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# The flood pulse in a semi-arid riparian forest: metabolic and biogeochemical responses to inter-flood interval

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1 Running Head: Semi-arid floodplain response to flood pulse

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6 **Biogeochemical and Metabolic Responses**  
7 **to the Flood Pulse in a Semi-Arid Floodplain**

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11 with 7 Figures and 3 Tables

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1 *Abstract:* Flood pulse inundation of riparian forests alters rates of nutrient retention and  
2 organic matter processing in the aquatic ecosystems formed in the forest interior. Along the  
3 Middle Rio Grande (New Mexico, USA), impoundment and levee construction have created  
4 riparian forests that differ in their inter-flood intervals (IFIs) because some floodplains are  
5 still regularly inundated by the flood pulse (i.e., connected), while other floodplains remain  
6 isolated from flooding (i.e., disconnected).

7 This research investigates how ecosystem responses to the flood pulse relate to forest IFI  
8 by quantifying nutrient and organic matter dynamics in the Rio Grande floodplain during  
9 three years of experimental flooding of the disconnected floodplain and during a single year  
10 of natural flooding of the connected floodplain. Surface and subsurface conditions in paired  
11 sites (control, flood) established in the two floodplain types were monitored to address  
12 metabolic and biogeochemical responses.

13 Compared to dry controls, rates of respiration in the flooded sites increased by up to 3  
14 orders of magnitude during the flood pulse. In the disconnected forest, month-long  
15 experimental floods produced wide spread anoxia of 4-week duration during each of the  
16 three years of flooding. In contrast, water in the connected floodplain remained well  
17 oxygenated (3-8 ppm). Material budgets for experimental floods showed the disconnected  
18 floodplain to be a sink for inorganic nitrogen and suspended solids, but a potential source of  
19 dissolved organic carbon (DOC). Compared to the main stem of the Rio Grande, flood water  
20 on the connected floodplain contained less nitrate, but comparable concentrations of DOC,  
21 phosphate-phosphorus, and ammonium-nitrogen.

22 Results suggest that floodplain IFI drives metabolic and biogeochemical responses during

1 the flood pulse. Impoundment and fragmentation have altered floodplains from a mosaic of  
2 patches with variable IFI to a bimodal distribution. Relatively predictable flooding occurs in  
3 the connected forest, while inundation of the disconnected forest occurs only as the result of  
4 managed application of water. In semi-arid floodplains, water is scarce except during the  
5 flood pulse. Ecosystem responses to the flood pulse are related to the IFI and other measures  
6 of flooding history that help describe spatial variation in ecosystem function.

7 Keywords: inter-flood interval, flood pulse, floodplain, river, nutrients, respiration, riparian  
8 forest

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## INTRODUCTION

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In their natural state, riparian zones are intimately linked to the rivers they border (Gregory et al. 1991) and flooding facilitates the exchange of materials and energy between rivers and their floodplains (Junk et al. 1989, Mayack et al. 1989, Bayley 1995). In the past century, flow regulation has reduced or eliminated hydrological and ecological interactions between many rivers and their floodplains. Dynesius and Nilsson (1994) showed that for the 139 largest river ecosystems of the northern one-third of the Earth, 77% of the total water discharge is strongly or moderately affected by fragmentation of river channels by dams, interbasin diversions, and irrigation. Disconnection of river channels from their historic floodplains, therefore, is a common ecological alteration in the U.S. and worldwide.

The flood pulse concept of Junk et al. (1989) and Bayley (1995) emphasizes that inundation of the floodplain creates and maintains riparian forests as some of the most productive and diverse ecosystems in the biosphere. In the flood pulse model, flooding is predicted to trigger an increase in the magnitude of biological processes that occur during

1 both the rising and falling limb of the pulse. For the most part, the model has emphasized the  
2 expansion of aquatic habitat and the importance of floods for aquatic communities and fish  
3 production (Bayley 1995, Odum et al. 1995) in large rivers of tropical and semi-tropical  
4 regions.

5 It is also clear that the flood pulse plays an important role in determining functional  
6 characteristics of floodplains and the rivers that inundate them. Foresberg et al. (1988)  
7 showed that mixing of river water with floodplain lakes of the Amazon River system altered  
8 concentrations of N and P in both particulate and dissolved forms. Smith et al. (2000) found  
9 that flooding from the Orinoco River determined the rate and extent of methane emission  
10 from floodplain habitats, with the highest values observed in flooded riparian forests. The  
11 flood pulse along the Ogeechee River, Georgia, USA, resulted in the net loss of floodplain  
12 organic matter (Cuffney 1988), consistent with the conclusions of Meyer and Edwards  
13 (1990) that linked that river's metabolism to floodplain inputs.

14 Recently, holistic models of rivers and streams have recognized the importance of  
15 groundwater/streamwater interaction (Findlay 1995). In this context, riparian forests have  
16 received attention because of their potential to act as nutrient filters that reduce nutrient loads  
17 originating from groundwater flow paths (Peterjohn and Correll 1984, Triska et al. 1993)  
18 under baseflow conditions. Far less study has addressed nutrient transport and retention in  
19 riparian forests during flooding or the influence of surface-groundwater interactions on  
20 ecosystem responses to the flood pulse.

21 In arid and semi-arid regions of the world, including the southwestern United States  
22 (Fisher et al. 1982, Molles and Dahm 1990), Australia (Walker et al. 1995), and southwestern

1 Africa (Jacobson et al. 1995), floods are major ecological organizers for lotic systems,  
2 floodplains, and riparian forests. While flash floods may be disturbances that result in pulsed  
3 mortality (Fisher et al. 1982), they also increase the extent of aquatic habitat (Stanley et al.  
4 1997) and result in transport that alters resource availability (Jacobson et al. 1995). In arid  
5 and semi-arid regions, ecosystem processes in the riparian forest may be limited by moisture  
6 availability (Ellis et al. 2002) and flooding should promote strong responses in the inundated  
7 floodplain.

8       Along the Middle Rio Grande of New Mexico in the southwestern United States, fifty  
9 years of flow regulation have had deleterious effects on the riparian forest (Howe and Knopf  
10 1991, Bullard and Wells 1992). Regulation has favored the growth and dispersal of exotic  
11 species and eliminated sexual reproduction by many native species of riparian trees  
12 (Stromberg 2001). In addition, the absence of flooding has favored accumulation of forest  
13 floor wood and litter (Molles et al. 1995, Ellis et al. 1999), increasing the size of a relatively  
14 inactive organic matter pool rich in carbon (C). Further, impoundment has reduced peak  
15 discharge of the flood pulse while levees have bifurcated the riparian forests, creating  
16 relatively disconnected (i.e. outside of levees) and connected (river-side forests within the  
17 levees) floodplains. The flood pulse continues to regularly (i.e., on a nearly annual basis  
18 depending on the magnitude of discharge during spring snow melt, Slack et al. 1993)  
19 inundate connected floodplains while disconnected floodplains remain isolated from flooding  
20 for much longer periods of time. As a result, these riparian forests differ in their inter-flood  
21 interval (IFI, Molles et al. 1998). The floodplain along the Middle Rio Grande, like many  
22 other large river systems, has historically represented a mosaic of ecosystems with differing  
23 histories of flooding (e.g., different IFIs). Loss of connectivity between the river and

1 floodplain due to flow regulation and floodplain modification has shifted the distribution  
2 toward longer IFIs. At the same time, these changes and active management of riparian  
3 vegetation have favored the invasion and establishment of non-native species (Ellis et al.  
4 2002).

5 This study investigates how the IFI influences flood pulse regulation of metabolism and  
6 nutrient retention within a floodplain ecosystem dominated by native vegetation. Using  
7 experimental and natural flooding of the riparian forests along the Middle Rio Grande, we  
8 address how inundation influences forest floor respiration, and retention of dissolved organic  
9 carbon (DOC), inorganic nitrogen (N), and phosphorus (P). Water table elevation and  
10 groundwater biogeochemical structure were monitored to address surface-subsurface  
11 exchange during flooding and consider its role in ecosystem responses to the flood pulse.

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#### STUDY SITES

14 Study sites were established within the Bosque del Apache National Wildlife Refuge  
15 (Figure 1) along the Middle Rio Grande, New Mexico, USA, where the majority of refuge  
16 land is disconnected floodplain. The refuge's connected floodplain is located within the  
17 constructed levees (i.e. adjacent to the river) where river flooding during spring runoff  
18 commonly inundates the riparian forest. Forests of the connected floodplain have IFIs that  
19 range from 1-5 years, while the IFI for disconnected floodplains reflect 50 years of isolation  
20 due to reservoir and levee construction (Slack et al. 1993).

21 In 1991, a single pair of study sites was established within the disconnected floodplain  
22 (Figure 1) where riparian vegetation was dominated by native Rio Grande cottonwood



1 [*Populus deltoides* var. *wislizenii* (Wats.) Eckenwalder] with a subcanopy of Gooding's  
2 black willow [*Salix gooddingii* Ball.]. From 1993 to 1995, a 10 ha site on the disconnected  
3 floodplain (i.e., experimental flood site) was subject to flooding from a riverside irrigation  
4 canal (Figure 1). A site on the disconnected floodplain that did not receive any flooding  
5 during the study (i.e., outside-levee control) was located ca. 3.7 km north of the experimental  
6 flood site. In 1995, a pair of study sites was established on the connected floodplain (Figure  
7 1). The natural flood site was at a topographic low point and was flooded regularly during  
8 spring runoff. The inside-levee control site was located in an elevated portion of the  
9 connected floodplain and was protected from floods by remnant groin dikes.

10 A sampling web consisting of 12 radially arranged transects 100 m long (Figure 1) was  
11 established within each of the disconnected floodplain sites and used to monitor a suite of  
12 ecological responses to flooding (Molles et al. 1998). In March 1993, six sampling wells  
13 were installed in each site and the network expanded to 16 in March of 1994 with wells  
14 distributed relatively uniformly within each 3.14 ha sampling web (Figure 1).

15 Sampling sites within the connected floodplain consisted of 10 parallel transects 60 m  
16 long and 20 meters apart. Seven sampling wells were installed in February of 1995,  
17 uniformly distributed throughout each site. In the connected flood site, water flowed freely  
18 and inundation extended laterally for over 200 m from the riverbed to the levee.

19 Soils in the area are Typic Ustifluvents characterized as deep, somewhat poorly drained to  
20 well-drained soils on floodplains formed in recent alluvium (Johnson 1988). Permeability  
21 ranges from very rapid to very slow. Shallow soils (0-10 cm) contain 3-5% organic matter  
22 (OM) by weight with OM decreasing sharply with depth (CN Dahm, unpublished data).  
23 Variable drainage is often related to clay-rich layers encountered at various depths.

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METHODS

*Experimental flooding*

Water used for flooding the disconnected flood site was diverted from the Rio Grande and conveyed via irrigation canals to the refuge. Chemical composition of canal water was similar to that in the main stem of the Rio Grande (Digital Appendix 1). Water was routed onto the disconnected flood plot through groin dikes equipped with H-notched weirs. In 1994 and 1995, refuge personnel monitored discharge onto and from the plot. Floods lasted approximately 30 days and were designed to peak on May 31, the average date of maximal river discharge based on a 100 yr (1889 - 1990) hydrograph (Slack et al. 1993).

*Sampling wells and water table monitoring*

Sampling wells (3-4 m long) constructed from 5 cm diameter poly vinyl chloride (PVC) casing had 2-3 m of 25 µm slotted screen that extended 50 - 100 cm below the water table. A Solinst Model 101 Water Level Meter (Solinst, Georgetown, Ontario) was used to monitor depth to water table. Water levels, including surface water stage on flooded sites, were recorded daily (or every two days) for all wells during inundation and at variable intervals before and after flooding.

*Biogeochemical measures*

*Surface and groundwater sampling* – Temperature and dissolved oxygen (DO) were measured in surface and groundwater using a DO probe (Model 55, YSI Inc, Yellow Springs,

1 Ohio). Water samples were collected in 120 ml acid-washed HDPE bottles. Surface and  
2 well samples (n = 3 to 16 per sampling date) were collected from the disconnected sites at  
3 roughly weekly intervals before, during, and after flooding. During flooding, replicate  
4 samples also were collected from the source canal and Rio Grande. Within the connected  
5 floodplain, monitoring of flood and control sites was initiated one day prior to the onset of  
6 river flooding. Water samples were placed on ice, returned to the laboratory, filtered using  
7 pre-combusted glass fiber filters (Whatman GF/F, pore size 0.7  $\mu\text{m}$ ), and analyzed for DOC,  
8 phosphate-P ( $\text{PO}_4\text{-P}$ ), nitrate-N ( $\text{NO}_3\text{-N}$ ), and ammonium-N ( $\text{NH}_4\text{-N}$ ).

9 *Nutrient and sediment retention* – During the experimental floods of 1994 and 1995,  
10 triplicate inlet and outlet samples were collected daily and used to generate material budgets.  
11 Samples collected in 1994 were analyzed for chemical constituents and 1995 samples  
12 analyzed for total suspended sediments (TSS). Daily input and output loads were calculated  
13 as the product of daily discharge and concentration. Retention was calculated as the  
14 difference between input and output loads. During experimental flooding, water discharge  
15 out of the plot was substantially lower than input discharge reflecting surface water loss.  
16 Assuming that all hydrologic loss resulted from groundwater recharge, we calculated a  
17 corrected output load as the product of outlet concentration and total water input in order to  
18 address how biological processes influenced material retention.

19 *Analytical Techniques.* – Nitrate- plus nitrite-nitrogen (herein  $\text{NO}_3\text{-N}$ ) was quantified by  
20 colorimetric analysis following Cd reduction (Wood et al. 1967) on a Technicon  
21 Autoanalyzer II. Soluble reactive phosphorus (Murphy and Riley 1962, used to represent  
22  $\text{PO}_4\text{-P}$ ) and  $\text{NH}_4\text{-N}$  (Solorzano 1969) were also analyzed on a Technicon Autoanalyzer II  
23 using the ascorbic acid and phenohypochlorite methods, respectively. Total inorganic

1 nitrogen (TIN) was determined as the sum of  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$ . Dissolved organic carbon  
2 (DOC) was measured by wet persulfate digestion (Menzel and Vaccaro 1964) on an  
3 Oceanographic International model 700 total carbon analyzer. Total suspended solids (TSS)  
4 were determined through gravimetric analysis of unfiltered samples following standard  
5 methods (Standard Methods, APHA 1998).

6

### 7 *Floodplain metabolism*

8 Chambers made of 30.5 cm diameter x 20 cm length PVC pipe were used to measure  
9 forest floor respiration. At each site, 5 chambers were inserted to ca. 10 cm depth while  
10 taking care to avoid severing large roots. Metabolism chambers therefore enclosed forest  
11 floor litter, shallow soils, and fine roots. Thus, respiration rates reported in this study include  
12 microbial and fine root responses and are referred to as forest floor metabolism to emphasize  
13 inclusion of all constituents. In flooded sites, chambers were fitted with connectors on  
14 opposite sides to allow sampling with a peristaltic pump. PVC caps fitted with a Teflon  
15 septum and a central manual stir bar were used to seal the tops of the chambers at the  
16 beginning of each incubation. Between sampling dates metabolism chambers were left in  
17 place with the caps removed.

18 Metabolism incubations occurred for 2-4 h concurrently at each study site during  
19 which  $\text{CO}_2$  concentrations inside the chamber were sampled every 30-45 minutes. In non-  
20 flooded sites, 25 ml of chamber headspace was removed using a 60 ml nylon syringe via the  
21 septum and placed in an evacuated 15 ml serum vial. The method of Kling et al. (1992) was  
22 used to extract dissolved  $\text{CO}_2$  from inundated chambers installed in flooded sites following 1

1 minute of circulation using a peristaltic pump (Geotech, Denver, Colorado). Head space  
2 gases were analyzed for CO<sub>2</sub> using a gas chromatograph (Buck Scientific, Pennsylvania,  
3 USA) equipped with a thermal conductivity detector. Respiration rate was calculated as the  
4 slope of CO<sub>2</sub> concentration vs. time as determined by linear regression. Units for respiration  
5 were converted to mg OM m<sup>-2</sup> d<sup>-1</sup> assuming that OM was 50% C.

6

7

### *Statistical analyses*

8 The influences of flooding on the connected and disconnected floodplain forests were  
9 generally assessed using a non-replicated design due to constraints related to site size and  
10 water delivery capacity. The vast majority of our results, therefore, are presented using  
11 descriptive statistics only (sensu Hurlbert 1984). While restricted in their application,  
12 inferential statistics were used to assess temporal changes in nutrient concentrations within or  
13 between sites. Pearson correlation coefficients were calculated to compare solute behavior  
14 between sites and between surface and groundwater environments. Within the disconnected  
15 flood site, we used t-tests to address differences in solute concentrations between input and  
16 output water. A paired t-test was used to compare solute concentrations in the main channel  
17 of the river with those measured in surface waters of the natural flood plot.

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## RESULTS

22

### *Hydrology*

23

Before flooding, depth to water in the disconnected floodplain was 250 cm in the control

1 site and 200 cm in the flood site (Figure 2, Digital Appendix 2). During flooding, floodplain  
2 sediments were fully saturated and water table elevation at the experimental flood site was  
3 above the forest floor within 1-2 weeks (Figure 2, Digital Appendix 2). Surface water depth  
4 varied from 1-2 m along the western border of the flood site and was 150 cm at a designated  
5 monitoring site (location C, Figure 2). As water was drained from the site, water table  
6 elevation dropped rapidly (Figure 2, Digital Appendix 2) and returned to pre-flood levels.

7 On the connected floodplain, initial depth to water in the natural flood site was nearly 1 m  
8 greater than in the inside-levee control site (Figure 2). Following 17 days of flooding, water  
9 table elevation in the natural flood site had increased 123 cm, but maximal elevation was still  
10 147 cm underground. Surface water was present for 69 days and depth averaged  $15.8 \pm 1$   
11 cm, with little spatial or temporal variation (Figure 2). After loss of surface water, water  
12 table elevation in the natural flood site was nearly equal to that observed before inundation.  
13 Throughout the monitoring period, water table elevation in the inside-levee control site  
14 remained relatively unchanged.

#### 15 *Temperature and Dissolved Oxygen*

16 Water temperatures in the disconnected floodplain averaged 17 – 21 °C (Digital Appendix  
17 3). In the absence of flooding, average groundwater temperatures in the outside-levee  
18 control and experimental flood sites were nearly identical (i.e., within 0.5 °C). During  
19 flooding, groundwater in the experimental flood site warmed by ca. 3-4 °C and approached  
20 surface water temperatures.

21 Temperatures during river flooding of the connected floodplain were comparable to those  
22 observed during experimental flooding of the disconnected forest site (Digital Appendix 4).

1 Within the connected floodplain, average groundwater temperatures of the inside-levee  
2 control and natural flood sites differed by only 0.3 °C and both warmed ca. 3 °C during  
3 flooding. Average groundwater temperatures of the natural flood and inside-levee control  
4 sites were significantly correlated over the course of flooding ( $r = 0.92$ ,  $P < 0.0001$ ,  $n = 17$ ).

5 Water used for experimental flooding on the disconnected floodplain was well oxygenated  
6 (ca. 7 mg/L, 87 % saturation, Digital Appendix 1), but once on the site, DO concentrations in  
7 surface water dropped rapidly (Figure 3A). In 1993, surface water initially contained less  
8 than 3 mg/L DO (ca. 40% saturation) after which concentrations dropped to ca. 0.5 mg/L.  
9 Flooding induced a slight increase in groundwater DO (Figure 3A), but average  
10 concentrations remained low ( $1.33 \pm 0.13$  mg/L, 14% saturation). At the same time, DO in  
11 groundwater of the control site averaged just  $0.88 \pm 0.03$  mg/L. Spatial and temporal  
12 variation in surface and groundwater DO during the 1994 and 1995 experimental floods (data  
13 not shown) were nearly identical to those described for the 1993 flood.

14 In 1994, deeper areas of the above-ground floodwaters were thermally stratified and  
15 characterized by a positive heterograde oxygen curve (Figure 3B). Water temperatures at the  
16 designated monitoring site (Figure 1) declined from 23.8 to 18.2 °C over 150 cm depth. At  
17 the same time, DO concentration at 10 cm depth was just 2.3 mg/L, but concentrations  
18 increased to 5.2 mg/L at 90 cm depth then decreased to less than 0.1 mg/L on the forest floor.  
19 Maximum DO corresponded to a water temperature of ca. 21 °C, a value similar to that of  
20 inlet water. Comparable temperature and DO patterns were recorded during the 1995 flood.

21 In the connected floodplain, surface water was well oxygenated and DO increased with  
22 time (Figure 3C). Across 69 days of flooding, DO averaged  $5.39 \pm 0.28$  mg/L (59%  
23 saturation) and there were no vertical gradients in DO or temperature. Flooding increased

1 groundwater DO concentrations from less than 1 to over 3 mg/L and DO remained elevated  
2 over pre-flood and control concentrations for approximately 3 weeks (Figure 3C).  
3 Groundwater DO in the connected control site averaged  $0.57 \pm 0.04$  mg/L (6% sat.)  
4 throughout the flood and was comparable to DO recorded in connected flood site  
5 groundwater prior to inundation (Figure 3C).

6

7

### *Biogeochemistry*

8 *Inorganic N and P* - Inlet water used to flood the disconnected forest contained  $143 \pm 12$   
9  $\mu\text{g/L}$   $\text{NO}_3\text{-N}$  (Digital Appendix 1). Mean  $\text{NO}_3\text{-N}$  in surface and groundwater ranged from 3  
10 to 28  $\mu\text{g/L}$  across space (i.e. outside-levee control and experimentally flooded sites) and  
11 across time (Digital Appendix 5). Average  $\text{NO}_3\text{-N}$  in surface water during flooding was  
12 consistently lower than in groundwater, but mean concentrations were all less than 10  $\mu\text{g/L}$ .  
13 Groundwater concentrations during flooding tended to be lower than pre- or post-flood  
14 periods (Digital Appendix 5).

15 Concentrations of  $\text{PO}_4\text{-P}$  in surface and groundwater during experimental flooding ranged  
16 from 29-82  $\mu\text{g/L}$  (Digital Appendix 5). During experimental floods,  $\text{PO}_4\text{-P}$  was highest in  
17 surface water (62 to 82  $\mu\text{g/L}$ ) while average groundwater concentration ranged from 27-51  
18  $\mu\text{g/L}$ . Concentrations varied little (i.e.,  $< 10 \mu\text{g/L}$ ) during flooding.

19 Temporal patterns in  $\text{NO}_3\text{-N}$  were more apparent during river inundation of the natural  
20 flood site (Digital Appendix 6). During the first 13 days of flooding, surface  $\text{NO}_3\text{-N}$   
21 concentrations increased rapidly from  $30 \pm 9 \mu\text{g/L}$  to  $177 \pm 33 \mu\text{g/L}$ . Over the next 7 days,  
22  $\text{NO}_3\text{-N}$  in surface water declined sharply to concentrations lower than those observed at the



1 onset of flooding. Concentrations then increased steadily over the next 40 days, reaching  
2 levels comparable to those observed during the initial stages of flooding (Digital Appendix  
3 6). Groundwater  $\text{NO}_3\text{-N}$  in both natural flood and inside-levee control sites remained low  
4 during the period of flooding ( $4 \pm 1 \mu\text{g/L}$  and  $6 \pm 2 \mu\text{g/L}$ , respectively).

5 Inundation of the connected floodplain also resulted in dramatic increases in  $\text{PO}_4\text{-P}$   
6 concentrations during the initial stages of flooding (Digital Appendix 6). On the first day of  
7 natural flooding, average surface water  $\text{PO}_4\text{-P}$  was  $105 \pm 25 \mu\text{g/L}$  and concentrations doubled  
8 by day 3 exceeding  $200 \mu\text{g/L}$ . Afterward,  $\text{PO}_4\text{-P}$  levels dropped sharply and averaged  
9 between  $50$  and  $70 \mu\text{g/L}$  over the remainder of the flood. Over 16 sample dates, groundwater  
10  $\text{PO}_4\text{-P}$  in flood and control sites were similar and correlated ( $r = 0.86$ ,  $P < 0.001$ ) with  
11 initially high (i.e.,  $100 \mu\text{g/L}$ ) then steadily declining concentrations.

12 Floodwaters of the disconnected site were enriched in  $\text{NH}_4\text{-N}$  (Figure 4). While inlet  
13 water contained only  $35 \mu\text{g/L}$   $\text{NH}_4\text{-N}$  (Digital Appendix 1), surface waters averaged  $110\text{-}$   
14  $130 \mu\text{g/L}$  across the three floods (Figure 4A). Groundwater  $\text{NH}_4\text{-N}$  in the control site of the  
15 disconnected floodplain averaged  $137\text{-}190 \mu\text{g/L}$  across the three floods and there were no  
16 distinct temporal trends over the course of any single flood (data not shown).

17 In contrast, groundwater  $\text{NH}_4\text{-N}$  of the experimental flood site showed strong responses to  
18 inundation (Figure 4B). During each flood, groundwater  $\text{NH}_4\text{-N}$  concentrations declined  
19 sharply from much higher pre-flood concentrations (Figure 4B). Following the loss of  
20 surface water,  $\text{NH}_4\text{-N}$  concentrations rebounded to levels greater than those observed for pre-  
21 flood means (Figure 4B). Over the course of 3 years of experimental flooding, pre-flood  
22 concentrations averaged  $142 \pm 47$ ,  $330 \pm 58$ , and  $506 \pm 49 \mu\text{g/L}$ . Thus, pre-flood  $\text{NH}_4\text{-N}$

1 concentrations increased 150 and 300  $\mu\text{g/L}$  following the 1993 and 1994 floods (Figure 4B).

2 River flooding of the connected floodplain generated a transient pulse of  $\text{NH}_4\text{-N}$  in surface  
3 water of the natural flood site that raised concentrations to  $489 \pm 124 \mu\text{g/L}$  after which they  
4 dropped to  $25 \pm 12 \mu\text{g/l}$  within the first 11 days of flooding (Digital Appendix 7).

5 Concentrations then remained very low (i.e.  $< 5 \mu\text{g/L}$ ) until the final day of flooding when  
6  $\text{NH}_4\text{-N}$  averaged  $23 \mu\text{g/L}$ .

7 In the connected floodplain, groundwater  $\text{NH}_4\text{-N}$  concentrations were notably higher than  
8 those recorded in surface water. Moreover, concentrations in the inside-levee control plot  
9 ( $200\text{-}600 \mu\text{g/L}$ , Digital Appendix 7) were often an order of magnitude higher than in the  
10 natural flood plot. Groundwater means in control and flood plots were significantly  
11 correlated ( $r = 0.74$ ,  $n = 16$ ,  $P < 0.001$ ) and generally lower during the flooding period  
12 (Digital Appendix 7).

13 *Dissolved Organic Carbon* - Surface flood water in the experimental flood site was  
14 enriched in DOC compared to inlet water (Figure 5A, Digital Appendix 1). Surface DOC  
15 averaged  $4.8 \pm 0.7$ ,  $15.1 \pm 1.2$ , and  $16.3 \pm 1.5 \text{ mg/L}$  in 1993, 1994, and 1995, respectively,  
16 while maximum average concentrations were 12, 18, and 22  $\text{mg/L}$  during the same years.  
17 Experimental floods resulted in dramatic increases in groundwater DOC. During the first  
18 flood, DOC increased from pre-flood values of  $4 \text{ mg/L}$  to more than  $30 \text{ mg/L}$  with maximal  
19 values greater than  $70 \text{ mg/L}$ . Concomitant with decreasing water levels (Digital Appendix 2),  
20 groundwater DOC then declined sharply to concentrations only slightly greater than those  
21 observed at the onset of flooding (Figure 5B). DOC averaged  $17.5 \pm 2.3 \text{ mg/L}$  during the  
22 flood. In the second experimental flood, groundwater DOC increased to over  $20 \text{ mg/L}$  the

1 first week and averaged  $17.8 \pm 0.8$  mg/L throughout the monitoring period. Average  
2 concentration during the third flood was  $15.0 \pm 0.8$  mg/L, more than 5 mg/L greater than the  
3 mean pre-flood concentration (Figure 5B).

4 River flooding of the connected floodplain generated a brief spike in surface water  
5 DOC after which concentrations declined rapidly and remained low (Figure 5C). Surface  
6 water DOC averaged  $15.3 \pm 1.3$  mg/L on the first day of the flood, but was half that value  
7 ( $7.1 \pm 0.6$  mg/L ) by the third day. Groundwater DOC in the flooded site was closely  
8 correlated ( $r = 0.95$ ,  $n = 15$ ,  $P < 0.0001$ ) to surface water DOC and both decreased steadily  
9 during the first two weeks of flooding. After two weeks, concentrations remained low (i.e., <  
10 5 mg/L) and stable for the remainder of the flood (Figure 5C). During most of the flood,  
11 average values for surface water were less than those in flooded groundwater and both were  
12 3-5 mg/L lower than groundwater of the inside-levee control site where concentrations were  
13 relatively stable through time.

#### 14 *Floodplain Material Retention*

15 Input-output budgets for the second and third experimental floods illustrated that the  
16 disconnected floodplain consumed water and acted as a sink for  $\text{NO}_3\text{-N}$ , but also perhaps as a  
17 DOC source (Table 1). Approximately  $363,000 \text{ m}^3$  of water was added to the flood site in  
18 1994 while only 58% ( $209,000 \text{ m}^3$ ) as much water was used for flooding in 1995 (Table 1).  
19 Nevertheless, the flood site retained similar amounts of water each year ( $127,000$  and  
20  $143,000 \text{ m}^3$ ) representing 39% and 61% of hydrologic inputs (Table 1).

21 Mean TSS over 30 days of hydrologic input was  $111.8 \pm 9.0$  mg/L, while average output  
22 concentration ( $16.0 \pm 2.5$  mg/L) was significantly lower ( $P < 0.0001$ , t-test of inlet and outlet  
23 concentrations). Of the TSS load introduced in 1995, 93% was retained within the flood site

1 (Table 1). Input and output concentrations were statistically similar for  $\text{NH}_4\text{-N}$  ( $P = 0.6$ ) and  
2  $\text{PO}_4\text{-P}$  ( $P = 0.2$ ), with mean concentrations differing by only 5 and 18  $\mu\text{g/L}$ , respectively  
3 (Figure 6). Mean  $\text{NO}_3\text{-N}$  output concentration (18  $\mu\text{g/L}$ ) was four-fold lower than input  
4 concentration (71  $\mu\text{g/L}$ ,  $P < 0.0001$ , Figure 6). Mean output DOC was 0.5  $\text{mg/L}$  higher than  
5 input concentration ( $P < 0.02$ ).

6 Without correcting for hydrologic loss, the experimental flood site acted as a sink for all  
7 monitored solutes with retention representing between 30 and 87 % of input loads (Table 1).  
8 Once corrected for hydrologic loss, however, the extent of retention differed for specific  
9 solutes. Corrected inputs and outputs for  $\text{NH}_4\text{-N}$  were evenly balanced and retention was  
10 only 2% of total input. Hydrologic corrections for  $\text{NO}_3\text{-N}$  loads only slightly reduced (87vs.  
11 79%, Table 1) retention, suggesting strong biological and chemical control. Overall, the  
12 experimentally flooded site retained over 50% of all TIN introduced during flooding. For  
13  $\text{PO}_4\text{-P}$ , corrected retention was 17% of the total input load. Correcting for hydrologic loss  
14 showed the floodplain to be a net source of DOC with output representing 114% of input  
15 (Table 1).

16 Comparison of main stem and natural flood site surface waters indicated that the  
17 connected floodplain retained solutes in a manner generally similar to the disconnected  
18 floodplain (Table 2). Average concentration for  $\text{NH}_4\text{-N}$  and  $\text{PO}_4\text{-P}$  in the floodplain and  
19 main stem of the Rio Grande were similar to concentrations observed in the surface water of  
20 the experimental flood and did not differ significantly ( $P > 0.05$ ) from one another (Table 2).  
21 Although DOC concentrations were nearly 1  $\text{mg/L}$  higher in the natural flood site compared  
22 to the river's main stem, mean concentrations were not significantly different ( $P = 0.09$ ). In

1 contrast, NO<sub>3</sub>-N in the main stem of the Rio Grande (ca. 300 µg/L) was three times higher (P  
2 = 0.008) than in the natural flood surface water.

3

4

#### *Forest Floor Respiration*

5 Experimental flooding of the disconnected floodplain stimulated forest floor respiration  
6 (Figure 7). Prior to flooding, respiration rates in the outside-levee control and experimental  
7 flood sites were similar and these rates were comparable to those recorded on the outside-  
8 levee control site later during the flooding period (Table 3). Inundation resulted in  
9 immediate respiratory responses that lasted throughout and following the flood. Initial DO  
10 concentrations in the metabolic chambers were less than 1 mg/L and no DO was detected in  
11 subsequent samples during respiration assays in 1994 or 1995. Following five days of  
12 inundation, respiration rates were 100 times greater than pre-flood rates or concomitant  
13 control rates (Figure 7). Respiration in the experimental flood site continued to climb for two  
14 weeks, reaching a plateau value of nearly 2000 mg OM m<sup>-2</sup> d<sup>-1</sup> (Figure 7). At the same time,  
15 respiration in the outside-levee control site remained low and varied only 2-fold (Figure 7,  
16 Table 3). After flooding, respiration on the experimental flood site dropped sharply but rates  
17 for saturated sediments assayed one day after the loss of surface water were 10 times the  
18 respiration rate measured at the outside-levee control site on the same day (Figure 7). The  
19 flood-induced increase in forest floor respiration was consistent across the 1994 and 1995  
20 floods with average 1995 respiration rates approximately double those recorded in 1994  
21 (Table 3).

22 Respiratory responses to river flooding of the natural flood site were similar in kind, but  
23 lower in magnitude (Table 3) than those observed in the experimental flood site. Respiration

1 at the inside-levee control site was 50-95% of the rates recorded for outside-levee control  
2 (Table 3). During flooding, forest floor respiration in the natural flood site was 65 times  
3 greater than measured for the outside-levee control (Table 3). After 56 days of flooding,  
4 respiration rates were nearly 500 mg OM m<sup>-2</sup> d<sup>-1</sup> or one quarter to one half of rates observed  
5 during month-long flooding of the experimental flood site (Table 3). Unlike conditions  
6 during experimental flooding, metabolism chambers inundated by river water remained well  
7 oxygenated during respiration assays with minimum DO values never less than 4 mg/L.

## 9 DISCUSSION

### 11 *Hydrology and the flood pulse*

12 The IFI is proposed as a conceptual descriptor of a site's flooding history and used to  
13 summarize aspects of the flood pulse including time since last flood and average time  
14 between floods (Molles et al. 1998). While their IFIs were not specifically quantified, the  
15 disconnected and connected floodplains investigated in this study are examples of long and  
16 short IFI forests. Levee construction and floodplain fragmentation have dictated the IFI for  
17 the disconnected floodplain. Flow regulation has clearly altered the extent and timing of Rio  
18 Grande discharge (Slack et al. 1993), but river inundation of the connected floodplain  
19 represents a more 'natural' version of the seasonal flood pulse compared to experimental  
20 flooding of the disconnected floodplain. The experimental flood pulses applied to the  
21 disconnected forest lasted approximately 30 days while the natural flood inside of the levees  
22 inundated the forest for more than 70 days. Both the natural and experimental floods fell

1 within the historical range of values for duration and seasonal timing (Slack et al. 1993).

2 Hydrometric data showed that the flood pulse influenced both surface and subsurface  
3 conditions. During inundation of the experimental flood site, flooding saturated nearly 2 m  
4 of unsaturated zone during each of the three experimental floods. Mixing of surface and  
5 groundwater was illustrated by changing water table depth and temperature profiles.

6 In contrast, two free water surfaces were maintained throughout the flood pulse at the  
7 natural flood site. A deep unsaturated zone ( $> 150$  cm) separated surface water from  
8 groundwater. However, depth to groundwater decreased rapidly during the first two weeks  
9 of flooding while water table depth in the control site remained relatively constant. Similar  
10 groundwater temperatures at the inside-levee control and natural flood sites were consistently  
11 lower than surface water temperatures, suggesting relatively little mixing between surface  
12 and groundwater. On the other hand, groundwater DO in the flood site was immediately  
13 elevated by onset of flooding, and groundwater DOC concentrations closely tracked those in  
14 surface water.

15 These data suggest that flood pulse inundation has strong influence on floodplain  
16 groundwater environments. During flooding, groundwater and surface water interaction  
17 differed greatly between sites on the connected and disconnected floodplain. Previous work  
18 on linkage between streams and alluvial aquifers in semi-arid regions suggests that flooding  
19 enhances groundwater flow away from the channel toward floodplain and riparian areas  
20 (Marti et al. 2000). Surface and groundwater of the natural flood site probably remained  
21 distinct due to clay-rich horizons and extensive silt deposits characteristic of shallow soils of  
22 the connected floodplain (L. McFadden, University of New Mexico, unpublished data).  
23 These fine-grained materials overlie coarser sediments suggesting that flow regulation may

1 be structuring floodplain soils in a manner that retards hydrologic exchange. Whether  
2 increased water table elevations in the connected floodplain reflected 1) localized infiltration  
3 and recharge not represented by monitoring wells, 2) the influence of enhanced horizontal  
4 groundwater flow, or 3) pressure changes associated with flooding in the main channel  
5 remains unknown.

6

7 *Forest floor detritus, respiration, and anoxia during the flood pulse*

8 Inundation of the forest floor and aquifer sediments of the long IFI forest quickly rendered  
9 water anoxic during each of the annual floods. Once the site was flooded, DO imported in  
10 flood water entered the system at a depth dictated by water temperature as was reflected in  
11 the positive heterograde DO curves. At the same time, water in close proximity to the forest  
12 floor was anoxic and groundwater DO remained very low (near detection limit) throughout  
13 the disconnected forest.

14 Depending on how the annual cycle of the flood pulse influences primary productivity,  
15 root respiration, decomposition of woody and non-woody vegetation, and water residence  
16 time (Junk et al. 1989, Megonigal et al. 1997, Robertson et al. 2001), floodplains may  
17 produce and retain enough OM to render floodwaters anoxic on an annual basis (c.f.  
18 O'Connell et al. 2000). Hamilton et al. (1997) described a six-week anoxic event in the  
19 Pantanal wetland of the Paraguay River, Brazil where inundation of stored senescent  
20 vegetation, leaching of soils, and processing of detritus and liberated DOC removed all  
21 oxygen.

22 Similar reasoning explains anoxia during flooding of the experimental flood site.



1 Isolation from the flood pulse has resulted in the accumulation of large standing stocks of  
2 woody biomass (33-38 Mg/ha) and leaf litter (1.1 - 2.1 kg OM m<sup>-2</sup>) on the disconnected  
3 floodplain (Ellis et al. 1999, 2002). These values are comparable to those measured at the  
4 inside-levee control site, a site also isolated from the flood pulse. In contrast, standing stocks  
5 of wood in the natural flood site were approximately three times lower and leaf litter OM was  
6 an order of magnitude less than at all other sites (Ellis et al. 1999). In this manner, OM  
7 standing stock reflects the IFI characteristic of each riparian setting with larger stocks in  
8 areas less frequently influenced by the flood pulse. In the long IFI floodplain, the flood pulse  
9 liberated DOC at concentrations greater than those observed by Hamilton et al. (1997) in the  
10 Pantanal.

11 On the natural flood site, OM stocks were lower and DOC concentrations were elevated  
12 only during the first day of flooding after which concentrations remained low for more than  
13 two months. Thus, patterns of DOC concentration appear linked to the distribution of OM on  
14 the forest floor. Ultimately, the amount and forms of C available for processing during  
15 flooding differed substantially among the study sites. These differences probably reflect how  
16 forest IFI alters the flood pulse influence on metabolic activity.

17 On the experimental flood site, flooding increased respiration by two orders of magnitude  
18 despite anoxic conditions. Our estimates of system respiration were limited to forest floor  
19 (i.e. benthic) environments and did not include water column processes that would have  
20 contributed to whole-system respiration. High DOC availability in surface water, low water  
21 column clarity, and greatly reduced DO at shallow depths suggest substantial water column  
22 respiration.

23 On the natural flood site, the flood pulse caused more than a 50-fold increase in respiration,

1 but maximum rates were only one half to one quarter of rates recorded during flooding of the  
2 experimental flood site. The lower respiration rates and well oxygenated waters of the  
3 connected floodplain may be attributed to lower OM standing stocks (Ellis et al. 2002) and  
4 hydrologic exchange between the main stem and short IFI floodplains that may lower water  
5 residence times.

6

7 *Nutrient dynamics and material retention*

8 *Hydrologic mass balance* – During each of the floods applied to the disconnected  
9 forest, hydrologic flux through the output weir was 40-60% of the water added during  
10 flooding. Water loss from the flooded forests no doubt resulted from both evapotranspiration  
11 (ET) and groundwater recharge. Natural flooding of the cottonwood forests appears to  
12 reduce ET compared to unflooded sites (CN Dahm, unpublished data) and the influence of  
13 flooding on ET may have differed substantially between floodplain types given the fully  
14 saturated rooting zone of the experimental flood site and unsaturated soils characteristic of  
15 natural flooding. Nevertheless, application of an ET estimate derived from natural flood sites  
16 along the Rio Grande (6 mm/d, J. Cleverly, University of New Mexico, unpublished data)  
17 suggest that ET accounted for approximately 15% of water loss from the experimental flood  
18 site during 1994 and 1995. Thus, ca. 85% of the water leaving the flooded plot contributed  
19 to groundwater discharge, resulting in extensive fluxes through the forest floor and saturation  
20 of over 2 m of soils and sediments.

21 *Total suspended sediments* - Both short and long IFI portions of the Rio Grande floodplain  
22 acted as sinks for suspended sediments. Over 90% of the sediment entering the experimental

1 flood site was deposited on the forest floor. Areal rates determined from retention  
2 calculations (Table 1) showed that experimental flooding deposited 6.7 g dry mass sediment  
3  $\text{m}^{-2} \text{d}^{-1}$ , a rate similar to the 8.0 g dry mass  $\text{m}^{-2} \text{d}^{-1}$  reported by Ellis et al. (1998) using  
4 ceramic tiles to quantify net deposition rates during the 1995 experimental flood. A great  
5 deal of nutrient load in rivers and streams is associated with particulate transport (Meybeck  
6 1982). Applying preliminary atomic ratios for forest floor sediments (CN Dahm,  
7 unpublished data) to net deposition rates illustrates the importance of particulate retention.  
8 Rates of N and P retention via sediment deposition are very similar to those recorded for  
9 dissolved constituents, suggesting that total nutrient retention may be double that reported  
10 here. In the case of C, however, daily rates of particulate deposition are  $135 \text{ mg m}^{-2} \text{d}^{-1}$  while  
11 dissolved materials appear to have been released at a rate of  $75 \text{ mg m}^{-2} \text{d}^{-1}$ . These fluxes  
12 suggest that the experimental flood site may have been a sink for particulate C, but a source  
13 of DOC. While no material budgets were generated for the natural flood site, Ellis et al.  
14 (1996) measured net silt deposition rates of  $155 \text{ g dry mass m}^{-2} \text{d}^{-1}$  during the 1995 flood,  
15 suggesting considerable particulate retention of N, P, and C in the connected floodplain. A  
16 more complete understanding of nutrient and C retention and processing in these floodplain  
17 forests should assess the role of particulate transport and deposition.

18 *Dissolved organic carbon* – The extent to which floodplains act as sources of OM that  
19 fuel lotic metabolism is closely related to the balance of OM production and decomposition  
20 on the floodplain, and the timing and duration of the flood pulse (Meyer and Edwards 1990,  
21 Hamilton et al. 1997). We argue that this balance is in turn related to the IFI.

22 Material budgets for the experimental flood of 1994 suggested that the inundated forest of  
23 the disconnected floodplain acted as a source of DOC. Calculated output load, however, was

1 based on concentrations measured only in surface water. Far more C was exported from the  
2 site if groundwater concentrations are considered. The vast majority of water added to the  
3 site contributed to groundwater recharge and, therefore, left the site with material loads  
4 dictated by interaction with the forest floor and shallow sediments. Groundwater DOC  
5 during flooding averaged 10-20 mg/L (2-4 times the concentration in output water), but  
6 maximum values were greater than 80 mg/L even after recharge caused mixing with ambient  
7 groundwater of lower DOC content. Adding these values to the C budget would increase  
8 output loads nearly four-fold. Thus, infrequent flood pulse inundation of long IFI forests  
9 may export substantial amounts of DOC to both the river and groundwater ecosystems.

10 Inundation of the natural flood site resulted in only a moderate and transient increase in  
11 DOC. When compared over the course of flooding, DOC concentrations in the connected  
12 floodplain were not significantly different from those in the river (Table 2). Wainright et al.  
13 (1992) documented that floodplain soils of the Ogeechee River were a source of DOC despite  
14 regular inundation. At the same time, flooding decreased soil respiration (Cuffney 1988), a  
15 response very different from that observed for floodplains along the Middle Rio Grande.  
16 Similar to the experimental flood site, leaching of C from forest floor detritus and soils may  
17 fuel high rates of respiration observed during flooding. However, DOC supplied from soils  
18 and detritus may be consumed by forest floor respiration resulting in a balance between C  
19 liberation and consumption (i.e., steady-state, Molles et al. 1998).

20 *Phosphate-phosphorus* - In general,  $\text{PO}_4\text{-P}$  behaved conservatively in both connected and  
21 disconnected floodplains. In floodwater sources, the relative supply of  $\text{PO}_4\text{-P}$  compared to  
22 inorganic N was high (atomic N:P ~ 5 - 14) for both the main river and conveyance canals

1 (Digital Appendix 1). Atomic ratios for floodplain soils (C:P = 86, N:P = 3.4, C:N. Dahm,  
2 unpublished data) suggest that low forest floor demand for P and high P availability resulted  
3 in little biological influence on net P retention in both experimental and natural flood sites.

4 Others have observed that floodplains may act as P sources. In some cases, anoxia in  
5 floodplains may lead to P release and increases in PO<sub>4</sub>-P (e.g. Van den Brink et al. 1993). In  
6 this manner, anoxia during experimental flooding of disconnected forest may have resulted in  
7 the release of sorbed P. At the same time, elevated respiration rates may be tied to enhanced  
8 P mineralization such that both physical and biological processes may have increased output  
9 loads and decreased net retention.

10 *Inorganic nitrogen* – In contrast to P dynamics, net retention of dissolved inorganic N was  
11 observed during flooding of both experimental and natural flood sites. This was most  
12 notable for NO<sub>3</sub>-N. Despite input concentrations in excess of 100 µg/L, NO<sub>3</sub>-N  
13 concentrations in the experimental flood site were low throughout the forest during the  
14 course of each flood. Given the extensive anoxia and enhanced DOC availability observed in  
15 surface and groundwater of the experimental flood site, low concentrations may in part  
16 reflect loss of NO<sub>3</sub>-N via denitrification, a process commonly associated with anoxia in  
17 riparian zones. At the same time, low DO availability would suppress rates of nitrification.

18 Despite the similarity in water chemistry of flood source waters (i.e., canal and Rio  
19 Grande, Digital Appendix 1), N concentrations in surface water of the short IFI floodplain  
20 differed greatly from those in the long IFI forest. While NH<sub>4</sub>-N dominated TIN in the  
21 surface water of the experimental flood, NO<sub>3</sub>-N was the dominant form in surface water of  
22 the natural flood site. Despite concentrations that ranged widely and included maximum  
23 values in excess of 500 µg/L, flood water on the connected floodplain always contained less

1 NO<sub>3</sub>-N than was observed in the main stem of the Rio Grande. Over more than two months  
2 of flooding, differences in concentration suggested that processes in the connected floodplain  
3 removed more than 2/3 of the NO<sub>3</sub>-N load.

4 At the same time, floodplain processes appeared to have little net effect on NH<sub>4</sub>-N  
5 concentration. Net retention in the experimentally flooded forest was nearly zero based on  
6 material mass balance (Table 1). At the same time, concentrations did not differ significantly  
7 between the Rio Grande and floodwaters of the natural flood site (Table 2). We suggest,  
8 however, that these results belie the dynamic nature of this solute and the extensive  
9 processing of NH<sub>4</sub>-N that appears to occur in both long and short IFI forests during the flood  
10 pulse.

11 An immediate and abrupt increase in NH<sub>4</sub>-N characterized the initial stages of the flood  
12 pulse in the natural flood site after which concentrations dropped to very low levels for the  
13 remainder of the flood. The spike in NH<sub>4</sub>-N may have been associated with desorption from  
14 sediments or inclusion of very fine (i.e. clay) particles mobilized from the forest floor during  
15 the early stages of flooding. It is also possible that mineralization of organic N associated  
16 with forest floor detritus (as particulate C or liberated DOC) may have introduced substantial  
17 amounts of NH<sub>4</sub>-N to the well-oxygenated floodwaters. Ammonium liberated in this manner  
18 may have then been nitrified to produce the observed increase in NO<sub>3</sub>-N (Sanchez-Perez and  
19 Tremolieres 1997).

20 Inundation of the experimental flood site liberated NH<sub>4</sub>-N in groundwater and surface  
21 water and increased concentrations by as much as an order of magnitude compared to inlet  
22 water. Mid-flood declines in groundwater NH<sub>4</sub>-N probably resulted from a combination of

1 dilution, sorption, and uptake. At the same time, outlet  $\text{NH}_4\text{-N}$  concentrations did not differ  
2 significantly from inlet concentrations. Thus, flooding may both liberate  $\text{NH}_4\text{-N}$  from forest  
3 soils and sediments during the rising limb of the flood pulse and promote its potential  
4 sequestration by microbes associated with detrital stores and soils of high C:N content (Ellis  
5 et al. 2002) or by plant uptake.

6 Comparable N processing has been described for other floodplain systems. Through a  
7 mass balance approach, Lewis and Saunders (1989) determined that the floodplain of the  
8 Orinoco River acts as both a N sink and source. They evoked a terrestrial (i.e. floodplain)  
9 source for  $\text{NH}_4\text{-N}$  and sink for  $\text{NO}_3\text{-N}$  to balance material loads between upstream and  
10 downstream locations. They emphasized that an exceptional biological demand for  $\text{NO}_3\text{-N}$   
11 must be associated with the floodplain because of the observed changes in load and the  
12 apparent lack of demand by the river itself. The extent to which the floodplain acts as a  
13 source or sink of materials, both in tropical and semi-arid systems, depends on spatial  
14 distribution of the flood pulse, its duration, and the IFI characteristic of the inundated  
15 floodplain.

16

### 17 *IFI, reorganization, and floodplain management*

18 We propose that the IFI influences the structure and function of floodplain environments  
19 through connectivity with other landscape elements (i.e. main channel and floodplain  
20 aquifers). Lorenz et al. (1997) defined an ‘ecosystem indicator’ as a ‘measurable quantity  
21 having significance beyond what is actually measured because it provides information on  
22 ecosystem condition’. Others have identified soil respiration and material retention as useful  
23 ecosystem indicators (Lorenz et al. 1997, Tockner et al. 2000). Results from our study have

1 shown that in floodplain ecosystems these variables are closely linked to the IFI  
2 characteristic of a patch of riparian forest.

3 In this study, we used riparian forest sites that represent extreme values for the IFI (i.e. ca.  
4 annual vs. 50 year intervals) to see how very different hydrologic histories organize response  
5 to the flood pulse. For any river system, variable duration and intensity of river discharge,  
6 differences in floodplain manipulation, and geomorphic complexity of the fluvial landscape  
7 will interact to dictate the IFI distribution among patches of riparian forests. The  
8 manipulated flooding used in this study may be employed in the process of riparian  
9 restoration (Molles et al. 1998). Knowledge of the IFI distribution may provide critical  
10 guidance for floodplain restoration (Buijse et al. 2002). At the same time, it provides a  
11 conceptual basis for understanding floodplain responses to aquatic-terrestrial interaction.

12

13

14

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22

23



LITERATURE CITED

- 1  
2  
3 American Public Health Association, American Water Works Association, Water  
4 Environment Federation. 1998. Standard Methods for Examination of Water and  
5 Wastewater, 20<sup>th</sup>ed., American Public Health Association, Washington, D.C.  
6  
7 Bayley, P. B. 1995. Understanding large river-floodplain ecosystems. *Bioscience* **45**: 153-  
8 158.  
9  
10 Bormann, F. H., and G. E. Likens. 1979. Catastrophic disturbance and the steady state in  
11 northern hardwood forests. *American Scientist* **67**: 660-669.  
12  
13 Buijse, A. D., H. Coops, M. Staras, L. H. Jans, G. J. Van Geest, R. E. Grifts, B. W. Ibelings,  
14 W. Oosterber, and F. C. J. M. Roozen. 2002. Restoration strategies for river floodplains  
15 along large lowland rivers in Europe. *Freshwater Biology* **47**: 889-907.  
16  
17 Bullard, T. F., and S. G. Wells. 1992. Hydrology of the Middle Rio Grande from Velarde to  
18 Elephant Butte Reservoir, New Mexico. United States Department of Interior, Fish and  
19 Wildlife Service Resource Publication **179**: 1-51.  
20  
21 Cuffney, T. F. 1988. Input, movement and exchange of organic matter within a coastal  
22 blackwater river-floodplain system. *Freshwater Biology* **19**: 305-320.  
23

1 Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in  
2 the northern third of the world. *Science* **266**: 753-762.

3

4 Ellis, L. M., M. C. Molles, Jr., and C. S. Crawford. 1996. Seasonal flooding and riparian  
5 forest restoration in the Middle Rio Grande Valley. Final Report, Cooperative Agreement 14-  
6 16-0002-91-228. U.S. Fish and Wildlife Service, New Mexico Ecological Field Office,  
7 Albuquerque, NM.

8

9 Ellis, L. M., M. C. Molles, Jr., and C. S. Crawford. 1999. Influence of experimental  
10 flooding on litter dynamics in a Rio Grande riparian forest, New Mexico. *Restoration*  
11 *Ecology* **7**: 193-204.

12

13 Ellis, L. M., C. S. Crawford, and M. C. Molles, Jr. 2002. The role of the flood pulse in  
14 ecosystem-level processes in southwestern riparian forests: a case study from the Middle Rio  
15 Grande. Pages 51-107 in B. A. Middleton, editor. *Flood Pulsing in Wetlands: Restoring the*  
16 *Natural Hydrologic Balance*. John Wiley and Sons, Inc., Hoboken, NJ.

17

18 Findlay, S. 1995. Importance of surface-subsurface exchange in stream ecosystems: the  
19 hyporheic zone. *Limnology and Oceanography* **40**: 159-164.

20

21 Fisher, S. G., L. G. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in a  
22 desert stream ecosystem following flash flooding. *Ecological Monographs* **43**: 421-439.

1 Forsberg, B. R., A. H. Devol, J. E. Richey, L. A. Martinelli, and H. D. Santos. 1988. Factors  
2 controlling nutrient concentrations in Amazon floodplain lakes. *Limnology and*  
3 *Oceanography* **33**: 41-56.  
4

5 Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem  
6 perspective of riparian zones. *Bioscience* **41**: 540-551.  
7

8 Hamilton, S. K., S. J. Sippel, D. F. Calheiros, and J. M. Melack. 1997. An anoxic event and  
9 other biogeochemical effects of the Pantanal wetland on the Paraguay River. *Limnology and*  
10 *Oceanography* **42**: 257-272.  
11

12 Howe, W. H., and F. L. Knopf. 1991. On the imminent decline of Rio Grande Cottonwoods  
13 in central New Mexico. *The Southwestern Naturalist* **36**: 218-224.  
14

15 Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments.  
16 *Ecological Monographs* **54**:187-211.  
17

18 Jacobson, P. J., K. M. Jacobson, and M. K. Seely. 1995. Ephemeral Rivers and Their  
19 Catchments: Sustaining People and Development in Western Namibia. Windhoek, Desert  
20 Research Foundation of Namibia.  
21  
22  
23

1 Johnson, W. R. 1988. Soil survey of Socorro County area, New Mexico. USDA, Soil  
2 Conservation Service in cooperation with the US Department of the Interior, Bureau of Land  
3 Management, Bureau of Indian Affairs, and New Mexico Agricultural Experiment Station.  
4 Soil Conservation Service, Washington.  
5  
6 Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain  
7 systems. Canadian Special Publication in Fisheries and Aquatic Sciences **106**: 110-127.  
8  
9 Kling, G. W., G. W. Kipphut, and M. C. Miller. 1992. The flux of CO<sub>2</sub> and CH<sub>4</sub> from lakes  
10 and rivers in arctic Alaska. *Hydrobiologia* **240**: 23-36.  
11  
12 Lewis, W. M., Jr., and J. F. Saunders, III. 1989. Concentration and transport of dissolved  
13 and suspended substances in the Orinoco River. *Biogeochemistry* **7**: 203-240.  
14  
15 Lorenz, C.M., G. M. Van Dink, G. M. Van Hattum, and W. P. Cofino. 1997. Concepts in  
16 river ecology: implications for indicator development. *Regulated Rivers: Research and*  
17 *Management* **13**: 501-516.  
18  
19 Marti, E., S. G. Fisher, J. D. Schade, and N. B. Grimm. 2000. Flood Frequency and stream -  
20 riparian linkage in arid lands. Pages 111-136 in J. B. Jones and P. J. Mulholland, editors.  
21 *Streams and Groundwaters*. Academic Press, New York.

22

1  
2 Mayack, D. T., J. H. Thorp, and M. Cothran. 1989. Effects of burial and floodplain  
3 retention on stream processing of allochthonous litter. *Oikos* **54**: 378-388.  
4  
5 Megonigal, J. P., W. H. Conner, S. Kroeger, and R. R. Sharitz. 1997. Aboveground  
6 production in southeastern floodplain forests: a test of the subsidy-stress hypothesis.  
7 *Ecology* **78**: 370-384.  
8  
9 Menzel, D. W., and R. F. Vaccaro. 1964. The measurement of dissolved organic and  
10 particulate carbon in seawater. *Limnology and Oceanography* **9**: 138-142.  
11  
12 Meybeck, M. 1982. Carbon, nitrogen, and phosphorus transport by world rivers. *American*  
13 *Journal of Science* **282**: 401-450.  
14  
15 Meyer, J. L., and R. T. Edwards. 1990. Ecosystem metabolism and turnover of organic  
16 carbon along a blackwater river continuum. *Ecology* **71**: 668-677.  
17  
18 Molles, M. C., Jr., C. S. Crawford, and L. M. Ellis. 1995. Effects of an experimental flood  
19 on litter dynamics in the middle Rio Grande riparian ecosystem. *Regulated Rivers* **11**: 275-  
20 281.  
21  
22 Molles, M. C., C. S. Crawford, L. M. Ellis, H. M. Valett, and C. N. Dahm. 1998. Managed  
23 flooding for riparian ecosystem restoration. *Bioscience* **48**: 749-756.

1  
2 Molles, M. C., Jr., and C. N. Dahm. 1990. A perspective on El Niño and La Niña: global  
3 implications for stream ecology. *Journal of the North American Benthological Society* **9**: 68-  
4 76.

5  
6 Murphy, J., and J. P. Riley. 1962. Determination of phosphate in natural waters. *Analytica*  
7 *Chimica Acta* **27**: 31-36.

8  
9 O'Connell, M., D. S. Baldwin, A. I. Robertson, and G. Rees. 2000. Release and  
10 bioavailability of dissolved organic matter from floodplain litter: influence of origin and  
11 oxygen levels. *Freshwater Biology* **45**: 333-342.

12  
13 Odum, W.E., E.P. Odum, and H.T. Odum. 1995. Nature's pulsing paradigm. *Estuaries* **18**:  
14 547-555.

15  
16 Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed:  
17 observations on the role of a riparian forest. *Ecology* **65**: 1466-1475.

18  
19 Robertson, A. I., P. Bacon, and G. Heagney. 2001. The responses of floodplain primary  
20 production to flood frequency and timing. *Journal of Applied Ecology* **38**: 126-136.

21

22

1

2 Sanchez-Perez, J., and M. Tremolieres. 1997. Variation in nutrient levels of the  
3 groundwater in the Upper Rhine alluvial forests as a consequence of hydrological regime and  
4 soil texture. *Global Ecology and Biogeography Letters* **6**: 211-217.

5

6 Slack, J. R., A. M. Lumb, and J. M. Landwehr. 1993. Hydroclimatic data network  
7 streamflow data set, 1874-1988. Water-Resources Investigation Report 93-4076. U.S.  
8 Geological Survey, Reston, VA.

9

10 Smith, L. K., W. M. Lewis, Jr., J. P. Chanton, G. Cronin, and S. K. Hamilton. 2000.  
11 Methane emissions from the Orinoco River floodplain, Venezuela. *Biogeochemistry* **51**:  
12 113-140.

13

14 Solorzano, L. 1969. Determination of ammonium in natural waters by the phenohypochlorite  
15 method. *Limnology and Oceanography* **14**: 799-801.

16

17 Stanley, E. H., S. G. Fisher, and N. B. Grimm. 1997. Ecosystem expansion and contraction in  
18 streams. *Bioscience* **47**: 427-436.

19

20 Stromberg, J. C. 2001. Influence of stream flow regime and temperature on growth rate of  
21 the riparian tree, *Platanu wrightii*, in Arizona. *Freshwater Biology* **46**: 227-239.

22

23

- 1 Tockner, K., D. Pennetzdorfer, N. Reiner, F. Schiemer, and J. V. Ward. 1999. Hydrological  
2 connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain  
3 system (Danube, Austria). *Freshwater Biology* **41**: 521-535.
- 4
- 5 Tockner, K., F. Malard, and J. V. Ward. 2000. An extension of the flood pulse concept.  
6 *Hydrological Processes* **14**:2861-2883.
- 7
- 8 Triska, F. J., J. H. Duff, and R. J. Avanzino. 1993. Patterns of hydrological exchange and  
9 nutrient transformation in the hyporheic zone of a gravel-bottom stream: examining  
10 terrestrial-aquatic linkages. *Freshwater Biology* **29**: 259-274.
- 11
- 12 Van den Brink, F. W. B., J. P. H. M. De Leeuw, G. Van Der Velde, and G. M. Verheggen.  
13 1993. Impact of hydrology on the chemistry and phytoplankton development in floodplain  
14 lakes along the Lower Rhine and Meuse. *Biogeochemistry* **19**: 103-128.
- 15
- 16 Wainright, S. C., C. A. Couch, and J. L. Meyer. 1992. Fluxes of bacteria and organic matter  
17 into a blackwater river from river sediments and floodplain soils. *Freshwater Biology* **28**: 37-  
18 48.
- 19
- 20 Walker, K. F., F. Sheldon, and J. T. Puckridge. 1995. A perspective on dryland river  
21 ecosystems. *Regulated Rivers* **11**: 85-104.
- 22



1

2 Wood, E. D., A. J. Armstrong, and F. A. Richards. 1967. Determination of nitrate in seawater  
3 by cadmium-copper reduction to nitrite. *Journal of the Marine Biological Association of the*  
4 *United Kingdom* **47**: 23-31.

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7

1 Table 1. Hydrologic and material budgets for the experimental flood site, 1994 and 1995.  
 2 Material loads were calculated as the summed product of daily discharge and mean inlet or  
 3 outlet concentration during the 1994 flood\*. Difference between input and output load is  
 4 presented as absolute and percent ( $[\text{input} - \text{output}/\text{input}] \times 100\%$ ) retention. Output loads  
 5 determined as the product of input discharge and mean outlet concentration were used to  
 6 calculate retention corrected for hydrologic loss to groundwater. na = not applicable.

	Input	Ouput	Absolute		Corrected
	<u>Load</u>	<u>Load</u>	<u>Retention</u>	<u>% Retention</u>	<u>% Retention</u>
<u>Water</u>					
1994 (m <sup>3</sup> )	363029	220261	142768	39	na
1995 (m <sup>3</sup> )	209300	81870	127430	61	na
<u>Materials</u>					
TSS (Mg)	23.9	1.6	22.3	93	na
NH <sub>4</sub> -N (kg)	10.4	6.2	4.2	41	2
NO <sub>3</sub> -N (kg)	26.9	3.4	23.5	87	79
TIN (kg)	37.3	9.6	27.7	74	58
PO <sub>4</sub> -P (kg)	26.3	13.1	13.2	50	17
DOC (Mg)	1.4	1.0	0.4	31	-14

7 \*TSS loads are based on 1995 samples and hydrologic fluxes

1 Table 2. Comparison of physical and chemical parameters between surface waters of the main stem Rio Grande and  
 2 connected floodplain forest. Data are mean  $\pm$  SE (n) for 10-15 sample dates during the first 40 days of flooding, May - July  
 3 1995. Results from paired t-tests (P) compare mean river and floodplain concentrations for all days (n) when samples were  
 4 simultaneously taken from the river and floodplain.

	River	Connected Floodplain	P (n)
Temperature ( $^{\circ}$ C)	19.6 $\pm$ 0.5 (14)	18.5 $\pm$ 0.5 (10)	0.0156 (7)
Dissolved Oxygen (mg/L)	7.8 $\pm$ 0.2 (14)	5.2 $\pm$ 0.3 (10)	0.0156 (7)
Oxygen Saturation (%)	100.2 $\pm$ 3.3 (14)	56.7 $\pm$ 3.8 (10)	0.0156 (7)
NH <sub>4</sub> -N (mg/L)	0.020 $\pm$ 0.007 (12)	0.081 $\pm$ 0.041 (14)	0.156 (7)
NO <sub>3</sub> -N (mg/L)	0.280 $\pm$ 0.029 (12)	0.093 $\pm$ 0.016 (14)	0.0078 (9)
PO <sub>4</sub> -P (mg/L)	0.074 $\pm$ 0.006 (11)	0.060 $\pm$ 0.015 (12)	0.31 (6)
DOC (mg/L)	5.1 $\pm$ 0.2 (10)	5.9 $\pm$ 0.7 (15)	0.09 (10)



1 Table 3. Floodplain forest floor respiration rates (mg OM m<sup>-2</sup> d<sup>-1</sup>). Data are means ± SE (n)  
 2 taken from the different floodplain forest types (disconnected, connected) in control (dry)  
 3 and flood (inundated by natural or experimental flood pulses) sites during pre-flood and  
 4 flooded periods. na = data not available

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	Control Plots		Flood Plots	
	flooding		flooding	
	pre-flooding	period	pre-flooding	period
Disconnected				
1994	5.2 ± 0.7(25)	7.7 ± 1.9(17)	1.9 ± 0.4(16)	1085 ± 392(12)
1995	18.3 ± 4.2(8)	14.5 ± 3.3(5)	11.0 ± 6.7(5)	1703 ± 756(3)
Connected				
1995	na	7.3 ± 1.6(3)	na	473 ± 119(3)

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1 **FIGURE LEGENDS**

2

3 **Figure 1.** Areal photograph of the riparian forest along the Middle Rio Grande (flow is from  
4 left to right) at the Bosque del Apache National Wildlife Refuge, San Antonio, New Mexico.  
5 The disconnected floodplain (A) is isolated from flooding by constructed levees. Portions of  
6 the riparian forest (B) found within the levees (i.e., the connected floodplain) are subject to  
7 inundation during annual high flows associated with spring runoff. The experimental flood  
8 site was an 11 ha area (outlined in white) within the disconnected forest that was flooded  
9 with water from a source canal for 30 days each year during May 1993-1995. White arrows  
10 denote the locations of inlet and outlet flumes used for water and material balance  
11 calculations. Radially aligned sampling transects (white lines) used in previous studies (see  
12 text) were equipped with 16 groundwater wells (white squares) established to monitor  
13 hydrologic and chemical characteristics of the flood pulse. A designated monitoring site (C)  
14 was used to characterize vertical chemical structure of surface waters during experimental  
15 flooding.

16

17 **Figure 2.** Depth to water table (relative to the ground surface, dashed line) in control (filled  
18 circles) and flood (open circles) during (A) 1995 experimental flooding of the disconnected  
19 forest, and (B) 1995 natural flooding of the connected floodplain. Open triangles in B  
20 indicate surface water depth in the connected forest. Data are means  $\pm$  SE. Arrows in this  
21 and subsequent figures denote the initiation of flooding and the loss of surface water. Flood  
22 day refers to the number of days of inundation with negative values indicating days before  
23 flooding.

1 **Figure 3.** Physical-chemical response to the flood pulse. A) Dissolved oxygen (mean  $\pm$  SE)  
2 during the first experimental flood (May - June 1993) for groundwater in the control (filled  
3 circles) and flooded site (open circles) and surface flood waters (open triangles). B) Vertical  
4 profiles (single measures) of temperature and dissolved oxygen recorded at the central  
5 monitoring location (see Figure 1) during the 1994 experimental flood. C) Dissolved oxygen  
6 (mean  $\pm$  SE) during natural flooding of the connected forest (symbols are as in A above).

7

8 **Figure 4.** Ammonium-N ( $\text{NH}_4\text{-N}$ ) responses to experimental flooding during 1993 (open  
9 circles), 1994 (gray squares), and 1995 (filled triangles) in A) surface water and B)  
10 groundwater of the disconnected forest. Data are means + SE from 5-16 monitoring points  
11 within the inundated site (see Figure 1).

12

13 **Figure 5.** Dissolved organic carbon (DOC) responses to the flood pulse. Data are means +  
14 SE (n = 5-16) during experimental floods of 1993 (open circles), 1994 (gray squares), and  
15 1995 (filled triangles) in A) surface water and B) groundwater of the disconnected forest. C)  
16 DOC (mean  $\pm$  SE) during river flooding of the connected forest. Data are from surface water  
17 (triangles) and groundwater of the flooded (open circles) and control (filled circles) sites  
18 within the connected forest.

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22 **Figure 6.** Comparison of inlet (filled bars) and outlet (open bars) concentration of

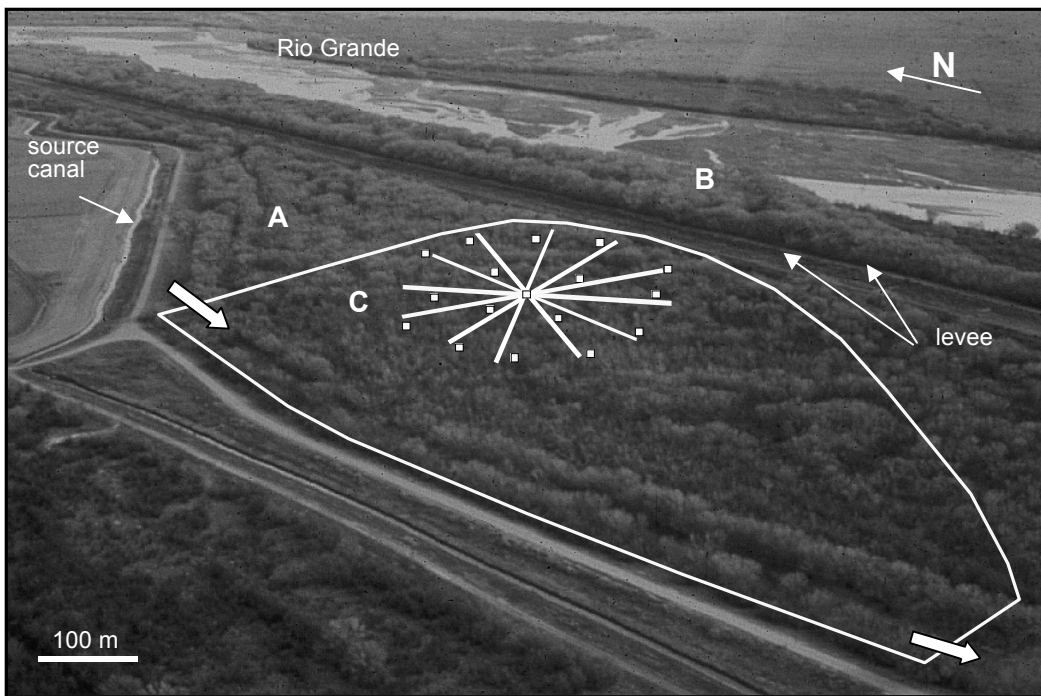


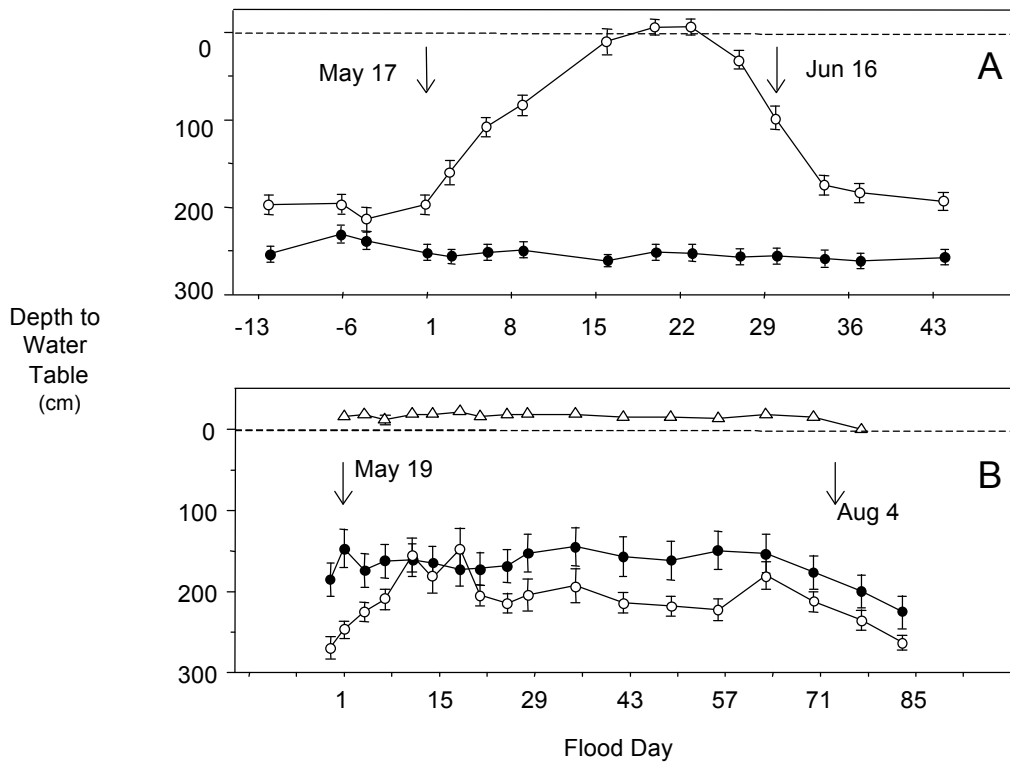
1 biogeochemically-active solutes (X) during the experimental flooding (1994) of the  
2 disconnected forest. Data are means  $\pm$  SE across all flooding days (n = 18-32) for water  
3 entering or leaving flumes. Significant differences ( $P < 0.05$ ) between inlet and outlet  
4 concentrations determined by t-tests are denoted by an asterisk.

5  
6 **Figure 7.** Time course of forest floor respiration ( $\text{mg OM m}^{-2} \text{ d}^{-1}$ ) in control (filled circles)  
7 and flood (open circles) sites during the second experimental flooding (May - Jun 1994) of  
8 the disconnected forest. Data are means  $\pm$  SE for five metabolic chambers at each site during  
9 each sampling date. Assays conducted on the flood site during flood day 31 were done in the  
10 absence of pooled surface water, but included moist forest floor litter and soils.

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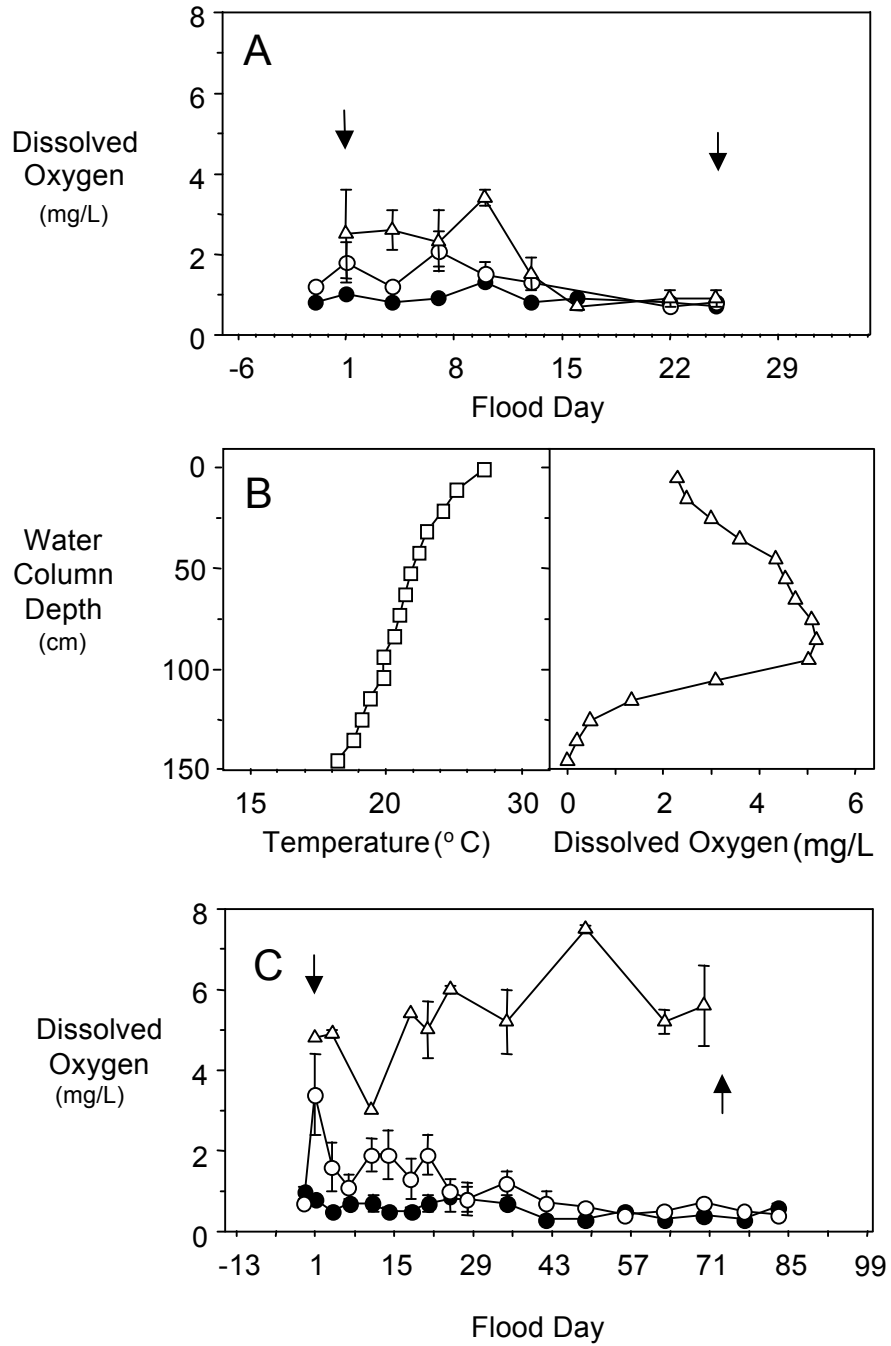
Valett et al. Figure 1



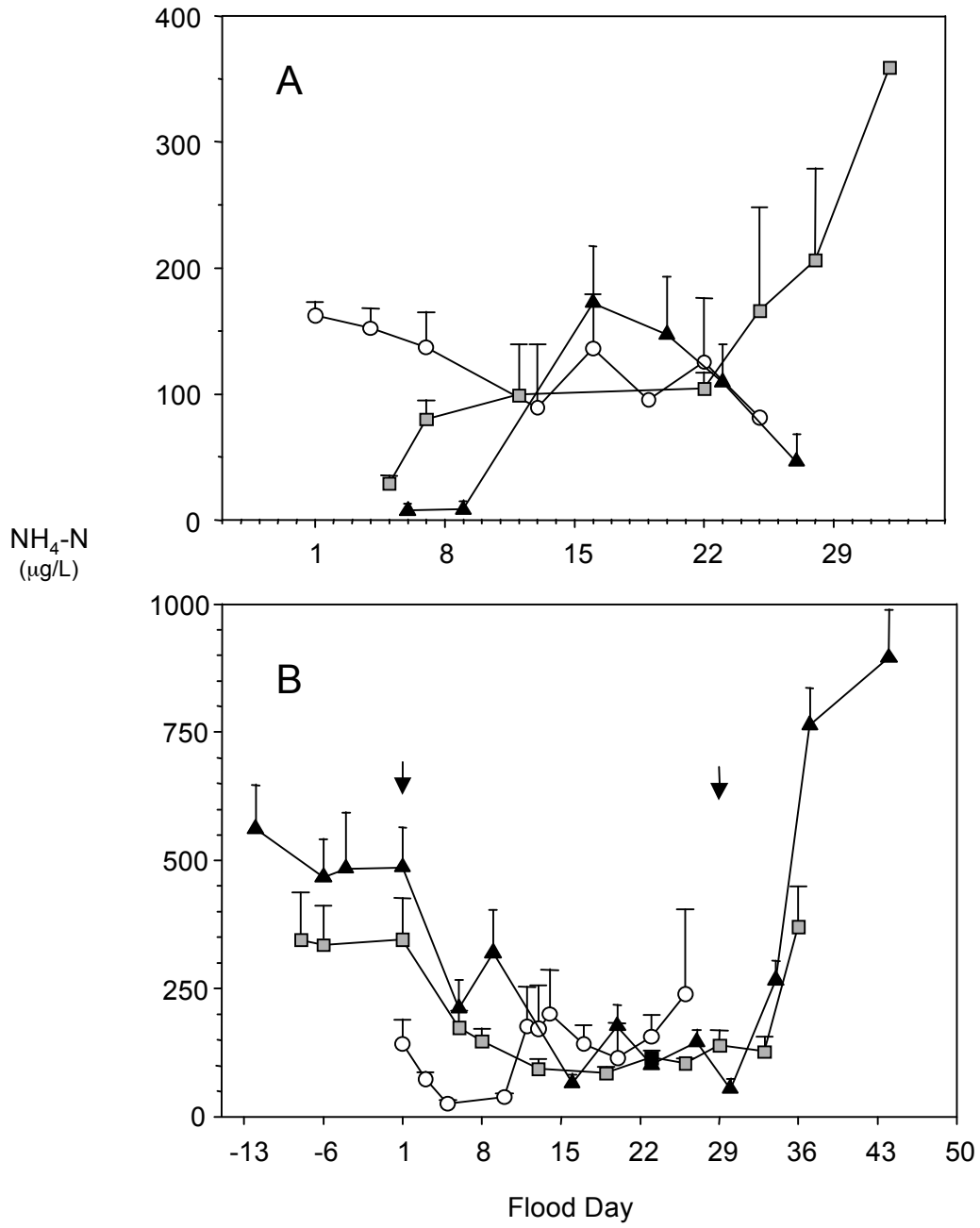


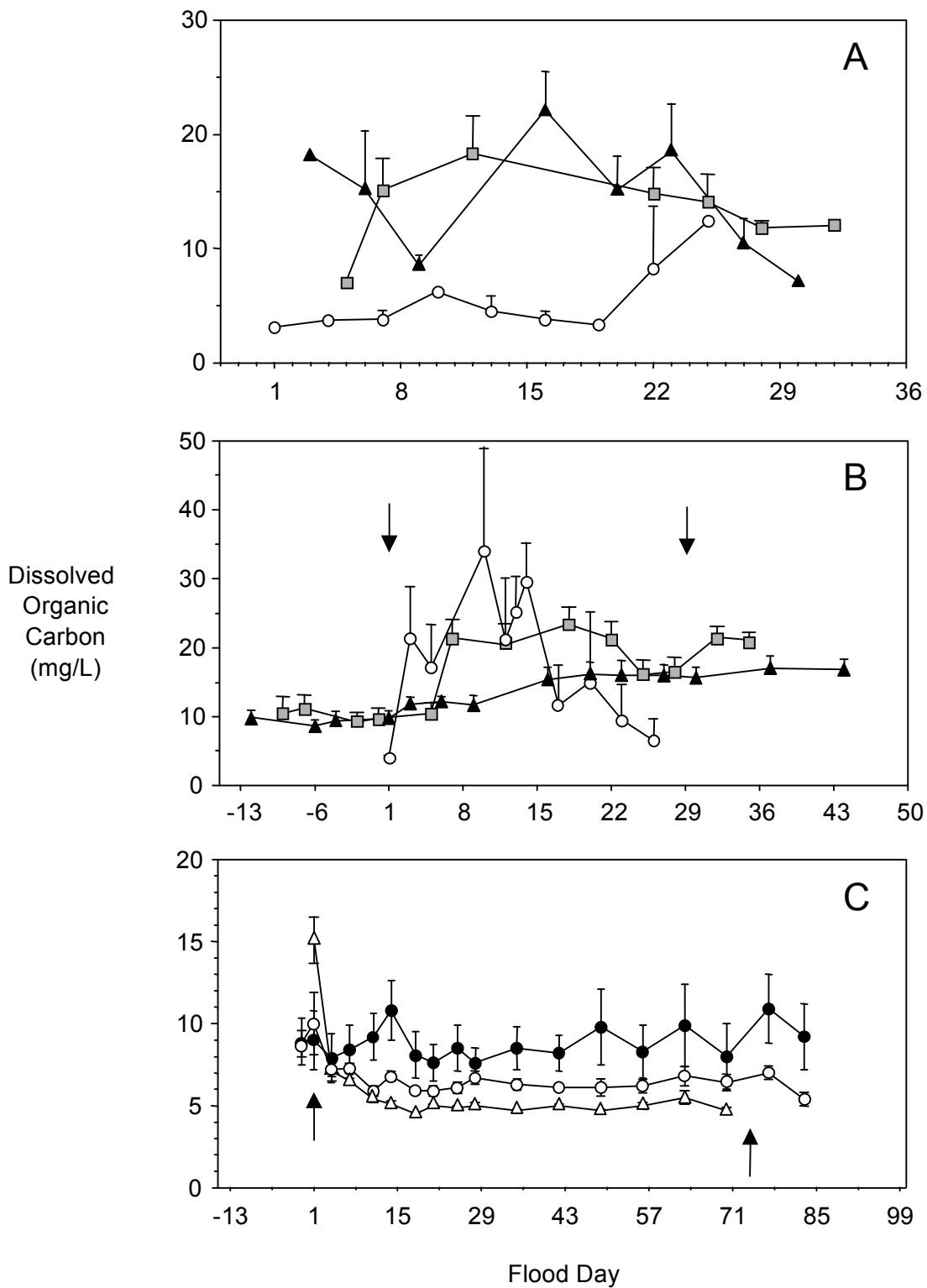
Valett et al.  
Figure 2

Valett et al. Figure 3



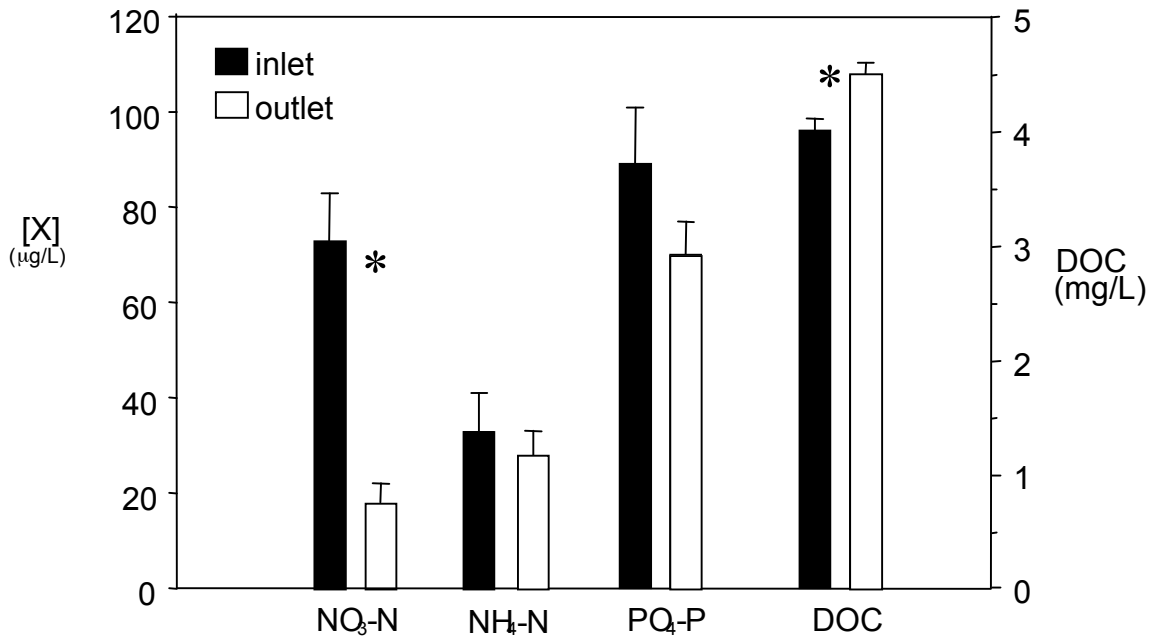
Valett et al. Figure 4





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Valett et al. Figure 6



Valett et al. Figure 7

