ENVIRONMENTAL CONTROLS ON RIPARIAN PLANT PRODUCTIVITY

by

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ABSTRACT

While much attention has focused on the decline of riparian forests in the southwestern United States, little mention is made of increases in vegetation along the Colorado River in the Grand Canyon. This research investigated rates of aboveground primary plant productivity and relationships between productivity and environmental controls along a topographic sequence of a single reattachment bar on the Colorado River. Environmental and plant productivity data were collected in May and July 1995. An elevation and nitrogen gradient were discerned by correlation analysis and principal components analysis. The elevation gradient was correlated with soil texture, soil moisture, soil organic matter, soil phosphorus concentrations and potential nitrogen mineralization for May 1995, and the same variables, minus potential nitrogen mineralization for July. The nitrogen component was strongly correlated with nitrate, ammonium, and total inorganic nitrogen in May 1995, and ammonium, total inorganic nitrogen, and potential nitrogen mineralization in July. Minimum annual aboveground productivity ranged from 0 to 2105 g/m^2, and averaged 615 g/m^2. The degree of correlation among environmental controls makes it difficult to definitively conclude what is controlling plant productivity, however, regression analysis suggests soil mositure is most significant in explaining productivity patterns. Environmental patterns indicate the role that geomorphic processes play in creating and maintaining riparian

environments in arid regions. If productivity has indeed increased since closure of Glen Canyon Dam, increased rates of nutrient use and storage by riparian ecosystems may exacerbate the overall importance of the riparian zone to the stream/riparian ecosystem.

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INTRODUCTION

Introduction

A staggering variety of plants inhabit the ecosystems of the world. While plant composition varies over space and time, different plant assemblages never cease to perform their vital function of creating biomass from solar energy and the basic elements of the earth. Biomass produced by these plants contains chemical energy which supports almost all other life forms. Because all other living organisms are dependent upon the energy harvested and stored by plants, primary productivity, or the accrual of biomass per unit area over time, has long been of interest to many scientists.

Riparian ecosystems are the ecotones between a stream and its adjacent uplands. Functioning as transitional zones between the aquatic and terrestrial ecosystems, riparian ecosystems are composed of steep gradients of environmental factors (Gregory et al., 1991) including soil moisture (Gemborys and Hodgkins, 1971; Johnson and Lowe, 1985), nutrient availability (Pinay et al., 1992), and soil texture (Rubin et al., 1990). These gradients create the substrate for vegetative development which reflect the underlying environmental controls. In the arid southwest, the gradients are exacerbated by extreme temperature and moisture deficits in the uplands, creating narrow riparian zones that stand in stark contrast to the adjacent uplands (Mitsch and Gosselink, 1993).

Two theories pervasive in ecological literature address riparian plant productivity: the flood-pulse theory (Junk et al, 1989) and the nutrient-spiralling theory (Newbould et al., 1981). The flood-pulse theory most directly addresses the riparian zone, suggesting that high productivity in riparian zones is maintained by the input of nutrients and sediments during seasonal flooding. However, other studies performed in the midwestern United States (Brown and Peterson, 1983; Mitsch and Rust, 1984) have indicated that the presence of flooding may not have a direct positive effect on productivity. Additionally, along the Colorado River in the Grand Canyon, results of several studies (Turner and Karpiscak, 1982; Stevens et al., 1995) indicate that vegetative development has increased since the closure of Glen Canyon Dam. These results suggest that in the arid southwest, flood disturbance may limit productivity, and that the flood-pulse theory may not be directly applicable.

Nutrient spiralling links the movement of nutrients through a stream system to physical transport by the stream and biological utilization of nutrients (Newbould et al., 1981). Four interacting components comprise a desert stream ecosystems: the surface stream, hyporheic, parafluvial, and riparian zones (Holmes et al., 1994). Fluxes occurring across the stream/riparian boundary provide pathways for nutrient transfers between adjacent ecosystems (Ward, 1989). Plant productivity increases biological uptake and utilitzation of nutrients, which suggests that riparian plant productivity may play a significant role in the overall movement and conservation of nutrients in desert stream ecosystems.

Research on the structure and function of riparian zones has increased in recent years, however, there is a paucity of data regarding the productivity of riparian ecosystems in the arid southwest (Mitsch and Gosselink, 1993). While riparian zones are stated to be productive and diverse (Nilsson, 1984), little quantitative literature exists on the subject of productivity, and what does exist has been generated from environments quite different from the deserts of the southwest. Given the importance of primary production to other ecosystem functions, the relationship of riparian productivity to the flood-pulse and nutrient spiralling theories, and the regional importance of riparian ecosystems in the arid regions, the lack of data for riparian plant productivity in the soutwestern United States indicates a need for quantitive study. The purpose of this study, therefore, is to quantify net aboveground primary productivity (NAPP) at a fluvial marsh along the Colorado River in the Grand Canyon and to investigate the dynamic relationship between plant productivity and environmental factors controlling it. This research will provide contributions to riparian ecological theory by: (1) quantifying spatial patterns of biomass accrual; (2) further refining the understanding of the relationship between these patterns and environmental controls at the scale of a single reattachment bar; (3) providing quantitative data that will lend itself to inclusion in models of nutrient spiralling, clarifying the role of the riparian zone in overall stream system nutrient retention; and (4) providing baseline data for an investigation into the validity of the flood-pulse theory.

Research Questions

The goals of this study are to understand the controls of NAPP in arid regions and to clarify the role of riparian plant productivity in the conservation and cycling of nutrients within a stream ecosystem. Kwagunt Marsh, located approximately 89 km (55 miles) downstream of Lee's Ferry along the Colorado River in the Grand Canyon, was selected for this study because it is located on a large alluvial bar with varied topography and substrate (Rubin et al., 1990), it has a variety of vegetation assemblages within close proximity to each other, and its physical and ecological history have been documented (Rubin et al., 1990; Stevens et al., 1995). Additionally, it was subjected to experimental flooding in April 1996, making this location and study appropriate for continuation in a test of the flood-pulse hypothesis.

This study quantitatively examines patterns of biomass accrual and community structure along a topographic sequence and examines the relationship of those patterns to environmental controls. The specific research questions investigated were:

(1) What patterns in community structure and NAPP emerge from quantitative analysis of the study area?

(2) How are the patterns in NAPP and community structure explained

by environmental conditions at the site?

LITERATURE REVIEW

The term ecosystem was first coined by Tansley (1935), to define a unit of study in ecology. The ecosystem, according to Tansley, is the basic unit of nature, and is comprised of "...not only the organism-complex, but also the whole complex of physical factors forming what we call the environment..." (Tansley, 1935 p. 299). Within a given ecosystem, biotic components interact with the physical environment in such a manner that the flow of energy leads to "...a characteristic trophic structure and material cycles within the system" (Odum, 1969 p. 262). By reducing the unit of biological study to a system, analysis progresses towards examination of the processes and functions performed by the system.

Research into primary productivity examines the flow of energy through an ecosystem. At the physiological level, research has determined the primary controls of plant productivity. Plant productivity can be understood as a biological input-output system, with primary climatic inputs being light energy, water, and CO_2 (Cooper, 1973). Utilization of these components is altered by temperature and nutrient stress (Cooper, 1973). While the theoretical factors controlling plant productivity are understood, there is a need for research to examine how these variables interact in different geographic regions and ecological communities (Mitsch and Gosselink, 1993).

While literature on wetland productivity is abundant (Keefe, 1972; Auclair et al., 1976; Mason and Bryant, 1974; Mitch and Ewel, 1979), a literature search yielded little research on productivity of riparian zones in the arid southwest. Smith and others (1991) investigated leaf area and branch length changes in riparian trees along diverted and undiverted reaches of Bishop Creek in California. They concluded that in diverted area, water stressed plants produced smaller leaves and had lower leaf area per unit branch length. Similarly, Stromberg and others (1993) investigated a variety of growth parameters for *Prosopis velutina* along a moisture gradient, finding that performance was significantly better in mesic (riparian), rather than xeric sites (uplands). Growth of *Salix exigua* and *Tamarix ramosissima* in relation to plant water relations was investigated by Stevens and Ayers (1993), who found that growth of *S. exigua* was negatively correlated with stage elevation, and that chronically low plant water potential resulted in decreased growth. Stevens and others (1995), in an investigation into fluvial marshes along the Colorado River, found mean standing ash-free mass to be 641 $g/c/m^2$, and stated that productivity is related to inundation regime, soil texture and patch age.

STUDY AREA

Kwagunt Marsh is located approximately 89 km downstream from Lee's Ferry along the Colorado River in the Grand Canyon (Figure 1). The marsh is located on a larger than average but mophologically representative reattachment bar (Rubin et al., 1990). The xeric environment above the riparian zone at Kwagunt Marsh supports Sonoran Desert vegetation, including the *Opuntia* sp., *Encelia frutescens*, *Lycium andersonii*, and *Acacia greggii*. Directly below the xeric zone, *Prosopis velutina* trees dominate in the Colorado River's historical Old Highwater Zone (OHWZ). Adjacent to the OHWZ, mature *Tamarix ramosissimi* trees dominate in what is known as the New Highwater Zone (NHWZ). The marsh exists on a low lying platform, and is separated from the NHWZ by a return channel. Vegetatively, the study area contains many common assemblages present along the course of the river. Specifically, within the study area, there are five distinct assemblages present. Assemblages are listed from the river to the return channel accordingly: a frequently innundated zone directly adjacent to the river, dominated by *Equisetum arvese*; a dense stand of *Phragmites australis* in lower elevations. a *Salix exigua/Equisetum hiemale* assemblage that often includes *Muhlenbergia asperifolia*: a *Tamarix ramosissimi* stand on higher elevations: and finally the return channel which is dominated by *Carex aquaitlus*. A map showing stage elevations, species common to each

Figure 1. Location of Kwagunt Marsh.

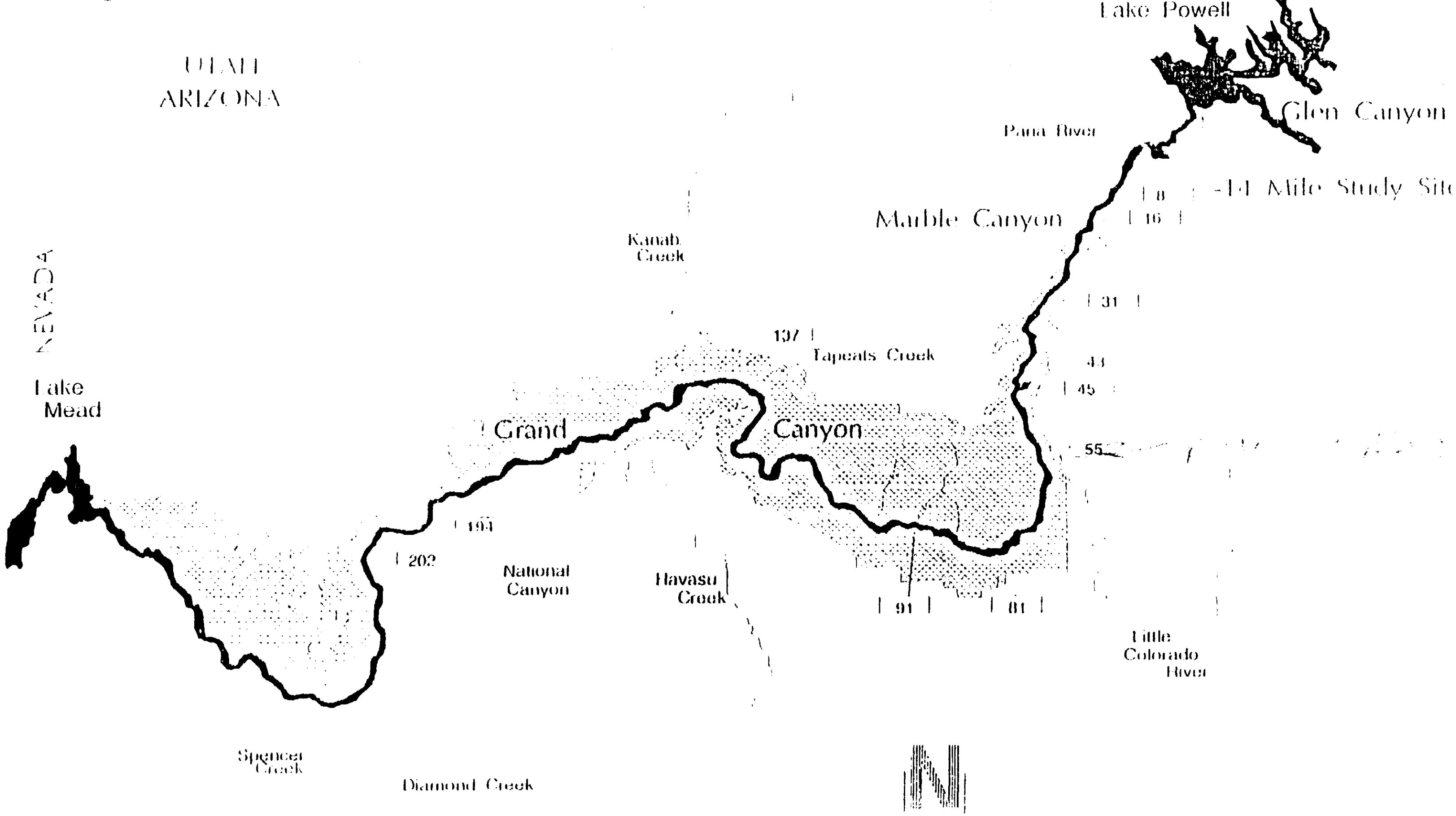
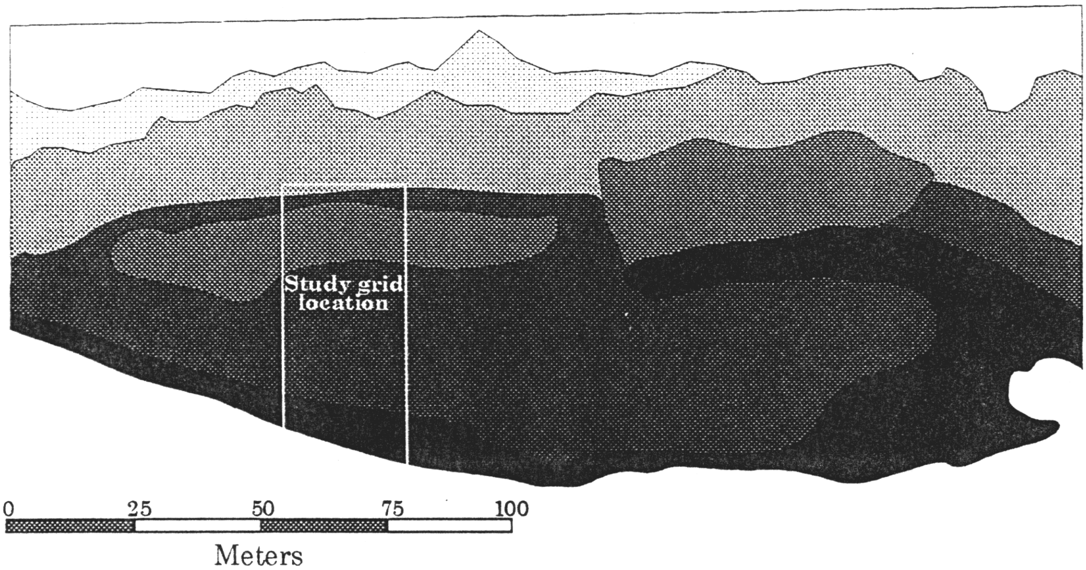


Figure 1. Location of Kwagunt Marsh. Marked river miles indicate locations of climatological studies performed in conjunction with this research. After Glen Canyon Environmental Studies (unpublished).

stage, and study grid location is provided as Figure 2. The base map and vegetative data were provided by L. E. Stevens from unpublished research.

The study area ranges in elevation from 843.093 to 844.821 meters above sea level. Because the river level changes based upon releases from Glen Canyon Dam, all discussions of quadrat locations relative to the river are based upon the river level when the original study grid was created in January 1995. Low elevation quadrats (843.093 m- 843.790 m; mean=843.356 m) were located between 0 and 40 m from the river, and in a return channel 65 m from the river. High elevation quadrats (843.893 m-844.821 m; mean=844.372 m), were located between 45 and 60 m from the river. The sedimentary history of the bar is detailed by Rubin and others (1990), who explain the processes causing the topographic features on the bar. The high elevation sites are the erosional remnants of a platform that was formed during a high flow event, and have a coarer texture than the lower elevation sites, which are the product of lower flow depositional events (Rubin et al., 1990).

The vegetative history of the Colorado River has been documented by Turner and Karpiscak (1982) and by Johnson (1990). Prior to the closure of Glen Canyon Dam, perennial vegetation along the Colorado River only grew above elevations that were not scoured seasonally by flooding (approximately 100,000 to 125,000 ft^3/s) in what is known as the Old Highwater Zone (Carothers and Brown, 1991). Following the closure of Glen Canyon Dam in



Represents stage elevations over 300,000 cfs. Composed of Sonoran desert vegetation, common species found in this zone include *Opuntia* sp., *Eriogonum inflatum*, *Encelia frutescens*, *Lycium andersonii*, and *Acacia greggii*.

Represents stage elevations between approximately 125,000 to 300,000 cfs. As a remnant of the Old Highwater zone, *Prosopis glandulosa* dominates. Other species include *Bromus rubens*, *Opuntia erinacea*, and *Guterrezia sarothroe*, *Baccharis emoryi* and *Baccharis salicifolia*.

Represents stage elevations between approximately 45,000 to 125,000 cfs. This zone is dominated by mature trees including *Tamarix ramosissimi*, *Prosopis glandulosa*, *Salix exigua*, *Baccharis emoryi*, and *Baccharis salicifolia*. Other species include *Bromus rubens*, *Guterrezia sarothroe*, *Equisetum* sp., and *Tessaria sericea*.

Represents stage elevations between approximately 28,000 to 40,000 cfs. A *Salix exigua/Equisetum* sp. assemblage frequently occurs, as do stands of juvenille *Tamarix ramosissimi*. Other species include *Baccharis emoryi*, *Bromus rubens*, *Prosopis glandulosa*, *Conyza canadensis*, *Carex aquatilus*, and *Sporobulus* sp.

Represents stage elevations between approximately 20,000 and 28,000 cfs. A *Salix exigua/Equisetum* sp. assemblage, along with stands of *Typha domingensis*, *Baccharis emoryi*, and *Phragmites australis* dominate. Other species include *Equisetum arvense*, *Carex aquatilus*, *Plantago major*, *Gnaphalium chilense*, *Melilotus* sp., *Muhlenbergia asperifolia*, and *Scirpus pungens*

Represents stage elevations below approximately 20,000 cfs. A variety of species are present, with no clear dominants. Species include *Juncus articulatus*, *Juncus ensifolius*, *Juncus bufonius*, *Scirpus pungens*, *Equisetum arvense*, *Equisetum* sp., *Tamarix ramosissimi*, *Typha domingensis*, *Juncus torreyi*, *Conyza canadensis*, *Muhlenbergia asperifolia*, and *Phagmites australis*.

Figure 2. Stage elevations and species associations are shown. Location of the study grid relative to the bar is shown as a white box, and a more detailed diagram of the study area is shown on Figure 3. Data provided by L. E. Stevens.

1963, river flow was stabilized and the cycle of annual flooding ceased. Changes in flow management that affect riparian vegetation include seasonal flow patterns, maximum and minimum discharges, nutrient and sediment transport, and water temperature (Johnson, 1990). The new flow patterns of the Colorado River allowed land between the river stage elevations of 100,000 to 33,000 cubic feet per second to be colonized by perennial vegetation (Carothers and Brown, 1991), and stable flows have created riparian ecosystems that are increasinly mesic when compared to pre-dam conditions (Johnson, 1990).

METHODOLOGY

Sampling Design

Because the objectives of this research were to examine NAPP along a topographic sequence, the research grid was established between January 9 and January 10, 1995 in the area of greatest topographic change across the alluvial deposit. A grid 25 x 65m in size was oriented across the study site with the long axis perpendicular to the river (see Figures 2 and 3). Along both axes, survey stakes were placed every five meters, creating a grid of fifty-four $25m^2$ study units, which are hereafter refered to as quadrats. Survey stake UTM coordinates are provided in APPENDIX A. All quadrats were named for the survey stake located in the upstream/canyon wall corner of each plot. Additional sampling trips were taken on May 3 through May 7, 1995 and from July 1 to July 7, 1995. Productivity and soil samples were collected from stratified locations within each quadrat to minimize trampling, disturbance, and the effects of boundaries during the May and July sampling trips. Individual samples were assumed to represent the environmental and ecological conditions over each quadrat.

Field Methods

Plant productivity for each quadrat was measured using a combination of harvest methods and allometric growth equations (Whittaker and Marks, 1975) during the May and July 1995 sampling trips. Loss due to death from the beginning of the growing season (early January) to May was assumed to

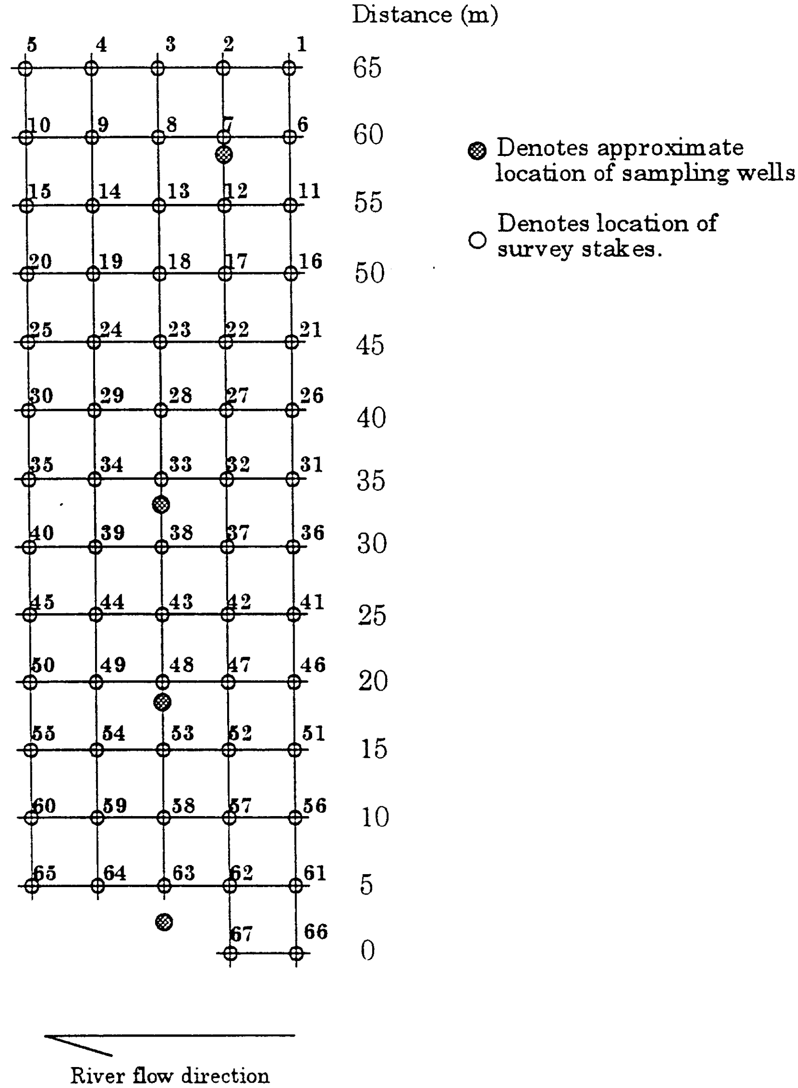


Figure 3. Kwagunt Marsh sampling grid and well locations. Locations of survey stakes, relative distances to the river at the time of study grid establishment, and groundwater wells are shown. The study grid orientation on the reattachment bar is shown in Figure 2. Survey stake identifying numbers are shown to the upper right of each stake in bold text, and correspond to the identifying numbers included in Appendices A, B, C, and D. Approximate distance to the river is shown at the far right of the study grid in plain text.

be zero, and could not be measured because litter samples had not been collected at the beginning of the growing season. Loss due to death from May to July was also assumed to be zero and an ANOVA test indicated that there was no significant ($p<0.01$) difference between the amount of litter present in May and the amount present in July.

To measure productivity of non-woody annual production, non-woody living biomass was collected from 0.10 m^2 circular plots in each quadrat. Samples were dried as long as possible in the field (approximately 3 days), then sealed and transported back to the lab. Samples were air dried for an additional two weeks at the lab, then weighed to the closest 0.1 g.

Due to the different growth forms of trees present at the site, several different methods were used to estimate NAPP of tree species. Tree density was measured by counting all trees in 1 x 1 m plots within each quadrat. Basal diameter (BD) and height were measured on *Salix exigua* and *Tamarix ramosissimi* seedlings located within the 1 x 1 m plots. Foliage harvests (leaves and new stems) in conjunction with BD and height measurements from approximately 30 *S. exigua* and 30 *T. ramosissimi* seedlings located across the study area were used to develop species specific relationships between tree dimensions and foliage production using regression equations. These equations were used to estimate foliage productivity on the censused *S. exigua* and *T. ramosissimi* trees located within the 1 x 1 m study plots. While *S. exigua* and *T. ramosissimi* seedlings grow from one long shoot, with relatively few large side branches, *Baccharis emoryi* produces many large side branches from its main trunk. For this reason, the *B. emoryi* growth form was not conducive to dimensional measurements and predictive equations used to predict *S. exigua* and *T. ramosissimi* foliage productivity. Therefore, *B. emoryi* foliage was harvested from three different trees in 0.10 m^2 circular plots that went from the ground through the canopy during the July 1995 sampling trip. These values were averaged, creating an estimate of productivity per 0.10 m^2 surface cover of *B. emoryi*. This value was multiplied by *B. emoryi* surface area cover, measured in each of the 1 x 1 m census plots, providing an estimate of *B. emoryi* foliage productivity. The methodology for *B. emoryi* trees was developed in time for May sampling, therefore, quantitative data for *B. emoryi* productivity up to May 1995 was not measured. To account for *B. emoryi* productivity in May, July values were used as a proxy, and might slightly overpredict productivity in plots with *B. emoryi*. Additionally, woody biomass accrual by tree species, while recognized as important, was not measured because instruments to measure the increase in tree trunk diameter within the appropriate margin of error were not available. Thus, productivity measurements are assumed to be slightly underpredicted in plots that contain trees.

To calculate the overall biomass accrual for each study quadrat, the 0.10 m^2 harvest plots were multiplied by 10 to estimate productivity on a 1m^2

basis, and was summed with the foliage productivity estimates for trees within the 1 x 1 m plots. All productivity data is presented as g/m^2.

Soil samples collected for analysis of nutrient content, soil moisture, and soil texture were gathered from each of the study quadrats. The soil samples were collected from a depth of 15 cm below ground surface, placed in plastic bags, and put on ice within 1 hour of collection. In addition, 4 wells, located approximately 5, 20, 35, and 60 m from the river, were sunk using 2 meter sections of PVC pipe during the May trip. (See Figure 3) From these wells, groundwater samples were collected from a depth of approximately 2 m below ground surface, filtered immediately, and placed on ice after collection.

A total of 54 quadrats were sampled in May. Only 48 quadrats were resampled in July because water levels had risen sufficiently that sampling was not practical in six quadrats.

Laboratory Methods

Within 10 days of collection, plant samples were air dried for 2 weeks in the laboratory, then weighed to the nearest 0.1 g. Harvested plant samples were sorted by species and weighed to provide quantitiatve data on community structure.

Soil samples provided measurements of soil texture, soil nitrogen concentrations, nitrogen mineraliztion potential, phosphorus concentrations, percentage soil moisture by weight, and percentage organic matter by weight.

To measure soil moisture, approximately 10g fresh soil samples were weighed and then dried for 72 hours. Soil moisture was calculated using the following equation (Allen, 1989):

Moisture (%) = (loss in weight on drying/initial sample weight)*100.

The percentage of organic matter in the soil was approximated by measuring loss-on-ignition. Dry soil samples were ashed at 550^0 C for 4 hours. Samples were re-wet, then dried at 60^0 C for 72 hours so that water bound to silts and clays would not be removed during the ashing process. Loss-on-ignition was calculated using the following equation (Allen, 1989):

Loss-on-ignition (%) = (wieght loss /initial sample weight)*100.

Soil texture was measured by sieving approximately 120g dry weight samples into five grain-size classes using U.S. standard sieve sizes:

> 2.000 mm	pebbble
2.000 - 0.600 mm	coarse sand
0.600 - 0.212 mm	medium sand
0.212 - 0.063 mm	fine sand
< 0.063 mm	silt

The percentage of each grain size weight to the total sample weight was then calculated for each sample. The percentage of silts in each soil sample was used as a proxy for soil texture (Stevens et al., 1995).

Nitrate (NO_3^-) and ammonium (NH_4^+) were extracted from 20g fresh soil using 200ml 6% KCl solution (Allen, 1989). Additional 20 g fresh soil samples from each locations were placed in unsealed plastic bags to allow aeration. The bags were incubated in a dark drawer at room temperature (approximately 26° c). To keep the samples at similar moisture levels as found in the field, samples were reweighed after 14 day, and dionized water was added to return the soils to original weight (Vitousek et al., 1982). After incubation, the samples were extracted using 200ml 6% KCl solution. Net nitrogen mineralization was calculated by subtracting the initial total inorganic nitrogen concentrations (TIN) from the TIN extracted from the incubated samples. Phosphorus was extracted from 10g fresh soil samples using 200 ml 2.5% acetic acid solution (Allen, 1989). All samples were corrected for soil moisture and are reported as μg of nutrient per gram dry weight soil (μg/g).

RESULTS

Environmental Data

Variables discussed in this section incude elevation above sea level (ELEV), the percentage of silts in the soil sample (SC), percent soil moisture (H_2O), percent soil organic matter (OM), soil phosphorus concentrations (SRP), soil nitrate concentrations (NO_3^-), soil ammonium concentrations (NH_4^+), total inorganic nitrogen concentrations (TIN), and nitrogen mineralization potential (NMIN). Environmental data are provided in APPENDIX B. Summary statistics for both the May and July datasets of these variables are provided in Table 1. In general, there were decreases in mean soil moisture, organic matter, phosphorus, nitrate, and nitrogen mineralization between May and July. There were increases from May to July in mean concentrations of ammonium and total inorganic nitrogen.

In order to test for normality in each of the variable distributions, a Kolmogorov-Smirnov one sample test was run on each of the environmental variables. All environmental variables except SRP in the May dataset, and SRP and NO_3^- in the July dataset were found to significantly deviate from a normal distribution ($p<0.01$). Therefore, in order to assess significant relationships between environmental variables in the study area, Spearman's rank-order correlations were generated for the environmental variables. Based upon correlations from May data, there appear to be two distinct groups of variables that are highly correlated (Table 2). The first

Table 1. Summary statistics for environmental variables.

	May N=54				July N=48*			
	Min	Max	Mean	S.D.	Min	Max	Mean	S.D.
ELEV	842.64	844.82	843.57	0.549	842.64	844.82	843.57	0.549
SC	1.360	65.350	27.980	19.073	1.360	65.350	27.980	19.073
H_20	0.750	42.060	15.450	11.371	0.240	28.293	14.861	9.579
OM	0.150	3.600	1.151	0.867	0.100	3.290	0.968	0.757
SRP	2.030	24.180	7.233	4.346	0.295	2.889	1.169	0.710
NO_3^-	0.000	0.780	0.104	0.172	0.000	0.018	0.006	0.004
$NH4^+$	0.000	4.270	0.631	0.652	0.000	5.325	1.015	0.813
TIN	0.000	4.490	0.735	0.733	0.002	5.331	1.0241	0.813
NMIN	-2.010	7.360	1..013	1.797	-4.014	4.261	-0.244	1.139

* July elevation and SC were calculated from 54 observations collected in January.

Elevatation (ELEV) is reported as m above sea level. Percentage silts (SC), soil moisture (H_20) and soil organic matter (OM) are reported as percentage of contribution to a soil sample by weight. Soil phosphorus (SRP), soil nitrate (NO_3^-), soil ammonium (NH_4^-) and total inorganic nitrogen (TIN) are reported as μg/g dry weight of soil. Potential nitrogen mineralization (NMIN) is reported as the total gain or loss of TIN in μg/g dry soil over 30 days.

Table 2. Spearman rank-order correlations between May environmental variables.

	ELEV	SC	H_2O	OM	SRP	NO_3^-	$NH4^+$	TIN	NMIN
ELEV	1.000								
SC	**-0.663**	1.000							
H_2O	**-0.686**	**0.785**	1.000						
OM	**-0.529**	**0.708**	**0.804**	1.000					
SRP	**-0.513**	**0.623**	**0.643**	**0.706**	1.000				
NO_3^-	-0.007	0.097	0.150	0.196	0.016	1.000			
$NH4^+$	-0.048	0.016	0.072	-0.044	0.032	**0.292**	1.000		
TIN	-0.035	0.049	0.094	-0.001	0.033	**0.500**	**0.954**	1.000	
NMIN	**-0.383**	**0.366**	**0.485**	**0.546**	**0.493**	-0.115	-0.240	-0.235	1.000

Environmental variables elevation (ELEV), percentage silt (SC), organic matter (OM), phosphorus (SRP), nitrate (NO_3^-), ammonium ($NH4^+$), total inorganic nitrogen (TIN), and potential nitrogen mineralzation (NMIN), are presented. Correlations significant at the 0.01 level are underlined in bold text. Correlations significant at the 0.05 level are shown in bold text only.

group includes the environmental variables elevation (ELEV), percentage of silts (SC), soil moisture (H_2O), soil organic matter (OM), soluable reactive phosphorus (SRP), and potential nitrogen mineralization (NMIN). The second grouping includes nitrate (NO_3^-), ammonium (NH_4^+), and total inorganic nitrogen (TIN). The pattern is similar for July, however, NMIN is correlated with the nitrogen measures rather than the other environmental factors (Table 3). A high degree of correlation among variables indicates that there is redundancy within a dataset. Thus, Principal Components Analysis (PCA) was used to reduce the number of variables by discerning major environmental gradients. For both May and July data, PCA generated two components explaining over 69% of the total dataset variation (Table 4). The two components were similar between sampling months. Component loadings indicate the elevation component (component 1) is strongly correlated with the variables ELEV, SC, H_2O, OM, and SRP, while the nitrogen component (component 2) is strongly correlated with the variables NH_4^+ and TIN (Table 4). NMIN was also correlated with the elevation component during May, however, it was correlated with the nitrogen component component in July, mirroring the patterns shown by Spearman rank-order correlations.

To discern how environmental variables change with distance from the river, means were calculated for each variable at 5 m intervals from the rivers edge. Four samples were used to compute each mean with

Table 3. Spearman rank-order correlation between July environmental variables.

	ELEV	SC	H_2O	OM	SRP	NO_3^-	$NH4^+$	TIN	NMIN
ELEV	1.000								
SC	**-0.653**	1.000							
H_2O	**-0.765**	**0.774**	1.000						
OM	**-0.713**	**0.761**	**0.895**	1.000					
SRP	**-0.759**	**0.678**	**0.743**	**0.722**	1.000				
NO_3^-	0.099	-0.212	-0.165	-0.061	-0.147	1.000			
$NH4^+$	-0.043	0.059	0.170	0.136	-0.025	**0.345**	1.000		
TIN	-0.039	0.053	0.166	0.132	-0.029	**0.357**	**0.999**	1.000	
NMIN	-0.044	0.047	-0.101	-0.070	0.039	**-0.286**	**-0.848**	**-0.844**	1.000

Environmental variables elevation (ELEV), percentage silt (SC), organic matter (OM), phosphorus (SRP), nitrate (NO_3^-), ammonium ($NH4^+$), total inorganic nitrogen (TIN), and potential nitrogen mineralzation (NMIN), are presented. Correlations significant at the 0.01 level are underlined in bold text. Correlations significant at the 0.05 level are shown in bold text only.

Table 4. Principal components analysis results for May and July.

	May			July		
Component	1	2		1	2	
% TV	41.88	27.10		44.73	28.36	
	Loadings			Loadings		
Component	1	2	Communality	1	2	Communality
ELEV	**-0.791**	0.037	0.627	**-0.856**	-0.219	0.781
SC	**0.879**	0.006	0.773	**0.869**	0.227	0.807
H_20	**0.913**	0.189	0.869	**0.947**	0.188	0.932
OM	**0.810**	-0.007	0.656	**0.807**	0.033	0.652
SRP	**0.710**	-0.025	0.505	**0.803**	0.213	0.69
NO_3^-	0.001	**0.667**	0.445	-0.210	-0.311	0.141
NH_4^+	0.052	**0.928**	0.864	0.334	**-0.917**	0.952
TIN	0.047	**0.982**	0.967	0.333	**-0.917**	0.952
NMIN	**0.609**	-0.362	0.502	-0.279	**0.770**	0.671

The percentage of total variance (TV) explained by each component. component loadings and communalties are shown. Bold loadings indicate that the variable is strongly explained by the given component.

the exception of locations at the rivers edge (0 m), where only two samples were collected. Tables 5 and 6 show May and July mean values at successive distances from the river. Figures 4 and 5 show transect graphs of mean SC, H_2O, OM, and SRP, along with a site topographic map for May and July. Additionally, Figures 6 and 7 show a site topographic map and transect graphs of NO3-, NH_4^+, TIN, and NMIN for May and July.

Two distinct environments seem to occur at the site, those located between 45 and 60 meters from the river, and those that are not (Figures 4, 5, 6, and 7). Sites located between 45 and 60 m from the river have higher elevations (mean = 844.28 m) and a lower percentage of silts (mean = 4.09%), less soil moisture (May mean=1.49%, July mean = 2.0%), less soil organic matter (May mean = 0.39%, July mean = 0.33%), and lower soluble reactive phosphorus concentrations (May mean = 3.28 μg/g, July mean = 0.45 μg/g). Sites located at distances between 0 and 40 m from the river, as well as locations 65 m from the river have lower elevations (mean = 843.24 m) and higher percentages of silts (mean = 37.76%), more soil moisture (May mean = 21.43%, July mean = 21.29%), greater amounts soil organic matter (May mean = 1.47%, July mean = 1.29%), and higher concentrations of soluble reactive phosphorus (May mean = 8.72 μg/g, July mean = 1.53 μg/g).

One-way ANOVA tests were performed on each variable to determine if there were statistically significant differences between the erosional

Table 5. May variable means at 5 m intervals.

Distance	Elev	SC	H_2O	OM	SRP	NO_3^-	NH_4^+	TIN	NMIN
65	843.48	20.69	15.73	0.91	5.32	0.22	1.56	1.78	-0.05
60	843.94	2.59	1.73	0.33	3.04	0.19	0.87	1.07	-0.34
55	844.62	3.46	1.10	0.35	3.74	0.06	0.30	0.36	0.13
50	844.56	5.61	1.88	0.48	3.70	0.03	0.51	0.54	0.10
45	843.98	4.70	1.24	0.38	2.62	0.02	0.48	0.50	0.58
40	843.53	45.99	21.38	1.72	7.59	0.19	0.47	0.66	0.44
35	843.26	52.09	28.39	2.58	8.97	0.08	0.41	0.49	1.67
30	843.23	38.74	21.70	1.65	9.85	0.13	0.60	0.73	2.09
25	843.34	33.69	19.72	2.16	12.64	0.17	0.67	0.84	3.44
20	843.44	34.11	19.23	0.59	11.85	0.18	0.75	0.93	1.28
15	843.33	31.21	18.08	1.10	9.71	0.00	0.56	0.56	1.07
10	843.23	34.60	19.81	1.43	9.91	0.05	0.48	0.53	0.44
5	842.88	44.06	26.89	1.06	6.05	0.06	0.62	0.68	0.99
0	842.70	52.37	23.38	1.26	5.30	0.03	0.45	0.48	3.69

Elevation is reported in m above sea level. Silt content (SC). soil moisture (H_2O). and organic matter (OM) are reported as the percentage contribution to a soil sample by weight. Phosphorus (SRP). nitrate (NO_3^-). ammonium (NH_4^+). and total inorgainc nitrogen (TIN) are reported as μg/g dry weight soil. Potential nitrogen mineralization (NMIN) is reported as the total gain or loss of TIN in μg/g dry soil over 30 days.

Table 6. July variable means at 5 m intervals.

Distance	ELEV	SC	H_2O	OM	SRP	NO_3^-	NH_4^+	TIN	NMIN
65	843.48	20.69	18.39	0.750	0.88	0.01	1.35	1.36	-0.90
60	843.94	2.59	1.65	0.26	0.43	0.00	0.90	0.90	-0.45
55	844.62	3.46	0.72	0.28	0.40	0.01	0.96	0.97	-0.35
50	844.56	5.61	0.81	0.43	0.45	0.01	0.66	0.67	-0.13
45	843.98	4.70	4.82	0.35	0.50	0.01	1.03	1.04	0.31
40	843.54	45.99	21.25	1.42	0.90	0.00	0.90	0.91	0.89
35	843.26	52.09	23.30	1.76	1.81	0.00	1.87	1.87	-1.03
30	843.23	38.74	24.15	2.04	2.02	0.00	0.66	0.67	0.02
25	843.34	33.69	21.30	1.53	1.97	0.01	1.01	1.01	-0.27
20	843.44	34.11	19.88	0.51	1.46	0.01	0.94	0.95	-0.28
15	843.33	31.21	19.85	0.85	1.65	0.00	0.92	0.92	-0.31
10	843.23	34.60	22.22	1.26	1.54	0.00	0.97	0.97	-0.44
5	842.88	44.06	N/A	N/A	N/A	N/A	N/A	N/A	N/A
0	842.70	52.37	N/A	N/A	N/A	N/A	N/A	N/A	N/A

Elevation is reported in m above sea level. Silt content (SC), soil moisture (H_2O), and organic matter (OM) are reported as the percentage contribution to a soil sample by weight. Phosphorus (SRP), nitrate (NO_3^-), ammonium (NH_4^+), and total inorgainc nitrogen (TIN) are reported as μg/g dry weight soil. Potential nitrogen mineralization (NMIN) is reported as the total gain or loss of TIN in μg/g dry soil over 30 days.

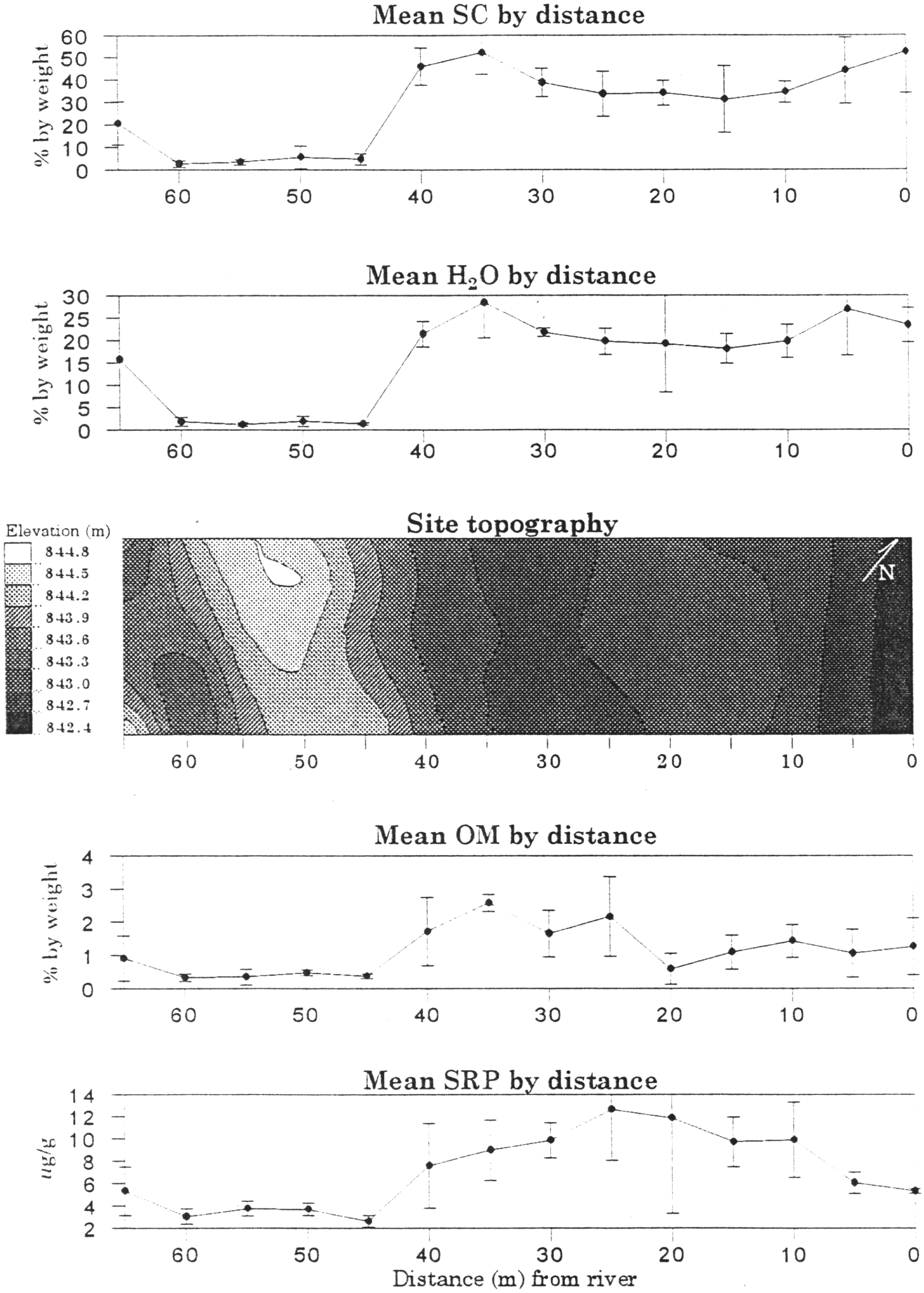


Figure 4. Spatial patterns of environmental variables in May. Silt content (SC), soil moisture (H_2O), soil organic matter (OM), and phosphorus (SRP) are averaged at 5 m intervals from the river. X-axes show distance from the river at the time of study grid establishment. Error bars represent one standard deviation.

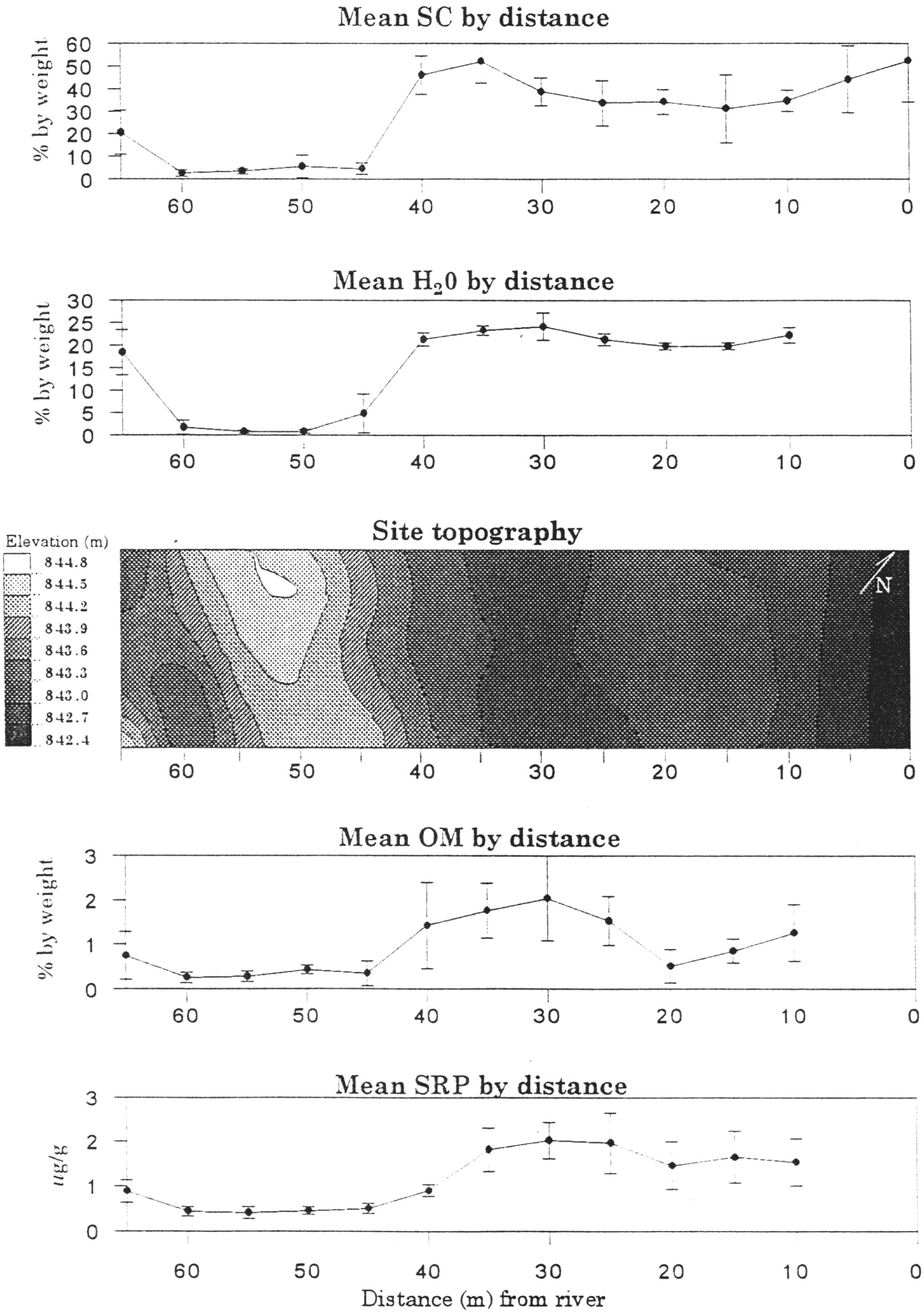


Figure 5. Spatial patterns of environmental variables in July. Silt content (SC), soil moisture (H_2O), soil organic matter (OM), and phosphorus (SRP) are averaged at 5 m intervals from the river. X-axes show distance from the river at the time of study grid establishment. Error bars represent one standard deviation.

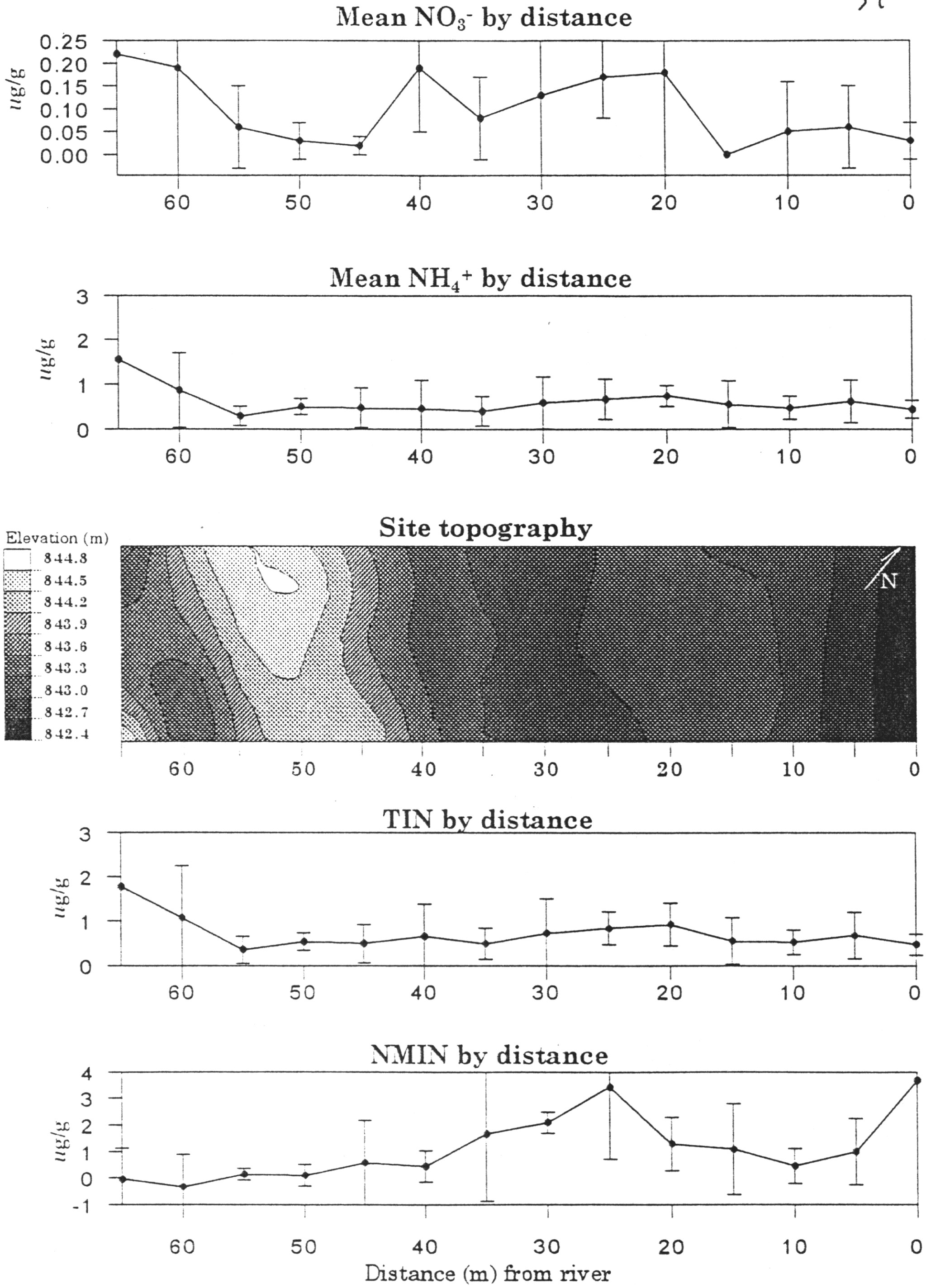


Figure 6. Spatial patterns of nitrogen variables in May. Nitrate (NO_3^-), ammonium (NH_4^+), total inorganic nitrogen (TIN), and potential nitrogen mineralization (NMIN) are averaged at 5 m intervals from the river. X-axes show distance from the river at the time of study grid establishment. Error bars represent one standard deviation.

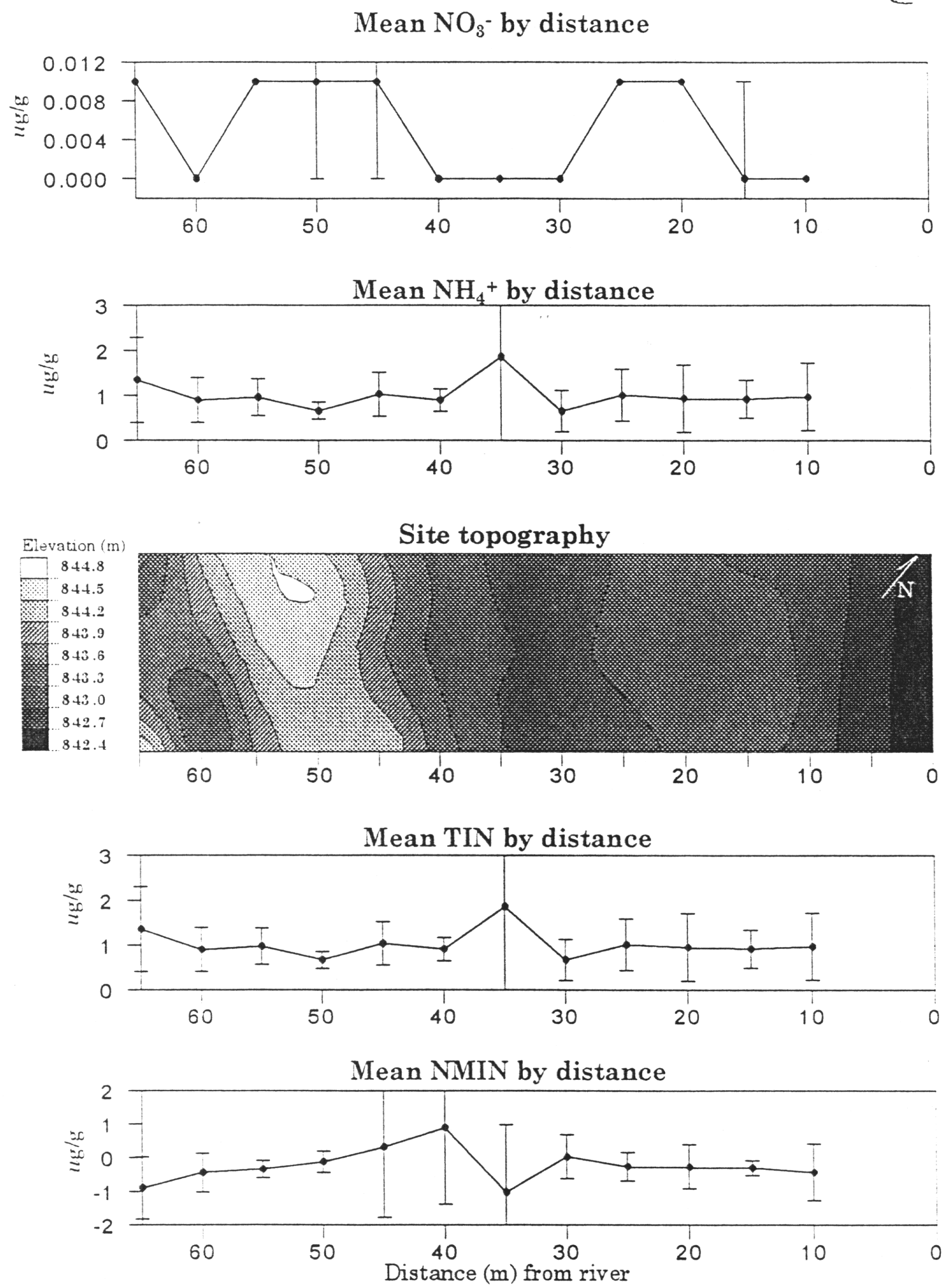


Figure 7. Spatial patterns of nitrogen variables in July. Nitrate (NO_3^-), ammonium (NH_4^+), total inorganic nitrogen (TIN), and potential nitrogen mineralization (NMIN) are averaged at 5 m intervals from the river. X-axes show distance from the river when the study grid was established. Error bars represent one standard deviation.

surfaces present between 45 and 60 m from the river, and depositional surfaces between 0 and 40 m and at 65 m from the river. ANOVA results are presented in Table 7. The only variables that were not significantly different were NO_3^- and NMIN in July.

While NMIN was significantly correlated with ELEV, SC, H_2O, OM, and SRP data collected during the May sampling trip, none of the other soil nitrogen variables (NO_3^-, $NH4^+$, TIN) are significantly correlated with other environmental variables, nor do they appear to have distributional pattern similar to other variables (see Figures 6 and 7). July data indicate that while the soil nitrogen measures NO_3^-, $NH4^+$, TIN, and NMIN are significantly correlated with each other, they are not significantly correlated with any other environmental variables. Soil nitrogen predominantly occurred as NH_4^+, with NO_3^- concentrations larger than $NH4^+$ concentrations found in only four quadrats sampled in May and two quadrats sampled in July. Nitrogen mineralization during May appears to be a significant contributor to nitrogen availability, with the flux of mean net nitrogen mineralization being greater than mean TIN in the soil. In July, however, mean net nitrogen minerization was negative, indicating that more nitrogen was lost rather than gained over the thirty day incubation period. This suggests that nitrogen limitiation might be more severe in July than in May.

An additional source from which plants aquire nutrients from is in the water stored in beach sediments. Duplicate samples collected in May 1995

Table 7. ANOVA results for May and July.

	May	July
ELEV	$p<0.001$	$p<0.001$
SC	$p<0.001$	$p<0.001$
H_20	$p<0.001$	$p<0.001$
OM	$P<0.001$	$P<0.001$
SRP	$P<0.001$	$P<0.001$
NO_3^-	$p=0.015$	$P=0.060$
NH_4^+	$p=0.002$	$p=0.002$
TIN	$p\leq0.001$	$p=0.002$
NMIN	$p<0.001$	$p=0.392$

Variables elevation (ELEV), silt content (SC), soil moisture (H_2O), soil organic matter (OM), phosphorus (SRP), nitrate (NO_3^-), ammonium (NH_4^+), total inorganic nitrogen (TIN), and potential nitrogen mineralization are tested for significant differences between erosional and depositional surfaces. Significant differences ($p<0.05$) between surfaces are shown in bold.

from each well location were averaged, and values are reported as mg/l in Table 8. NO_3^- ranged from 0.000 to 0.009 mg/l, $NH4^+$ ranged from 0.158 to 0.886 mg/l, and TIN varied from 0.158 to 0.891 mg/l. TIN increased in concentration from 5 to 35m from the river, but decreased at 60 m from the river. Phosphorus concentrations (SRP) did not follow the same pattern as nitrogen concentrations, were highest in the well located 20 m from the river, and were approximately equal at all other sample wells.

Plant Productivity

Because loss due to death and herbivory are assumed to be negligible, and because the beginning of the growing season was not known, all net aboveground productivity values are reported as standing biomass of understory herbaceous and tree foliage produced within the growing season. For this reason, no temporal component is included in the unit of measure. All productivity data are provided in APPENDIX C. Estimated productivity for individual plots ranged from zero to 1003.00 g/m^2 in May (mean 276.91 g/m^2), and zero to 2105 g/m^2 in July (mean= 614.71 g/m^2). Trees provided little of the actual biomass in most samples collected, as evidenced by the fact that productivity of herbaceous plants is greater than that of trees in 46 of 54 quadrats in May, and 43 of 48 quadrats in July. Quadrats in which the tree foliage productivity was greater than herbaceous vegetation productivity were all located at least 45 m from the rivers edge.

Productivity values measured at equal distances from the river were

Table 8. Groundwater geochemistry data for May 1995.

Distance from river (m)	NO_3^-	$NH4^+$	TIN	SRP
5	0.008	0.273	0.281	0.045
20	0.009	0.469	0.477	0.181
35	0.005	0.886	0.891	0.033
60	0.000	0.158	0.158	0.042

Samples collected 2 m below ground surface. All values are given in mg/l.

averaged and are plotted in Figure 8. Vegetation assemblages tended to change parallel to the river, therefore, with the exception of approximately two distance intervals from the river (25 m and 65 m) averaged productivity values were from the same basic assemblage type. In general, during both sampling months, productivity was highest for quadrats found from 10 to 40 m of the river, and for the quadrats located 65 m from the river. Quadrats located within 5 m from the river had low productivity, presumably due to disturbance and removal of vegetation by the river. Quadrats located on the topographic rise between 45 and 60 meters also had relatively low productivity.

In order to understand how productivity is related to environmental variables, Spearman's rank-order correlations were calculated. Results are presented in Table 9. To further explore the relationship between productivity and environmental variables, a regression analysis was run using pairwise combinations of the variables selected from the two groups of autocorrelated variables discerned using PCA. For both the May and July datasets, observations collected within 5 m of the river were discarded for the regression analysis due to the fact that the biomass had potentially been removed from these sites by highwater flows, and quantitative measures of disturbance had not been calculated or measured. Biomass accumulation from the beginning of the growing season to May appears to be most readily explained by soil moisture and NH_4^+ concentrations (Figure 9).

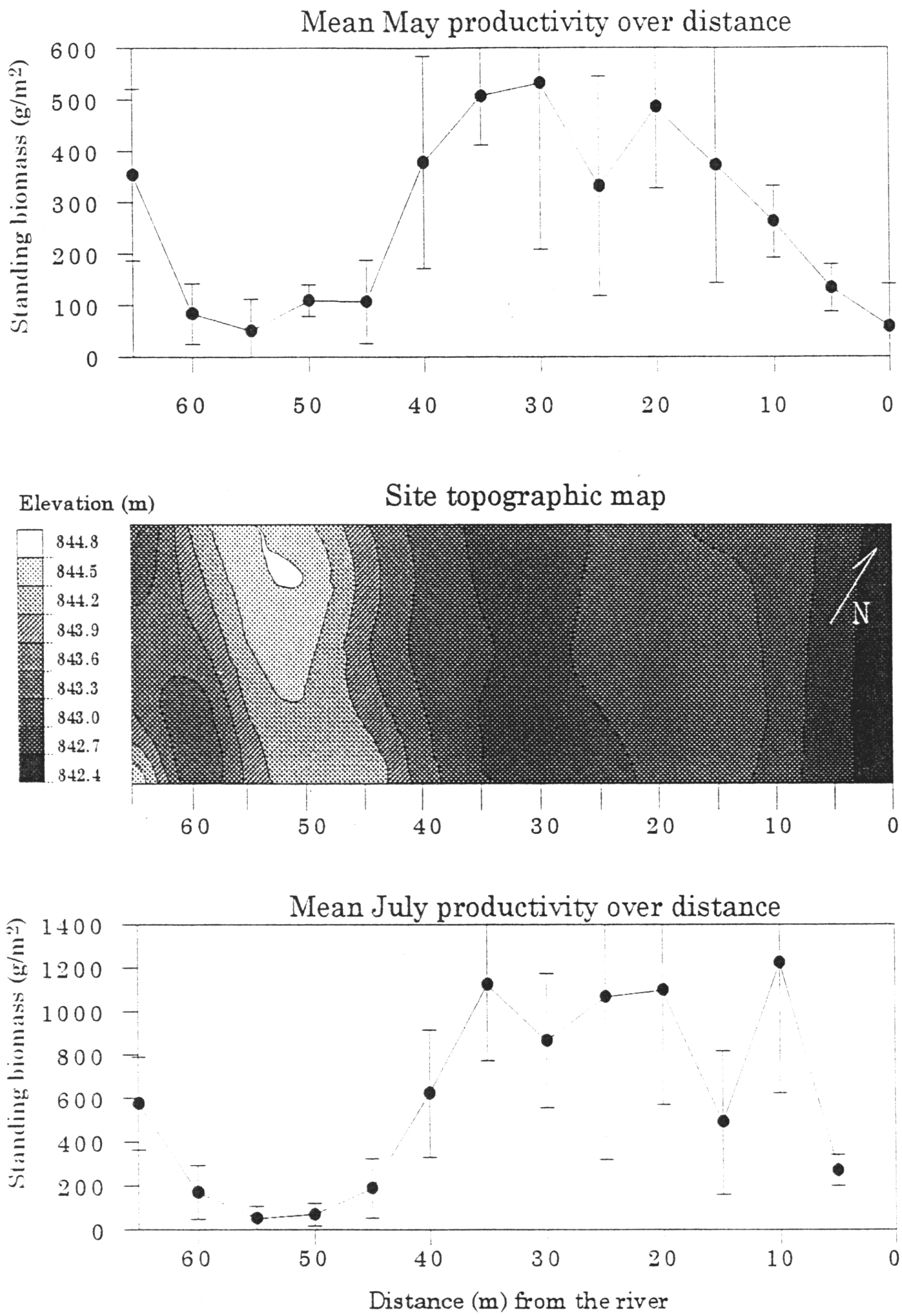


Figure 8. Spatial patterns of plant productivity in May and July. Productivity is averaged at 5 m intervals from the river. X-axes show distance from the river when the study grid was established. Error bars indicate one standard deviation.

Table 9. Spearman rank-order correlations between environmental variables and productivity.

	May productivity	July productivity
ELEV	**-0.284**	**<u>-0.686</u>**
SC	**<u>0.466</u>**	**<u>0.677</u>**
H_2O	**<u>0.480</u>**	**<u>0.747</u>**
OM	**<u>0.507</u>**	**<u>0.702</u>**
SRP	**<u>0.578</u>**	**<u>0.624</u>**
NO_3^-	0.097	-0.211
NH_4^+	-0.057	0.070
TIN	0.010	0.059
NMIN	**0.273**	-0.024

Variables include: elevation (ELEV), silt content (SC), soil moisture (H_2O), phosphorus (SRP), nitrate (NO_3^-), ammonium (NH_4^+), total inorganic nitrogen (TIN), and potential nitrogen mineralization (NMIN). Correlations significant at the 0.01 level are underlined in bold text. Correlations significant at the 0.05 level are shown in bold text only.

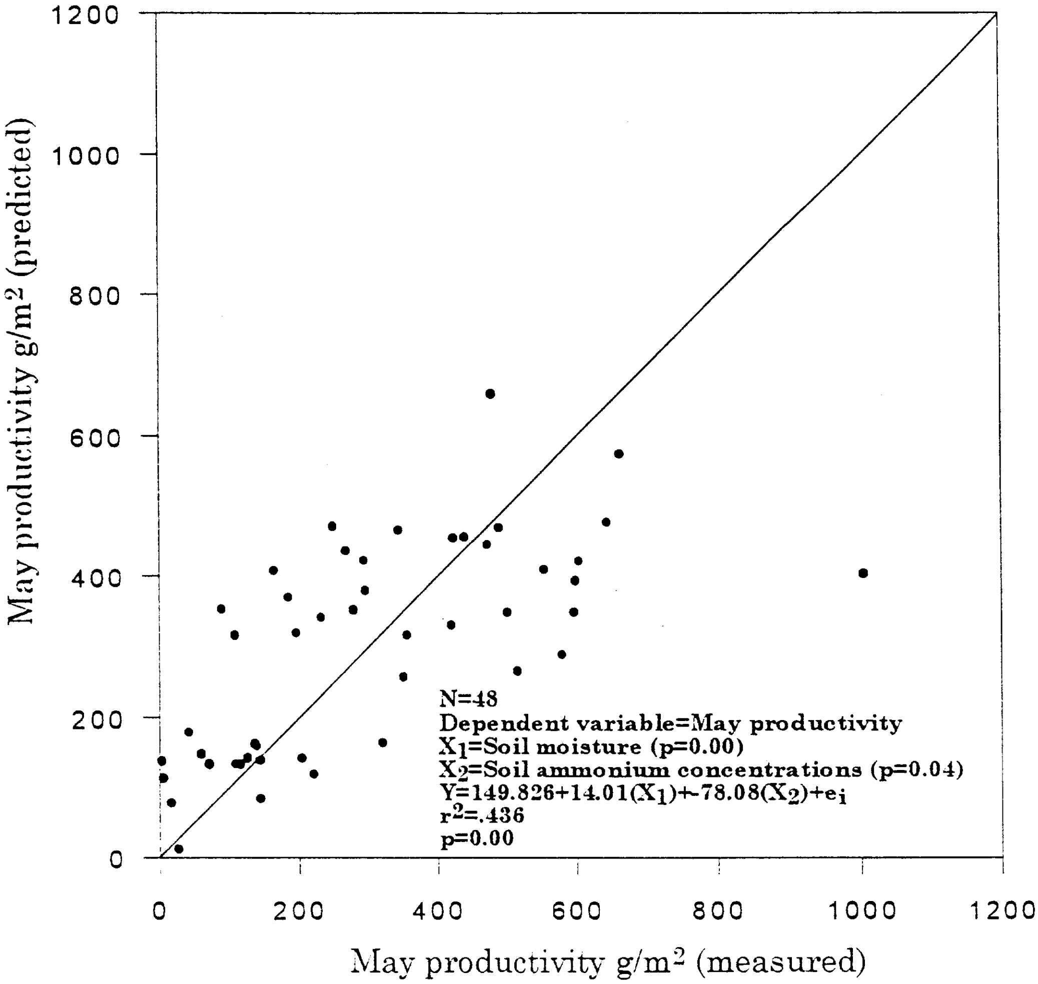


Figure 9. May plant productivity model results.

A model using these variables was significant ($p<0.01$), and explains 44 % of the variations in plant productivity. For biomass accumulation to July, the most effective combination of paired variables was H_2O and NMIN, producing a significant model ($p<0.01$) that explains approximately 48 % of the variation in plant productivity (Figure 10). Residuals from both models were graphed as normal plots, and based upon visual analysis, did not appear to deviate from normality.

Individual Species Contribution to Productivity

Biomass was calculated as the percentage of each species per quadrat. Quantitative data on assemblage composition is provided in APPENDIX D. *Phragmites australis* was the dominant plant in terms of biomass during both May and July (Table 10), but was only found in plots between 5 and 35 m from the river. The second most dominant species during both sampling months was *Equisetum hiemale*, which was only found in plots at least 35 m from the river's edge. Overall, biomass was more evenly divided between species in May than in July, however, during both months, the majority of biomass at the site was composed of just several species. In May, over 80 percent of the biomass was produced by 4 species: *P. australis, E. hiemale, Salix exigua*, and *Scirpus pungens*. In July, over 80 percent of the biomass was produced by 3 species: *P. australis, E. hiemale*, and *S. exigua*.

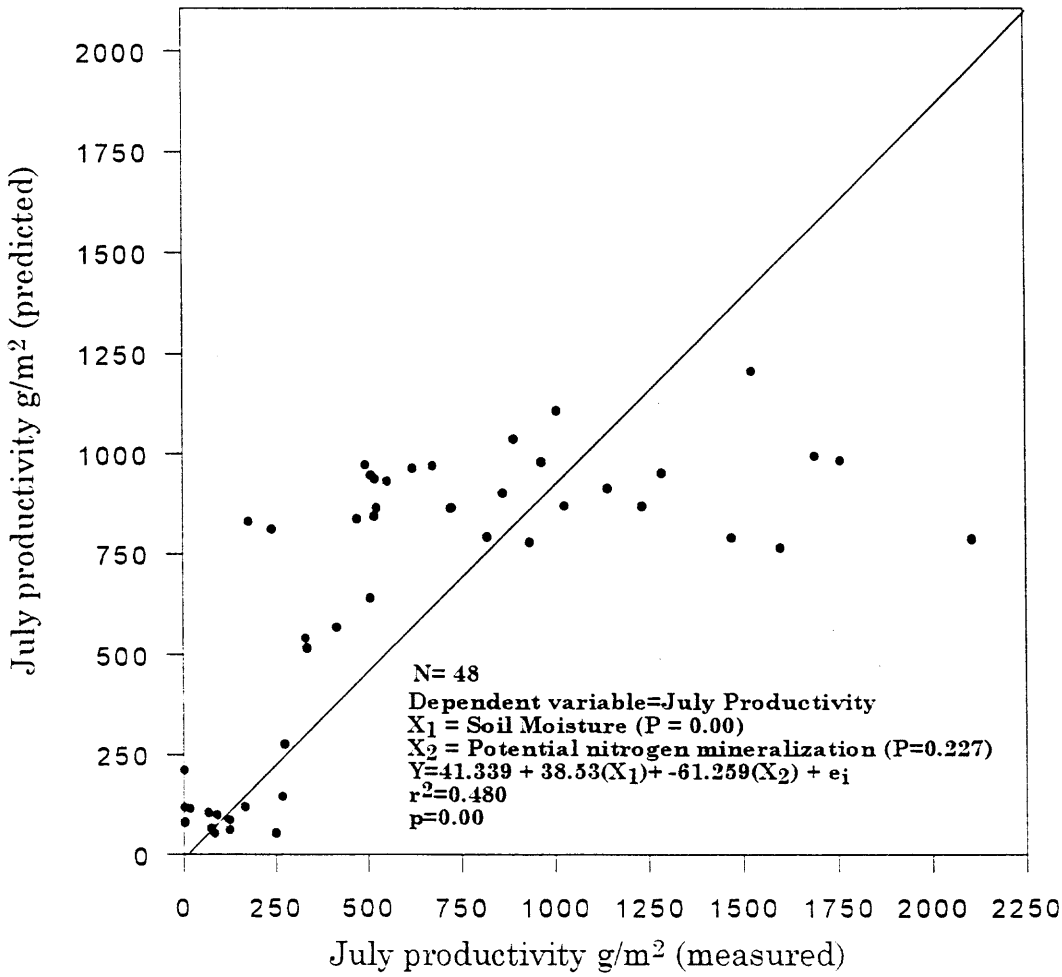


Figure 10. July plant productivity model results.

Table 10. Individual species contribution to productivity.

Species	May % total biomass	July % total biomass
Phragmites australis	44.61	58.10
Equisetum hiemale	20.08	19.14
Salix exigua	11.99	6.14
Scirpus pungens	6.77	4.28
Baccharis emoryi	6.56*	3.11
Tamarix ramosissimi	3.74	1.35
Equisetum arvense	2.45	0.09
Juncus sp.	1.62	0.00
Carex aquatilis	0.93	1.11
Muhlenbergia asperifolia	0.72	5.46
Conyza canadensis	0.27	1.19
Gnaphalium sp.	0.24	0.00
Plantago major	0.03	0.03

Species shown as the percent total biomass per month.

* Biomass contribution was based upon the productivity estimates from July.

DISCUSSION AND CONCLUSIONS

Discussion

The physical environment of reattachment bars vary topographically and environmentally. Rubin and others (1990) investigation into the sedimentary petrology of the bar indicates that many different fluvial events are responsible for the formation, maintenance, and current conditions of the bar. However, two geomorphic processes are ultimately responsible for the patterns found on reattachment bars: deposition and erosion. The results of this research suggest that these geomorphic processes strongly influence the patterns in environmental controls, and thus plant productivity.

Topographically, the study site contains a low lying platform bar created by the product of lower flow depositional events, as well as a topographic rise that is an erosional remnant of an earlier depositional event. All of the environmental variables, with the exception of nitrate and potential nitrogen mineralization in May, were significantly different between these erosional and depositional surfaces. Pinay and others (1990) investigated the linkage between erosional surfaces, depositional surfaces and environmental conditions on the Garonne River in France, finding that depositional surfaces had finer soil texture, higher soil moisture, higher nitrogen concentrations, and higher phosphorus concentrations in comparison to erosional surfaces. The findings of this research support Pinay and others (1990) research that it is vital to consider the geomorphic context of riparian zones. Additionally, it illustrates that, with regard to riparian environments and nutrient dynamics, geomorphic processes produce similar results in both temperate (France) and arid regions (Kwagunt Marsh).

The results of this study did indicate, however, that fertility of soils at Kwagunt Marsh were dramatically lower than soils found along the Garonne River (Pinay et al., 1990). Table 11 provides data comparing nutrient concentrations at Kwagunt Marsh and at the Garrone River in France (Pinay et al. 1990). Soil phosphorus concentrations at Kwagunt Marsh (May mean 7.22 μg/g, July mean 1.17 μg/g) were similar to those found along the Ottowa River in Canada, where reported mean values by vegetation type ranged from 4.4 μg/g to 7.8 μg/g (Day et al., 1988).

Hupp and Osterkamp (1985) examined how geomorphic processes influence riparian vegetation in Virginia, and found that vegetation patterns were best explained by hydrological processes associated with different landforms, as opposed to the effect of sediment texture. The results of my investigation, however, seem to suggest that this may not be the case on impounded rivers, where hydrological events effecting these landforms are less frequent. Specifically, Hupp and Osterkamp (1985) state that on Passage Creek, vegetation patterns were predominantly controlled by flow characteristics, and secondarily controlled by the effects of soil texture. They also, however, indicate that while these findings are supported by others, they are in disagreement with the findings of Frye and Quinn (1979), who

Table 11. Kwagunt Marsh soil nutrient concentrations compared to the Garonne River.

	Kwagunt Marsh--July		Garonne River--September	
	Erosional	Depositional	Erosional	Depositional
NO_3^-	0.007	0.005	12.4	32.0
NH_4^+	0.888	1.078	9.4	20.0
P	0.445	1.531	32.0	374.0

Soil nutrient contents are compared between Kwagunt Marsh and the Garonne River in France. Garonne River values from Pinay and others (1990). All values are repported as μg/g of dry soil.

conclude that edaphic gradients are responsible for species distribution. Kwagunt Marsh was scoured of all vegetation between 1983-1986 (Stevens et al., 1995). From 1986 to the conclusion of this research, Colorado River discharge did not exceed its mandated maximum of 892 m^3/s, a level that did not submerge vegetation located 5 m from the river's edge in January 1995. Therefore, it appears that when the effects of flooding are removed by impoundment and controlled releases from dams, the relative influence of soil texture is magnified.

Because of the lack of literature regarding riparian plant productivity in the arid southwest, it is difficult to directly compare the results of this study to others. Studies of marsh productivity have, however, been performed in locations other than the southwestern United States. Because productivity is generally reported in g/m^2/year, productivity of Kwagunt Marsh measured over the seven month period will be assumed to represent the minimum annual productivity for this site. Standing biomass at Kwagunt Marsh ranged from 0 to 2105 g/m^2. Mean standing biomass, and therefore mean minimum productivity at Kwagunt Marsh, was estimated to be no less than 615 g/m^2/year, which is in accordance with reported values for other freshwater marshes. Auclair and others (1976) report mean terminal shoot standing crop of 845 g/m^2 in a freshwater *Scirpus-Equisetum* wetland along Lake St. Francis, New York, while Day and others (1988) reported standing biomass along the Ottowa River ranged from 30 g/m^2 to 638 g/m^2.

more pronounced than in temperate zones. Auclair and others (1976) suggest that marsh systems have ample supplies of water. The fact that productivity is strongly related to soil moisture suggests that water budgets of riparian zones and marshes may be signifficantly different between geographic regions.

Marine organisms use nitrogen to phosphorus at a ratio of approximately 16:1, in what is known as the Redfield ratio (Redfield, 1958). Data taken from a study by Mason and Bryant (1975) found that the N:P ratio in *Phagmites communis* ranged from 3:1 to 2565:1. Excluding a single skewed ratio of 2565:1, the N:P ratio throughout the growing season in the Mason and Bryant (1975) study was 13.29:1. Because the *Phragmites* N:P ratio is reasonably close the Redfield ratio, it is assumed that it is appropriate to use the Redfield ratio to discuss potential nutrient limitation. By assuming the ratio which an organism uses nitrogen to phosphorus, the ratio can be used to evaluate potential nutrient limitation (Grimm and Fisher, 1986). Potential nitrogen limitation suggests that while absolute nitrogen levels might be above limiting levels, if plant are able assimilate nitrogen sufficiently to reduce the N:P ratio to below the the assummed tissue concentration ratio of 16:1, nitrogen concentrations will eventually limit productivity. Conversely if the N:P ratio is greater than 16:1, it suggests that phosphorus is potentially limiting (Grimm and Fisher, 1986). Soil N:P ratios at Kwagunt Marsh ranged from 0.001:1 to 5.014:1, indicating that based on soil data only, nitrogen is potentially limiting in the study area. In groundwater, the N:P ratio at Kwagunt Marsh ranged from 2.6:1 to 27.0:1, indicating that, based upon water chemistry, potential nutrient limitation may be spatially variable, with some locations potentially limited by nitrogen, and others potentially limited by phosphorus.

Nitrogen availability appeared to play a minor, but significant role in explaining plant productivity. Other researchers (Auclair et al., 1976; Day et al. 1988) have indicated that nutrient availability can promote or limit growth in wetlands. Two different measures of soil nitrogen, NH_4^+ concentrations in May, and nitrogen mineralization potential in July, were explanatory variables in regressions predicting productivity. Day and others (1988) suggest that riverine marshes can be conceptualized as following gradients of fertility, based upon their measurement of phosphorus concentrations, and disturbance, based upon their use of litter removal as a proxy variable. They found that sites tended to aggregate into locations with either high fertility and low disturbance, or low fertility and high disturbance. They noted that no sites with low disturbance and low fertility, or high disturbance and high fertility occur. At Kwagunt Marsh, disturbance has largely been removed, with the exception of vegetation found adjacent to the river's edge. Because the high disturbance sites were not sampled at Kwagunt Marsh, it is not possible to state whether high disturbance and high fertility sites exist at Kwagunt Marsh. However, because disturbance is absent from sites beyond 5 m from the river, low fertility and low disturbance sites not seen by Day and others (1988) emerged. These locations were found to have low standing biomass when compared to other non-disturbed sites.

It is not possible to directly compare rates of pre- and post-dam productivity along the Colorado River. Turner and Karpiscak (1980) did find that riparian vegetation has increased since the closure of Glen Canyon Dam. Because riparian zones act as nutrient sinks (Peterjohn and Correll, 1984; Pinay et al., 1992), if, indeed, riparian productivity has increased, there are potential ramifications to the overall nutrient budget of the entire stream ecosystem. Vitousek and Rieners (1975) studied the effects of ecosystem succession and nutrient retention. Following the general model of biomass accrual through successional time of Odum (1969), they indicate that retention rises rapidly as vegetative establishment and succession begin. Unless vegetation is disturbed, a steady state is eventually reached where ecosystem productivity is equal to zero, and elemental inputs equal outputs. If the assumption is made, based upon the fact that vegetation was scoured from the marsh in 1986, that the riparian ecosystem is the early successional stages, then it follows that the net biomass increment is increasing (Odum, 1969). Although nutrient use efficiency can change depending upon the nutrient availability (Keefe, 1972; Vitousek 1982), in general, with increased productivity generally comes increased nutrient use, and therefore, storage. These nutrients are inevitably extracted from the stream-riparian complex, in turn, reducing the amount of biologically available nutrients in the stream system. Controlled flows exacerbate the condition, in that disturbance, return to earlier successional states, and removal of biomass no longer occurs without overbank flooding, and therefore, nutrients are prevented from being returned to the stream. Therefore, assumming a fixed pool of nutrients in the stream-riparian complex, increased storage and utilization of nutrients in the riparian zone lead to decreased availability of nutrients in the stream system. Without additional information regarding the flux and overall nutrient pool sizes, however, it is difficult to predict the magnitude of these ramifications.

Conclusions

Objectives established for this research were to: (1) quantify spatial patterns in biomass accrual; (2) further refine the understanding between productivity patterns and environmental controls; (3) provide quantitative data that will lend itself to inclusion in models of nutrient spiralling; and (4) provide baseline data for an investigation into the validity of the flood-pulse theory. The first two objectives will be addressed in this section, and the final two objectives will be addressed in the future research section.

Minimally, productivity ranged from 0 to 2105 g/m^2/year. The mean minimum annual productivity was estimated to be 615 g/m^2/year. Highest productivity occurred in a dense stand of *Phragmites australis* not innundated by fluctuating water, and lowest productivity occurred in a sparse stand of *Tamarisk ramosissimi* located on the topographic rise between 45 and 60 m from the river. In May, over 80 percent of the biomass was produced by only four species: *P. australis, E. hiemale, Salix exigua,* and *Scirpus pungens.* In July, over 80 percent of the biomass was produced by only three species: *P. australis, E. hiemale,* and *S. exigua.*

Correlation analysis indicated variables were grouped together into clusters, and principal components analysis discerned the same groups of variables, indicating that two major environmental gradients were present at the site. The gradients were similar between months, however, potential nitrogen mineralization and soil nitrate concentrations did not conform to the same patterns in both sampling months. The elevation factor indicated that the elevation, soil texture, soil moisture, soil organic matter, and phosphorus concentrations, as well as potential nitrogen mineralization, in May, are all strongly related to each other. The nitrogen component explained the variations in nitrate, ammonium, and total inorgainc nitrogen in May, and the variations in ammonium, total inorganic nitrogen, and potential nitrogen mineralization in July. Additionally, significant differences in all environmental variables, except nitrate and potential nitrogen mineralization in May, were noted between the depositional and erosional surfaces at the study bar. A cursory look was taken at the groundwater geochemistry, which indicated that nutrient concentrations were spatially variable, suggesting that based upon water chemistry only, potential nutrient limitation could vary over space, with potential nitrogen limitation in some locations and potential phosphorus limitation in others. Based upon soil data only, however, nitrogen appears to be potentially limiting.

Plant productivity was significantly different between depositional and erosional surfaces at the bar. However, the high degree of correlation among variables makes it difficult to definitively state what is controlling plant productivity. The exploratory regressions analyzed in this research indicated that soil moisture was the most important variable in explaining productivity in both May and July. Additionally, two different measures of nitrogen availability, $NH4^+$ concentrations and nitrogen mineralization potential, also explained a small portion of the variation in productivity in May and July, respectively.

Future research

Changes in plant productivity have the potential to significantly effect nutrient budgets within the context of the entire stream ecosystem. The productivity rates measured in this research provide information fundamental to modelling nutrient spiralling. The productivity data from this research may be used in conjunction with either measured or estimated values of tissue nutrient concentrations to provide estimates of riparian nutrient use on reattachment bars. If the flux of nutrients through the stream system can be reasonably estimated, the magnitude of effect that riparian vegetation plays in the context of overall stream nutrient dynamics might be discerned.

Additionally, the study bar was subject to experimental overbank flooding in April 1996. The results in this research provide data for an experiment study on the effects of flooding on riparian plant productivity, and thus a test of the flood-pulse theory. The results of this study suggest that disturbance by overbank flooding will significantly surpress plant productivity in the short term. Additionally, because soil nutrient concentrations did not appear to be the most significant variables for explaining productivity, this research suggests that even if flooding brings a signficant influx of nutrients to the bar, productivity is not likely to significantly exceed the rates measured in this study.

Regarding the specific controls on plant productivity, the correlation between environmental variables makes it unlikely that further investigatios will resolve the question of what structures riparian plant productivity unless experimental methodologies are employed. Additionally, a potentially fruitful avenue of reserach might examine whether plants are more dependent upon groundwater or soils as a nutrient source. If plant nutrient sources are predominantly from groundwater, this research may have overlooked the importance of nutrients in explaining productivity. If groundwater is indeed the main nutrient source for riparian plants, the spatial variability of potential nutrient limitation is of greater consequence, and should be investigated further.

REFERENCES

Allen, S. E. (1989) *Chemical Analysis of Ecological Materials, 2nd edition.* London: Blackwell Scientific Publications.

Auclair, A. N. D., Bouchard, A., and Pajaczkowski, J. (1976) Plant standing crop and productivity relations in a *Scirpus-Equisetum* wetland. *Ecology*,Vol 57, 941-952.

Bendix, J. (1994) Scale, direction, and pattern in riparian vegetation-environment relationships. *Annals of the association of american geographers*, Vol 84, 652-665.

Brown, S. L., and Peterson, D. L. (1983) Structural characturistics and biomass production of two Illinois bottomland forests. *American Midland Naturalist*, Vol. 110, 107-117.

Carothers, S. W., and Brown, B. T. (1991) *The Colorado River through Grand Canyon - Natural History and Human Change.* Tucson: The University of Arizona Press.

Cooper, J. P. 1973. Control of photosynthetic production in terrestrial systems. In J. P. Cooper, ed., *Photosynthesis and productivity in different environments.* London: Cambridge University Press.

Day, R. T., Keddy, P. A., McNeill, J., and Carleton, T. (1988). Fertility and disturbance gradients: A summary model for riverine marsh vegetation. *Ecology*, Vol. 69, 1044-1054.

Frye, R. J., and Quinn, J. A. (1979) Forest development in relation to topography and soils in a flood-plain of the Raritan River, New Jersey. *Bulletin of the Torrey Botanical Club*, Vol. 106, 334-345.

Gemborys, S. R., and Hodgkins, E. J. (1971) Forests of small stream bottoms in the coastal plain of soutwestern Alabama. *Ecology*, Vol. 52, 70-82.

Gregory, S. V., Swanson, F. J., McKee, W. A., Cummins, K. W. (1991) An ecosystem perspective of riparian zones. *Bioscience*, Vol. 41, 540-551.

Grimm, N. B., and Fisher, S. G. (1986) Nitrogen limitation potential of Arizona streams and rivers. *Journal of the Arizona-Nevada Academy of Science*, Vol. 21, 31-43.

Holmes, R. M., Fisher, S. G., and Grimm, N. B. (1994) Parafluvial nitrogen dynamics in a desert stream ecosystem. *Journal of the North American Benthological Society*, Vol. 13, 468-478.

Hupp, C. R., and Osterkamp, W. R. (1985) Bottomland vegetation along Passage Creek, Virginia, in relation to fluvial landforms. *Ecology*, Vol. 66, 670-681.

Johnson, R. R., and Lowe, C. H. (1985) On the development of riparian ecology. In R. R. Johnson et al. eds., *Riparian ecosystems and their management*. Washington, D.C: U. S. Department of Agriculture, Forest Service, General Tech. Report RM-120.

Johnson, R. R. (1990) Historic changes in vegetation along the Colorado River in the Grand Canyon. In G. R. Mazolf, ed. *Colorado River ecology and dam management*. Wahington, D.C: National Academy Press.

Johnson, B. L., Richardson, W. B., and Naimo, T. J. (1995) Past, present, and future concepts in large river ecology. *Bioscience*, Vol. 45, 134-141.

Junk, W. J., Bayley, P. B., and Sparks, R. E. (1989) The flood pulse concept in river-floodplain systems. In D. P. Dogdge, ed. *Proceedings of the International Large River Symposium*. Can. Spec. Publ. Fish Aquat. Sci 106.

Keefe, C. W. 1972. Marsh production: A summary of the literature. *Contributions in Marine Science*, Vol. 16, 163-181.

Mason, C. F., and Bryant, R. J. (1975) Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha Angustifolia* L. *Journal of Ecology*, Vol. 63, 71-95.

Mitsch. W. J, and Ewel, K. C. (1979) Comparative biomass and growth of Cypress in Florida wetlands. *The American Midland Naturalist,* Vol. 101, 417-426.

Mitsch, W. J., and Gosselink, J. G. (1993) *Wetlands*. New York: Van Nostrand Reinhold.

Mitsch. W. J., and Rust, W. G. (1984) Tree growth responses to flooding in a bottomland forest in northeastern Illinois. *Forest Science*, Vol. 30, 499-

510.

Newbould, J. D., Elwood, J. W., O'Neill, R. V, and Van Winkle, W. (1981) Measuring nutrient spiralling in streams. *Canadien Journal of Fisheries and Aquatic Science*, Vol. 38, 860-863.

Nillson, C. (1984) Effects of stream regulation on riparian vegetation. In A. Lillehammer and S., J. Saltveit, eds. *Regulated rivers*. New York: Oxford University Press.

Odum, E. P. (1969) The strategy of ecosystem development. *Science*, Vol. 164, 262-270.

Pearsall, W. H., and Gorham, E. (1956) Production ecology I. standing crops of natural vegetation. *Oikos*, Vol. 7, 193-201.

Peterjohn, W. T., and Correll, D. L. (1984) Nutrient dynamics in an agricultural watershed: observation on the role of a riparian forest. *Ecology*, Vol. 65, 1466-1475.

Pinay, G, Fabre, A., Vervier, Ph., and Gazelle, F. (1992) Controls of C, N, P distribution in soils of riparian forests. *Landscape ecology*, Vol. 6, 121-132.

Redfield, A. C. (1958) The biological control of chemical factors in the environment. *American Scientist*, Vol. 46, 205-221.

Rubin, D. M., Schmidt, J. G., and Moore, J. N. (1990) Origin, structure, and evolution of a reattachment bar, Colorado River, Grand Canyon, Arizona. *Journal of Sedimentary Petrology*, Vol. 60, 982-991.

Smith, S. D., Wellington, A. B., Nachlinger, J. L., and Fox, C. A. (1991) Functional responses of riparian vegetation to streamflow diversion in the eastern Sierra Nevada. *Ecological Applications*, Vol. 1, 89-97.

Stake, E. 1967. Higher vegetation and nitrogen in a rivulet in Central Sweden. *Schweiz. S. Hydrol.*, Vol. 29,107-124.

Stevens, L. E., and T. J. Ayers. 1993. The influence of Glen Canyon dam operations on plant water relations and growth of native *Salix exigua* and exotic *Tamarix ramosissima* in the Colorado River Corridor, Grand Canyon National Park, Arizona. In *The effects of interim flows* *from Glen Canyon Dam on riparian vegetation along Colorado River in Grand Canyon National Park, Arizona: Final Report.* Grand Canyon: Grand Canyon National Park Service Report # CA8021-8-0002.

Stevens, L. E., Schmidt, J. C., and Ayers, T. J. (1995) Flow regulation, geomorphology, and Colorado River marsh development in the Grand Canyon, Arizona. Ecological Applications, Vol. 5, 1025-1039.

Stromberg, J. C., Wilkins, S. D., and Tress, J. A. (1993) Vegetation-hydrology models as management tools for velvet mesquite (*Prosopis velutina*) riparian ecosystems. *Ecological Applications*, Vol. 3, 307-314.

Tansley, A. G. 1935. The use and abuse of vegetational concepts. *Ecology*, Vol. 16, 284-307.

Turner, R. M., Karpiscak, M. M. (1980) Recent vegetation changes along the Colorado River between Glen Canyon Dam and Lake Mead, Arizona. *U.S.G.S. Professional Paper 1132.*

Vitousek, P. M., Gosz, J. R., Grier, C. C., Melillo, J. M., and Reiners, W. A. (1982) A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecological Monographs*, Vol. 52, 155-177.

Vitousek, P. M., and Reiners, W. A. (1975) Ecosystem succession and nutrient retention: a hypothesis. *Bioscience*, Vol. 25, 376-381.

Ward, J. V. 1989. The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society, Vol. 8, 2-8.

Whittaker, R. H., and Marks, P. L. (1975) Methods of Assessing Terrestrial Productivity. In Helmut Lieth, and R. H. Whittaker, eds. *Primary Productivity of the Biosphere*. New York: Springer-Verlag.

APPENDIX A

SAMPLE LOCATION COORIDINATES

ID	Easting	Northing
1	220808.4766	584224.4179
2	220811.4298	584219.9783
3	220813.9143	584215.7649
4	220817.3325	584212.7802
5	220819.9191	584207.1441
6	220812.8955	584227.0921
7	220815.5812	584223.0175
8	220818.1721	584218.8514
9	220820.7646	584214.7809
10	220823.6908	584210.4291
11	220816.4279	584229.8924
12	220819.3069	584225.8937
13	220822.1768	584221.5879
14	220825.0486	584217.6468
15	220827.4796	584213.4515
16	220820.6250	584232.6642
17	220823.4802	584228.6446
18	220826.4915	584224.5163
19	220829.2280	584220.5035
20	220831.8172	584216.5504
21	220824.7375	584235.5210
22	220827.4693	584231.3461
23	220830.3883	584227.0118
24	220833.3827	584222.9723
25	220835.9375	584218.8539
26	220828.7868	584238.2776
27	220831.5464	584234.0789
28	220834.2089	584229.9108
29	220837.0536	584225.7003
30	220840.0034	584221.7173
31	220832.9508	584240.9077
32	220835.8424	584236.7439
33	220838.6374	584232.6360
34	220841.3393	584228.3980
35	220844.2228	584224.3849
36	220837.2340	584243.5063
37	220839.2661	584239.1048
38	220842.4028	584235.5337
39	220845.3202	584230.7631
40	220848.6528	584226.8146
41	220841.3252	584246.4855
42	220843.3108	584242.2271
43	220846.5907	584238.2504
44	220849.3925	584234.0730
45	220852.4922	584230.0326
46	220845.5010	584249.3992
47	220848.4456	584245.1007
48	220851.1355	584241.0456
49	220853.6942	584236.8146
50	220856.3484	584232.6155
51	220849.[illegible]	584252.1295
52	220852.4273	584247.8061
53	220855.1584	584243.8929
54	220857.8021	584239.7295
55	220861.7709	584235.5702
56	220853.[illegible]	584255.0227
57	220855.8121	584250.3602
58	220859.5073	584246.3355
59	220862.3003	584241.9730
60	220864.8811	584237.7348
61	220857.3584	584257.6135
62	220860.5950	584253.5387
63	220863.3762	584249.2046
64	220866.7297	584245.1043
65	220868.5659	584240.9481
66	220862.1756	584260.2241
67	220864.4244	584256.4899

Sample location UTM coordinates.

APPENDIX B

ENVIRONMENTAL DATA

ID	ELEV	SC	H20	OM	NO3-	NH4+	TIN	NMIN	SRP
1	843.093	11.74	1.16	0.25	0.01	0.58	0.59	-0.07	4.03
2	843.395	14.18	3.96	0.47	0.63	0.51	1.14	-0.21	3.08
3	843.790	23.95	19.29	1.15	0.00	0.90	0.90	1.45	6.37
4	843.654	32.88	38.50	1.75	0.23	4.27	4.49	-1.39	7.82
6	844.471	2.86	1.13	0.44	0.78	1.95	2.73	-2.01	3.08
7	844.040	4.40	1.01	0.37	0.00	0.26	0.26	0.41	3.66
8	843.804	1.75	1.57	0.17	0.00	1.10	1.10	-0.42	3.34
9	843.432	1.36	3.22	0.33	0.00	0.19	0.19	0.67	2.09
11	844.761	4.69	0.87	0.15	0.20	0.60	0.80	-0.13	2.88
12	844.638	4.24	0.79	0.66	0.05	0.15	0.20	0.37	4.44
13	844.571	2.67	1.09	0.40	0.00	0.33	0.33	0.04	3.87
14	844.497	2.26	1.65	0.19	0.00	0.12	0.12	0.24	3.79
16	844.478	5.02	2.78	0.49	0.08	0.68	0.77	-0.30	3.18
17	844.821	12.89	1.03	0.60	0.00	0.37	0.37	0.63	4.52
18	844.508	2.97	2.97	0.45	0.00	0.65	0.65	-0.12	3.65
19	844.446	1.57	0.75	0.38	0.03	0.33	0.36	0.20	3.45
21	843.912	4.50	1.09	0.31	0.03	0.28	0.32	-0.09	2.70
22	844.085	8.29	1.24	0.34	0.00	1.12	1.12	-0.43	3.30
23	843.893	3.77	1.02	0.47	0.04	0.38	0.42	-0.13	2.45
24	844.033	2.23	1.62	0.40	0.00	0.15	0.15	2.95	2.03
26	843.496	53.32	22.00	1.55	0.32	1.38	1.70	-0.30	4.54
27	843.531	37.31	25.04	3.10	0.21	0.38	0.59	1.14	12.86
28	843.476	53.03	20.06	1.53	0.00	0.12	0.12	0.43	7.83
29	843.636	40.30	18.43	0.59	0.24	0.00	0.24	0.51	5.11
31	843.241	44.25	25.94	2.90	0.00	0.74	0.74	5.50	8.47
32	843.215	45.60	23.55	2.50	0.14	0.13	0.27	0.23	12.06
33	843.275	65.35	40.11	2.62	0.18	0.65	0.83	0.37	9.84
34	843.294	53.16	23.95	2.29	0.00	0.11	0.11	0.58	5.53
36	843.153	34.45	20.89	1.43	0.42	1.41	1.83	1.59	7.57
37	843.166	32.56	22.91	2.66	0.00	0.44	0.44	2.00	10.11
38	843.269	42.31	20.99	1.47	0.12	0.51	0.63	2.26	11.04
39	843.324	45.65	22.03	1.03	0.00	0.03	0.03	2.49	10.67
41	843.375	23.15	17.95	1.17	0.15	1.07	1.21	1.06	6.09
42	843.349	32.77	19.25	3.60	0.24	0.12	0.36	3.07	14.00
43	843.322	31.61	17.77	1.20	0.05	1.00	1.04	2.30	16.80
44	843.320	47.22	23.91	2.66	0.24	0.50	0.75	7.33	13.65
46	843.431	36.31	10.37	0.44	0.00	0.47	0.47	0.29	6.22
47	843.386	27.58	15.60	1.01	0.59	1.00	1.59	0.90	6.10
48	843.491	32.11	35.05	0.91	0.11	0.84	0.96	2.67	24.18
49	843.446	40.45	15.89	0.79*	0.00	0.70	0.70	1.24	10.90
51	843.291	51.39	20.71	1.18	0.00	1.10	1.10	3.55	12.55
52	843.377	31.78	20.15	1.53	0.00	0.12	0.12	0.60	9.32
53	843.323	16.01	13.43	0.35	0.00	0.91	0.91	-0.40	9.82
54	843.344	25.65	18.04	1.31	0.00	0.11	0.11	0.53	7.14
56	843.322	36.62	17.82	1.22	0.00	0.73	0.73	-0.04	10.47
57	843.260	37.41	17.16	1.33	0.00	0.13	0.13	0.66	11.19
58	843.189	27.54	19.04	0.83	0.00	0.59	0.59	-0.15	12.92
59	843.163	36.34	25.21	1.82	0.21	0.47	0.69	1.28	5.06
61	843.039	50.57	19.85	0.54	0.20	1.00	1.20	-0.53	5.74
62	842.954	43.41	22.38	0.51	0.00	0.00	0.00	1.09	6.36
63	842.806	23.91	42.06	2.05	0.05	0.52	0.57	2.53	6.77
64	842.702	58.33	23.26	1.15	0.00	0.96	0.96	0.86	4.82
66	842.749	39.47	20.69	0.66	0.06	0.59	0.65	0.02	5.45
67	842.643	55.27	26.08	1.86	0.00	0.31	0.31	7.36	5.16

May data for environmental variables elevation (ELEV), soil texture (SC), soil organic matter (OM), soil moisture (H2O), soil nitrate concentrations (NO3-), soil ammonium concentrations (NH4+), total soil inorganic nitrogen (TIN), potential nitrogen mineralization (NMIN), and soil phosphorus concentrations (SRP) are reported. ELEV is reported as meters above sea level. H2O is reported as percentage water by weight. SC is reported as percentage, by weight, of particles smaller than 0.063mm. OM is reported as the percentage loss on ignition. NO3-, NH4+, TIN, NMIN, and SRP are reported in micrograms per gram dry weight soil.

* Value was calculated as the mean of locations 46, 47, and 48.

ID	ELEV	SC	H20	OM	NO3-	NH4+	TIN	NMIN	SRP
1	843.093	11.74	13.08	0.35	0.01	1.22	1.23	-0.38	0.58
2	843.395	14.18	15.21	0.32	0.01	0.52	0.53	-0.22	0.91
3	843.790	23.95	22.32	0.89	0.01	2.71	2.72	-2.22	0.85
4	843.654	32.88	22.95	1.44	0.00	0.97	0.97	-0.78	1.20
6	844.471	2.86	0.89	0.13	0.01	1.24	1.25	-0.71	0.41
7	844.040	4.40	0.67	0.23	0.00	0.30	0.30	0.23	0.29
8	843.804	1.75	0.98	0.27	0.00	1.38	1.39	-1.08	0.47
9	843.432	1.36	4.04	0.43	0.01	0.67	0.67	-0.24	0.57
11	844.761	4.69	0.80	0.10	0.01	1.58	1.59	-0.70	0.32
12	844.638	4.24	1.09	0.31	0.01	0.73	0.74	-0.35	0.37
13	844.571	2.67	0.62	0.35	0.00	0.80	0.80	-0.25	0.31
14	844.497	2.26	0.38	0.37	0.01	0.74	0.75	-0.09	0.59
16	844.478	5.02	1.15	0.55	0.01	0.94	0.95	-0.53	0.34
17	844.821	12.89	0.56	0.32	0.00	0.51	0.51	0.17	0.44
18	844.508	2.97	1.27	0.45	0.01	0.60	0.61	0.07	0.50
19	844.446	1.57	0.24	0.38	0.01	0.61	0.62	-0.23	0.53
21	843.912	4.50	3.94	0.12	0.01	1.65	1.66	-1.37	0.39
22	844.085	8.29	1.52	0.18	0.00	0.96	0.96	0.03	0.48
23	843.893	3.77	11.17	0.75	0.01	1.05	1.05	-0.72	0.65
24	844.033	2.23	2.65	0.34	0.02	0.45	0.47	3.31	0.48
26	843.496	53.32	23.21	2.59	0.01	1.27	1.28	-0.47	0.90
27	843.531	37.31	21.20	0.81	0.00	0.69	0.69	0.23	0.86
28	843.476	53.03	20.82	1.83	0.01	0.86	0.87	-0.45	0.77
29	843.636	40.30	19.76	0.46	0.01	0.80	0.80	4.26	1.08
31	843.241	44.25	23.91	2.36	0.01	5.32	5.33	-4.01	1.81
32	843.215	45.60	21.69	1.30	0.00	0.64	0.64	0.19	2.47
33	843.275	65.35	23.76	2.22	0.01	0.83	0.84	0.06	1.30
34	843.294	53.16	23.83	1.15	0.00	0.67	0.67	-0.34	1.68
36	843.153	34.45	24.26	2.15	0.01	0.00	0.01	0.71	1.45
37	843.166	32.56	28.29	3.29	0.00	0.78	0.79	0.36	2.25
38	843.269	42.31	21.10	1.07	0.01	0.80	0.81	-0.25	2.02
39	843.324	45.65	22.94	1.64	0.00	1.06	1.07	-0.75	2.36
41	843.375	23.15	22.37	2.07	0.01	1.76	1.77	-0.73	1.62
42	843.349	32.77	19.80	0.80	0.00	0.51	0.52	0.27	1.30
43	843.322	31.61	20.73	1.47	0.01	1.15	1.16	-0.41	2.89
44	843.320	47.22	22.32	1.80	0.00	0.60	0.61	-0.22	2.09
46	843.431	36.31	20.37	0.68*	0.01	2.05	2.06	-1.25	1.26
47	843.386	27.58	19.01	0.64	0.00	0.67	0.67	0.11	0.81
48	843.491	32.11	19.48	0.54	0.01	0.36	0.36	0.00	1.83
49	843.446	40.45	20.68	0.36	0.01	0.69	0.70	0.02	1.94
51	843.291	51.39	18.85	1.11	0.01	1.38	1.39	-0.41	0.99
52	843.377	31.78	20.01	0.48	0.00	0.39	0.39	0.02	2.22
53	843.323	16.01	19.79	0.89	0.00	1.09	1.09	-0.44	2.05
54	843.344	25.65	20.74	0.93	0.00	0.80	0.80	-0.40	1.34
56	843.322	36.62	21.46	0.81	0.01	1.75	1.76	-1.14	2.33
57	843.260	37.41	20.19	0.92	0.00	0.00	0.00	0.64	1.43
58	843.189	27.54	23.11	1.09	0.01	1.30	1.31	-1.04	1.20
59	843.163	36.84	24.11	2.21	0.00	0.83	0.83	-0.24	1.22
61	843.039	50.57	NS	NS	NS	NS	NS	NS	NS
62	842.954	43.41	NS	NS	NS	NS	NS	NS	NS
63	842.806	23.91	NS	NS	NS	NS	NS	NS	NS
64	842.702	58.33	NS	NS	NS	NS	NS	NS	NS
66	842.749	39.47	NS	NS	NS	NS	NS	NS	NS
67	842.643	65.27	NS	NS	NS	NS	NS	NS	NS

July data for environmental variables elevation (ELEV), soil texture (SC), soil organic matter (OM), soil moisture (H20), soil nitrate concentrations (NO3-), soil ammonium concentrations (NH4+), total soil inorganic nitrogen (TIN), potential nitrogen mineralization (NMIN), and soil phosphorus concentrations (SRP) are reported. ELEV is reported as meters above sea level. H20 is reported as the percentage water by weight. SC is reported as the percentage, by weight, of particles smaller than 0.063mm. OM is reported as the percentage loss on ignition. NO3-, NH4+, TIN, NMIN, and SRP are reported in micrograms per gram dry weight soil. NS symbolizes not sampled.

* Value was calculated as the mean of locations 47, 48, and 49.

APPENDIX C

PRODUCTIVITY DATA

ID	Harvest	Foliage	Total	Litter
1	390	25.6	415.6	609
2	349	156.1	505.1	679
3	310	579.4	889.4	802
4	346	147.4	493.4	472
6	122	42.9	164.9	372
7	211	37.2	248.2	572
8	212	54.3	266.3	668
9	0	0.0	0.0	266
11	0	15.9	15.9	44
12	18	47.1	65.1	124
13	0	0.6	0.6	461
14	0	123.0	123.0	596
16	0	0.0	0.0	445
17	26	56.7	82.7	266
18	111	11.9	122.9	592
19	73	0.0	73.0	269
21	193	79.6	272.6	623
22	83	6.8	89.8	156
23	334	0.0	334.0	287
24	45	16.6	61.6	135
26	371	249.8	620.8	681
27	503	13.6	516.6	718
28	644	381.1	1025.1	1035
29	299	31.5	330.5	507
31	1447	76.0	1523.0	1745
32	589	135.8	724.8	757
33	1082	201.9	1283.9	1156
34	852	111.6	963.6	915
36	552	0.0	552.0	3116
37	1000	3.6	1003.6	1291
38	1197	34.3	1231.3	863
39	584	89.7	673.7	1893
41	508	0.0	508.0	1546
42	1932	173.5	2105.5	1176
43	495	28.0	523.0	666
44	1139	0.0	1139.0	2047
46	735	125.2	860.2	1309
47	1489	109.1	1598.1	665
48	1469	0.0	1469.0	448
49	356	115.1	471.1	1700
51	818	0.0	818.0	770
52	215	25.0	240.0	1153
53	177	0.0	177.0	858
54	689	32.7	721.7	989
56	518	0.0	518.0	637
57	932	0.0	932.0	1220
58	1688	0.0	1688.0	637
59	1755	0.0	1755.0	356
61	220	0.0	220.0	318
62	319	0.0	319.0	344
63	NS	NS	NS	NS
64	NS	NS	NS	NS
66	NS	NS	NS	NS
67	NS	NS	NS	NS

July plant productivity and litter are reported.
Data is divided into harvested biomass,
foliage estimates, total productivity, and litter.
Values are reported as grams per meter square
NS denotes not sampled.

ID	PHAU	EQHY	SCPU	MUAS	CAAU	EQAR	COCA	PLMA	SAEX	TARA	BAEM
1	0.00	94.12	0.00	0.00	0.00	0.00	0.00	0.00	5.88	0.00	0.00
2	0.00	70.33	0.00	0.00	0.00	0.00	0.00	0.00	29.67	0.00	0.00
3	0.00	36.29	0.00	0.00	0.00	0.00	0.00	0.00	15.74	0.00	47.98
4	0.00	1.97	0.00	0.00	68.97	0.00	0.00	0.00	29.05	0.00	0.00
6	0.00	75.17	0.00	0.00	0.00	0.00	0.00	0.00	24.83	0.00	0.00
7	0.00	86.07	0.00	0.00	0.00	0.00	0.00	0.00	13.93	0.00	0.00
8	0.00	80.56	0.00	0.00	0.00	0.00	0.00	0.00	6.08	13.36	0.00
9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	0.00
12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	0.00
13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	0.00
14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.84	88.16	0.00
16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17	0.00	34.62	0.00	0.00	0.00	0.00	0.00	0.00	0.00	65.38	0.00
18	0.00	90.98	0.00	0.00	0.00	0.00	0.00	0.00	9.02	0.00	0.00
19	0.00	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
21	0.00	72.52	0.00	0.00	0.00	0.00	0.00	0.00	27.48	0.00	0.00
22	0.00	92.61	0.00	0.00	0.00	0.00	0.00	0.00	7.39	0.00	0.00
23	0.00	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24	0.00	75.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	24.93	0.00
26	0.00	51.20	3.94	0.00	0.00	0.00	5.51	0.00	34.44	4.91	0.00
27	17.93	26.53	10.98	32.93	0.00	0.00	9.15	0.00	2.50	0.00	0.00
28	0.00	21.88	0.00	41.86	0.00	0.00	0.00	0.00	6.37	0.00	29.89
29	6.49	66.30	0.00	18.34	0.00	0.00	0.00	0.00	6.57	2.31	0.00
31	76.78	18.40	0.00	0.00	0.00	0.00	0.00	0.00	4.82	0.00	0.00
32	67.70	14.46	0.00	0.00	0.00	0.00	0.00	0.00	17.85	0.00	0.00
33	31.49	43.02	7.68	0.77	0.00	0.00	1.54	0.00	15.50	0.00	0.00
34	53.88	30.65	0.00	0.00	0.00	0.00	4.45	0.00	2.40	0.00	8.63
36	94.83	5.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
37	86.84	11.58	1.23	0.00	0.00	0.00	0.00	0.00	0.34	0.00	0.00
38	83.76	6.20	0.00	7.37	0.00	0.00	0.00	0.00	2.66	0.00	0.00
39	79.95	0.00	0.00	0.00	0.00	0.00	7.36	0.00	12.69	0.00	0.00
41	90.20	0.00	7.84	1.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00
42	47.36	44.58	0.00	0.00	0.00	0.00	0.00	0.00	6.80	1.26	0.00
43	0.00	0.00	94.94	0.00	0.00	0.00	0.00	0.00	5.06	0.00	0.00
44	99.16	0.00	0.00	0.00	0.00	0.00	0.84	0.00	0.00	0.00	0.00
46	61.03	0.00	16.27	8.14	0.00	0.00	0.00	0.00	14.56	0.00	0.00
47	89.48	0.00	1.21	2.12	0.00	0.00	0.60	0.00	0.00	0.00	6.59
48	82.67	0.00	10.00	6.00	0.00	0.33	1.00	0.00	0.00	0.00	0.00
49	57.44	0.00	12.76	0.00	0.00	0.00	5.32	0.00	0.00	24.48	0.00
51	94.19	0.00	0.00	5.81	0.00	0.00	0.00	0.00	0.00	0.00	0.00
52	76.00	0.00	8.00	4.00	0.00	2.00	0.00	0.00	0.00	10.00	0.00
53	0.00	0.00	93.41	0.00	0.00	0.00	6.59	0.00	0.00	0.00	0.00
54	88.27	0.00	2.67	4.68	0.00	0.00	0.00	0.00	0.00	0.00	4.38
56	67.63	0.00	0.00	28.78	0.00	0.00	2.88	0.72	0.00	0.00	0.00
57	71.28	0.00	0.00	28.72	0.00	0.00	0.00	0.00	0.00	0.00	0.00
58	86.05	0.00	0.00	8.72	0.00	0.29	4.65	0.29	0.00	0.00	0.00
59	99.22	0.00	0.26	0.00	0.00	0.52	0.00	0.00	0.00	0.00	0.00
61	66.99	0.00	25.84	2.39	0.00	4.78	0.00	0.00	0.00	0.00	0.00
62	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
63	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
64	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
66	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
67	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

July species composition, calculated as the percentage contribution to overall biomass from a sample location is provided. NS denotes not sampled.

Key

PHAU	Phragmites australis
EQHY	Equisetum hiemale
SCPU	Scirpus pungens
MUAS	Muhlenbergia asperifolia
CAAU	Carex aquatilis
EQAR	Equisetum arvense
COCA	Conyza canadensis
PLMA	Plantago major
SAEX	Salix exigua
TARA	Tamarix ramosissimi
BAEM	Baccharis emoryi