson and Andersson 1999) can be significant. However, rates of water column nitrification in limesink wetlands are likely to be low because ambient concentrations of NH_4 are relatively low and the pH values of the wetlands are acidic, conditions that are generally not conducive to nitrification (Brock and Madigan 1988). Furthermore, oxygen consumption continued well beyond the period in which background NH_4 would be used up. Finally, the additions of excess NH_4 in the substrate amendment experiments did not appear to further stimulate oxygen consumption.

Assuming that heterotrophic oxygen consumption is the dominant mechanism of oxygen removal, the observed trends in oxygen consumption among wetlands is indicative of differences in organic matter bioavailability. In both the short and long-term experiments, there were consistent differences in oxygen consumption rates among the limesink wetlands (Figures 5 and 6). These differences were consistent with the ecological gradient with the highest rates in W20, followed by W19, and then W18. Therefore, among the organic matter components that are being utilized, those in W20 appear to be more reactive, on average, than those in W19 and W18, respectively.

Further relationships between organic matter bioavailability and microbial oxygen consumption in the wetlands were also drawn out in the nutrient amendment experiments (Table 3). With few exceptions, growth was almost always stimulated by the addition of glucose, with inorganic nutrients having little or no effect. In many instances, glucose additions caused a complete depletion of oxygen within 24 h. Glucose is a very labile form of organic carbon that can be taken up by microbes through both group translocation and active transport (Brock and Madigan 1988). It appears that microbial communities in limesink wetlands can quickly assimilate added glucose leading to an increase in oxygen consumption. Rapid assimilation of glucose implies that there are very low ambient concentrations of highly bioavailable organic compounds, such as glucose. If other organic compounds such as free amino acids have a similar stimulatory effect on oxygen consumption, then the production rate of these highly bioavailable compounds is collectively less than the microbial demand for these compounds. What does become available must be quickly taken up by microbial communities, otherwise oxygen consumption rates would be higher and inorganic substrates may become growth limiting. Alternatively, sources of highly bioavailable DOC may be excluded as a function of the experimental design, in which case, oxygen consumption rates would be underestimated compared to those *in situ*.

The observation that inorganic nutrients rarely stimulated oxygen consumption provides supportive evidence that the supply of moderately bioavailable organic matter is a dominant factor supporting microbial metabolism. Further support for a larger pool of moderately bioavailable organic matter came from the long-term incubations (Figure 6). Strong linearity among all incubations was consistent with continued availability of all substrates throughout the incubation. In W18 and W19, rates appeared to taper off slightly over the time course, particularly between 290 and 360 h in W18. Decreasing oxygen consumption rates could result from several factors, including removal of the source of highly bioavailable organic compounds, reduced concentrations of organic matter of moderate bioavailability, or depletion of an inorganic nutrient. In W20, oxygen consumption was clearly linear over the time course indicating no change in rates of organic matter utilization and no nutrient depletion. Although small reductions in oxygen consumption rates were evident in some of the wetlands, it can be concluded that ambient pools of organic matter and nutrients can sustain continued oxygen consumption for at least 2 weeks.

Although there appear to be small pools of highly labile organic matter and larger pools of moderately bioavailable organic matter, their magnitudes relative to the biorefractory organic matter fractions remain unknown. Even though patterns of both DOC and respiration showed increases over the course of the study, only W18 showed a strong relationship between the concentration of DOC and oxygen consumption rates ($r^2 = 0.91$, $p < 0.05$). In W19, W20 and W5, there was not a strong relationship between oxygen consumption and DOC concentration. It appears as though the concentration of DOC by itself is not a good indicator of bioavailability of organic matter in these wetlands.

Ecological implications

The isolated limesink and riparian wetlands showed a number of different biogeochemical attributes which varied consistently across the previously documented ecological gradient (Figure 8). Initial DOC and lignin concentrations were highest in the closed canopy system (W18), lower in the cypress savanna (W19), and lowest in the marsh savanna (W20). Although DOC and lignin concentrations changed over time, the relative differences among wetlands remained essentially the same. The reverse pattern was evident for

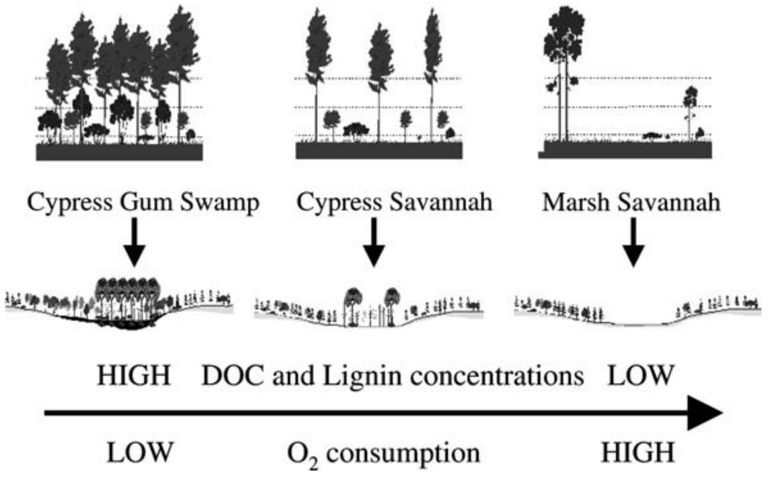

Figure 8. Conceptual model of the ecological gradient of limesink wetlands and the observed trends relating to organic matter composition and oxygen consumption.

oxygen consumption, in which the closed canopy system had the lowest rates with progressively higher rates as canopy cover decreased. In summary, the marsh savanna had the lowest ambient DOC concentrations, the largest changes in its DOM composition, and the highest rates of water column oxygen consumption.

The changes in organic matter composition based on changes in $\delta^{13}C$ and dissolved lignin (Table 2) were consistent with the ecological gradient. Inherent within this gradient is sunlight intensity which ranges from extremely low in cypress swamps and riparian wetlands to full sunlight in the marsh savannas. These results are consistent with photochemical degradation because dissolved lignin, which is highly photoreactive, decreased progressively with higher light intensity, and microbial activity increased progressively with higher light intensity, presumably at the expense of labile photoproducts. However, sunlight can also contribute to the observed changes by supporting algal production. Higher rates of algal production at increasing light levels are consistent with reductions in lignin concentrations by dilution with lignin-free DOC. Higher rates of microbial respiration may also be expected if algal DOM is more bioavailable than vascular plant derived DOM in wetlands. Intuitively, photochemical processes and algal production must both be occurring, but determining the magnitude of these different processes will require further study.

The isolated limesink and the riparian wetlands shared some other common attributes. All wetlands appeared to be continually undersaturated in oxygen concentrations and at times, nearly anoxic (Table 1). This results from the combination of water column oxygen consumption and benthic metabolism. Although benthic metabolism was not directly estimated in this study, high rates can be inferred because of the large quantity of benthic leaf litter and low rates of organic matter accumulation over time. With occasional exceptions of P depletion, all wetlands appeared to have an adequate inorganic nutrient supply that could support measured rates of oxygen consumption for periods as long as 15 d (Figure 6a–d). Microbial growth in all wetlands was most often stimulated by labile organic carbon (Table 3).

The observations regarding substrate limitation were informative in terms of contrasting ecosystem-level process. Craft and Chaing (2002) determined that overall primary productivity in cypress savanna wetlands within this same study area was primarily P-limited. Observations from the growth limitation experiments in this study indicate that there is usually, but not always, bioavailable P present in the water column. Therefore, the pool of microbially bioavailable P does not appear to represent an available source of P to vascular plant production, which probably extracts most of its P requirement from soils. A stronger P demand in the wetland soils by both plants and microbial communities may contribute to a greater depletion of available P in soils relative to the water column. In contrast, rates of microbial oxygen consumption in the water column were usually limited by the bioavailability of organic carbon.

However, occasional P-limitation suggests that P may be the most important inorganic compound controlling microbial growth.

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