Influence of Experimental Flooding on Litter Dynamics in a Rio Grande Riparian Forest, New Mexico

Lisa M. Ellis¹ Manuel C. Molles, Jr.¹ Clifford S. Crawford¹

Abstract

Flow regulation, which has largely eliminated flooding along the Rio Grande in central New Mexico, has substantially changed the riparian ecosystem. We investigated managed flooding as a means of restoring ecosystem function. After collecting baseline data during 1991 and 1992 in two riparian forest sites that had not flooded for about 50 years, we flooded an experimental site for 27-32 days during late spring of 1993, 1994, and 1995, leaving the reference site unflooded. During the final year of the study we compared these sites to two additional sites located within the riverside levee, one of which has been flooding naturally while the second remained largely unflooded. Three years of experimental flooding did not change the total biomass of either woody debris or forest-floor litter at the experimental flood site. Both woody debris and forest-floor litter, however, were significantly lower at the natural flood site than at the experimental flood site and two unflooded sites. Leaf and wood decomposition rates increased with flooding. The decay rate for cottonwood logs at the unflooded site (0.010 per year) predicted a half-life of 69.3 years, while the decay rate of 0.065 per year after 3 years of experimental flooding predicted a half-life of 10.6 years. This suggests that a decade of annual flooding may be used to restore the organic debris to pre-regulation levels. Flooding may also have caused

¹Department of Biology, University of New Mexico, Albuquerque, NM 87131, U.S.A. an increase in litter production. These results suggest that experimental flooding has initiated a process of restoring ecosystem function within the riparian forest.

Introduction

C easonal flooding is an integral component of river-Ufloodplain ecosystems, providing a hydrologic connection that controls a variety of functional responses (Junk et al. 1989; Sparks et al. 1990; Gregory et al. 1991; Bayley 1995). Along unregulated systems, the aquaticterrestrial interaction drives the transfer of water, nutrients, sediment, particulate organic matter, and organisms, with important fluxes operating laterally as well as downstream (Gregory et al. 1991). This "flood pulse" promotes biological productivity and helps to maintain ecological diversity in riparian ecosystems (Junk et al. 1989; Bayley 1995). Throughout much of the world, however, riparian ecosystems have been hydrologically disconnected from adjacent rivers due to extensive regulation, including dam construction, channelization, water diversion, and irrigation (Benke 1990; National Resource Council 1992; Dynesius & Nilsson 1994; Poff et al. 1997). This has altered wetland and riverine ecosystems, leading to declines in native riparian vegetation along regulated rivers (Reily & Johnson 1982; Fenner et al. 1985; Rood & Hinze-Milne 1989; Rood & Mahoney 1990; Stromberg & Patton 1991; Poff et al. 1997). Increasing awareness of the critical link between rivers and adjacent floodplains has led to recent efforts to restore the "natural flow regime" to several large river systems (Dahm et al. 1995; Koebel 1995; Collier et al. 1997; for review see Poff et al. 1997) and to understand the ecological role of floods as disturbances (Michener & Haeuber 1998).

In riparian forests, one result of decreasing the periodic influx of river water has been the accumulation of leaf litter and woody debris. This may be particularly important in arid systems, where the lack of moisture throughout most of the year inhibits microbial activity on the soil surface and thus inhibits decomposition (Facelli & Pickett 1991). For example, along the Rio Grande through central New Mexico, large amounts of leaf litter and woody debris have accumulated since flow regulation began (Molles et al. 1995). The availability of essential nutrients such as nitrogen from this litter depends on factors affecting rates of accumulation and decomposition, including moisture (Bell et al. 1978; Day 1983; Facelli & Pickett 1991). Insufficient moisture leads to decreased rates of decomposition, which immobilizes nutrients and materials and may inhibit plant growth. Along the Rio Grande, accumulations of organic matter also may have contributed to an increased fire frequency in riparian forests (Stuever 1997; Ellis et

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al. 1998), which threatens human populations in addition to the native biota.

The hydrology of the Rio Grande was once characterized by periodic flooding due to spring snow melt from high mountain catchments and intense summer thunderstorms, but dams and riverside levees now prevent most flooding (U.S. Army Corps of Engineers 1958; Crawford et al. 1993). In addition to large accumulations of organic matter, changes to the floodplain ecosystems include decreased establishment of native vegetation such as *Populus deltoides* subsp. *wislizenii* (Rio Grande cottonwood) and the spread of exotic trees (Howe & Knopf 1991; Crawford et al. 1993; Crawford et al. 1996). In 1991 we began a study of the Rio Grande riparian ecosystem in central New Mexico to assess the effects of restoring seasonal flooding to a forest that had not flooded for about 50 years.

After collecting baseline data, we flooded a forest site for 1 month during each of 3 successive years to simulate historic low-intensity flooding, while continuing to monitor an unflooded reference site. Here we consider the effects of flooding on litter dynamics in this system. We predicted that flooding would (1) decrease the quantity of wood and leaf litter present on the forest floor, (2) increase rates of wood and leaf decomposition, and (3) initially decrease rates of litter production. During the final year of the study we monitored a naturally flooded forest site to provide a comparison with a riparian forest in which the flood pulse had been maintained.

Study Sites and Experimental Flooding

Two study sites were established during the summer of 1991 in mixed cottonwood forest at the Bosque del Apache National Wildlife Refuge, elevation approximately 1400 m, Socorro County, New Mexico (Fig. 1). The Refuge contains approximately 14.5 km of the Rio Grande and its associated riparian vegetation. The study sites were located 3.7 km apart in a strip of continuous forest 200-300 m wide, with each intensive study area approximately 3.1 ha in size. The canopy of each was dominated by Rio Grande cottonwood ranging from 8 m to 15 m in height, with a subcanopy of Salix gooddingii (Goodding willow) and Tamarix ramosissima (saltcedar). Understory shrubs included Baccharis glutinosa (seepwillow) and Forestiera neomexicana (New Mexico olive) in varied proportions, as well as scattered Elaeagnus angustifolia (Russian olive), Prosopis pubescens (screwbean mesquite), Lycium torreyi (wolfberry), and Amorpha fruticosa (desert indigobush). A variety of herbaceous understory species was also present, but both composition and abundance varied among years (unpublished data).

The sites were approximately 0.5 km west of the Rio Grande and separated from it by the low-flow conveyance channel and riverside levee that parallel the river



Figure 1. Location of study sites within Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico. The four study sites are the experimental flood site (EF), the natural flood site (NF), reference 1 (R1), and reference 2 (R2); refuge headquarters is indicated (HQ). The location of the refuge is indicated on the inset map of New Mexico.

(Fig. 1). After collecting baseline data at both sites for two years, we inundated one site, designated the "experimental flood" site, for approximately 1 month during each of the following 3 years: 17 May-12 June 1993, 19 May-19 June 1994, and 17 May-17 June 1995. Floods were timed to match the historical peak flow of the upper Rio Grande, based on the mean annual hydrograph for 1889–1990 at the U.S. Geological Survey's Embudo gauging station (Slack et al. 1993), located upstream from major regulation sites. Water was taken from a riverside canal via a water diversion structure and included a combination of water diverted directly from the Rio Grande, irrigation return flows from agricultural fields, and groundwater recharge accumulated in the nearby low flow channel (J. Taylor, personal communication). Experimental floods inundated approximately 10 ha of riparian forest floor at the experimental flood site during 1993, 1994, and 1995. Flood water depth varied from nearly 20 cm to 200 cm across the site due to topographic variation; average depth was about 50 cm. Throughout the study the second site, reference 1, remained unflooded.

In 1994 a section of forest within the refuge was flooded directly from the Rio Grande, which provided a comparison with a more naturally flooded site (the "natural flood" site). This riparian forest was approximately 200 m east of the primary sites and was bounded on the east side by the Rio Grande and on the west by the levee (Fig. 1). In August 1994 an additional dry reference site (reference 2) was established south of the natural flood site in an area largely protected from flooding by a groin dike. These riverside sites cover approximately 1.1 ha each and contained a primarily cottonwood canopy, with understory vegetation including saltcedar, seepwillow, New Mexico olive, and Russian olive. Herbaceous understory vegetation was sparse, particularly at the natural flood site where the overstory was more dense. In 1995, flooding at the natural flood site lasted for approximately 2.5 months from mid-May through late July, and surface water height measured at one typical location averaged about 20 cm throughout the flood.

Rainfall varied considerably during the study (Fig. 2), reflecting the El Niño–Southern Oscillation phenomenon that affects many semiarid regions, including the south-western United States (Nicholls 1988). Locally, El Niño events result in increased fall, winter, and spring precipitation, as experienced in 1991–1992 and 1992–1993 (Dahm & Moore 1994; Fig. 2). Winter precipitation was relatively high during 1994–1995, but spring precipitation was low. In both 1990–1991 and 1993–1994, winter precipitation was relatively low (though normal), with more of the annual precipitation arriving during the summer monsoon season.



Figure 2. Precipitation at Bosque del Apache National Wildlife Refuge during 1991–1992, illustrating a year with increased fall, winter, and spring precipitation, and during 1993–1994, illustrating a year with relatively low winter precipitation. Data are presented by water-year and are averaged for two locations within the refuge.

Methods

Biomass of Woody Debris

Woody biomass was measured after flooding in 1995 following the linear and planar intersect methods of Van Wagner (1968) and Brown (1971, 1974). Wood on the ground was measured along 20 transects distributed throughout each of the four study sites; each transect extended 2 m above the ground. Standing dead snags were excluded. Each piece of wood intersecting the transect was defined as either fine woody debris (FWD, ≤ 2 cm diameter) or coarse woody debris (CWD, >2 cm diameter). FWD was classified by diameter size (0–0.5 cm, 0.51–1.0 cm, 1.01–2.0 cm), and the number of intersections of each class was summed over transects 2 m in length for each of the smallest two classes and 5 m in length for the largest class. CWD was counted along transects 15 m long. Each piece of CWD was classified as cottonwood, saltcedar, seepwillow, and "other," and by decomposition class. Decomposition classes were: 1 (slight/none) = little or no bark slippage, wood sound, with little or no decay throughout; 2 (moderate) = partial or complete bark slippage, decay extending to core, split wood with center decay but with sound outer layers; and 3 (advanced) = partial or complete bark slippage, wood decayed throughout. For each piece of CWD, the diameter at the point of intersection was measured.

Woody biomass was estimated following formulas of Van Wagner (1968) and Brown and Roussopoulos (1974). For FWD, 0–2.00 cm diameter:

$$mass(kg/ha) = \frac{1.2337 \times 10^5 S d_q^2 n}{L},$$

where *S* is mean density (g/cm³), d_q^2 is the quadratic mean diameter (cm), *n* is the number of intersections per sample plane, and *L* is the length of the sample plane (cm). Quadratic mean diameters (average squared diameters) were calculated from preliminary sample measurements throughout the sites. For CWD, >2.00 cm diameter:

mass(kg/ha) =
$$\frac{1.2337 \times 10^5 S_x \sum d_q^2}{L},$$

where S_x is mean density for each species based on decomposition stage, Σd_q^2 is the sum of individual squared diameters, and *L* is the length of the sample plane.

Density estimates used for biomass calculations were based on diameter and mass measurements of preliminary samples oven-dried to constant weight (Appendices 1 & 2). For FWD, all species were combined in each size class and extent of decomposition was not considered. For CWD, density estimates were calculated for each of the three species and three decomposition classes, with mean values of these used for pieces not identifiable to species. Biomass of FWD, CWD, and total woody debris (FWD + CWD) was averaged within each of the four sites and compared among sites by analysis of variance (ANOVA), followed by multi-way t tests to distinguish differences among sites; square-root-transformed data were used for CWD and total biomass (ANOVA procedure). All statistical procedures (here and following) used the SAS system (SAS Institute, Inc. 1989).

Forest Floor Litter

Samples of the standing stock of organic matter were collected from the forest floor at the experimental flood and reference 1 sites each spring and fall beginning in September 1991. Collections were made at riverside sites only in 1995. During each collection, 10×10 cm samples of all litter above the mineral soil layer were collected from randomly chosen locations distributed throughout each site. Samples were taken to the lab, dried in a 60°C oven to constant weight, and weighed. Subsamples were ground with a Wiley Mill and ashed at 500°C in a muffle furnace for 2 hours to determine the ash-free dry-weight of organic matter.

For each collection, the average ash-free dry-weights of forest floor litter at the experimental flood and reference 1 sites were compared by an independent-samples t test on log-transformed data (TTEST procedure). Comparisons among all four sites were made for spring and fall of 1995 by analysis of variance on log-transformed weights for each collection, followed by multiple t tests (ANOVA procedure).

Leaf Decomposition

Cottonwood leaves were collected in mid-October each year, prior to abscission, from at least 10 individual trees at a site near the study areas and were air dried to constant weight (usually several days) before being placed in mesh bags. Bags were made of fiberglass screening (15×15 cm, 1-mm mesh), and each contained 5 g of leaves. Twenty bags were arranged in a 5×4 bag grid at the experimental flood and reference 1 sites in early November of each year (1991, 1992, 1993, 1994); bags were covered with a coarse-mesh hardware cloth cage to deter animal interference. Five bags were then collected randomly from each site on each of four dates each year: (1) the same day the bags were placed at the sites, to correct for handling loss to bag contents during the installation; (2) the following April, prior to flooding; (3) June, immediately after flooding; and (4) early November, approximately one year after installation. Bags were installed in a similar way at the riverside sites in November 1994. The post-flood collections for riverside sites were made in early August 1995, since the natural flood site remained inundated until late July; those bags were under water for 2.5 months. In the lab, contents of litter bags were removed, dried at 60°C for 48 hours, weighed, and ground with a Wiley Mill; subsamples were ashed in a 500°C muffle furnace for 2 hours to determine ash-free dry-weights of leaves.

We compared ash-free dry-weights of leaves in decomposition bags at the experimental flood and reference 1 sites across years using a separate ANOVA (GLM procedure) for the pre-flood (November and April) and postflood (June and the following November) collections. Since neither site was flooded during the 1991–1992 season, the "post-flood" collections for that year were analyzed separately from other years. Because decomposition at the natural flood and reference 2 sites was measured during 1 year only, data were not analyzed statistically but instead patterns were compared visually.

Wood Decomposition

Cottonwood logs were placed at the experimental flood and reference 1 sites in June 1991 to estimate the rates of wood decomposition in flooded and nonflooded forests. Logs were cut into 1-m sections from fallen trees located several kilometers south of the study sites. Those dead trees were supported above the ground by the branches of other trees that had fallen previously. Initial diameters averaged 12.74 \pm 0.29 cm at the experimental flood site and 13.04 ± 0.26 cm at reference 1. Single disks approximately 3 cm thick were removed from both ends of each log as the logs were cut, and then were analyzed in the lab for initial moisture and organic content. Logs were initially very dry, without bark, and of sound wood. Each log was weighed in the field and marked for identification, and 20 were placed in a row at each site. Logs at the experimental flood site were anchored with rebar stakes to prevent movement during flooding. Four logs were collected from each site in April 1993, prior to experimental flooding. Additional sets of four logs were collected from each site in November 1994 and 1995, representing 2 and 3 years of annual flooding at the experimental flood site, respectively.

Logs subsequently collected from sites were oven-dried at 60°C until they reached constant weight (2–3 weeks) and re-weighed. Three disks were cut from each log, one at each end and one at a random location along the log. Several ground subsamples were taken from each disk with an electric drill and then combined and ashed in a 500°C muffle furnace for 2 hours to determine the ash-free dry-weight of each log. We calculated pre-flood (1991– 1993) and post-flood (1993–1995) decay rates based on the single exponential model discussed by Olson (1963):

$$y_t = y_0 e^{-kt},$$

where y_o is the initial mass of material, y_t is the mass left at time t, and k is the decay rate constant (expressed per unit time). This model assumes uniform density in the logs. We then compared pre-flood and post-flood decay rates between the two study sites using Wilcoxon Rank Sum tests for each period (NPAR1WAY procedure).

Litter Production

Litter production was monitored at the experimental flood and reference 1 sites beginning in 1991. Litter traps consisted of rubber tubs (50 cm diameter by 10 cm deep) placed on the ground and left for litter collection between September and the following March of each year. Tubs had small drainage holes to avoid accumulating rainwater. Twelve litterfall traps were present at each site, and their contents were collected monthly. Litter production was collected at the national flood and reference 2 sites during the final two seasons. In 1994 a flood in late August inundated traps at the natural flood site, and thus the September collection at that site may have missed some leaf fall. Thereafter, litterfall traps at the natural flood site were placed approximately 3 feet above ground on PVC pipe stands to keep samplers above water level. Observations suggest that stands did not affect the amount of litter trapped relative to traps placed on the ground.

Litter samples were oven-dried at 60°C for 48 hours and weighed. During the first three litterfall seasons at the experimental flood and reference 1 sites, the cumulative dry-weight (g/m²) for the entire litter sample leaves of all plant species, twigs, reproductive partswas computed monthly. During the 1994-1995 and 1995–1996 seasons, samples at all four sites were sorted to separate cottonwood leaves from other materials in the litter and weighted for each sample. Cumulative total litter measurements at each site during 1994–1995 accurately predicted the cumulative weight of cottonwood leaves (experimental flood, $r^2 = 0.89$, p = 0.0001; reference 1, $r^2 = 0.94$, p = 0.0001; natural flood, $r^2 = 0.99$, p =0.0001; reference 2, $r^2 = 0.91$, p = 0.0001; CORR procedure); this provided an estimate of the total biomass of cottonwood leaves produced during the first three seasons at the experimental flood and reference 1 sites based on total litterfall each year determined by the following regression equations: experimental flood, cumulative weight of leaves = $(0.690) \times (\text{cumulative weight})$ of litter) - 1.134; reference 1, cumulative weight of leaves = $(0.707) \times (\text{cumulative weight of litter}) - 1.052.$

We compared total annual leaf fall at the experimental flood and reference 1 sites during the study using a profile analysis with time as the within-subject effect and flood treatment as the between-subjects effect (multivariate analysis of variance with yearly contrast transformations, ANOVA procedure; von Ende 1993). Yearly contrasts in total leaf fall were made between the two pre-flood litterfall seasons and between each of the post-flood seasons with the 1992–1993 pre-flood season. A similar profile analysis was made of all four sites during the final 2 years, with contrasts made between the years. A Bonferroni adjustment was used to correct the experiment-wise error rate for these multiple contrasts.

Results

Biomass of Woody Debris

Total biomass of woody debris measured in 1995 was significantly lower at the natural flood site (13.7 Mg/ha) than at the other three sites (33.7–38.8 Mg/ha), which did not differ significantly from each other based on multiple *t* tests (ANOVA: $F_{3,76} = 9.36$, p = 0.0001; Fig. 3). Biomass of coarse woody debris was also lower at the natural flood site than at the other three sites ($F_{3,76} = 6.27$, p = 0.0007), while fine woody debris was greatest at reference 1 ($F_{3,76} = 18.25$, p = 0.0001; Fig. 3). Multiple *t* tests indicated significantly more FWD at the experimental flood site than at the natural flood site, but neither of those sites differed significantly from reference 2.

Distribution of woody biomass along transects varied among sites (Fig. 4). All transects at the natural flood site contained less than 30 Mg/ha of woody debris, with a range of only 3.8–22.5 Mg/ha. In contrast, biomass estimates along transects at reference 2 ranged from 4.9 to 106.9 Mg/ha, representing a more patchy distribution than at the natural flood site. The distribution of woody debris was more similar between the experimental flood and reference 1 sites, with most transects at both sites containing 30–40 Mg/ha total biomass (Fig. 4).



Figure 3. Biomass of total woody debris and coarse woody debris (CWD, diameter >2 cm) were significantly lower at the natural flood site than at other sites, which did not differ from each other. Reference 1 had more fine woody debris (FWD, diameter ≤ 2 cm) than other sites, while the experimental flood site had more FWD than did the natural flood site. Values are the estimated total biomass (Mg/ha) averaged across 20 transects for each site in 1995; vertical bars indicate standard errors.



Figure 4. Sites differed in the distribution of total woody biomass among sample transects. Transects at the natural flood site had consistently lower woody biomass, while woody biomass at other sites was more patchily distributed, with some transects containing much higher quantities of wood. Values along the horizontal axis represent midpoints of biomass size classes; biomass was estimated along 20 transects at each of the sites.

Forest Floor Litter

Three seasons of experimental flooding did not affect the quantity of forest-floor litter. The biomass of litter was greater at reference 1 than at the experimental flood site during 1991 and 1992 (*t* test; September 1991:



Figure 5. Accumulations of forest-floor litter were not affected by 3 years of experimental flooding. The experimental and reference 1 sites differed from each other in 1991 and 1992, but not for the remaining collections. For both collections in the final year, however, accumulations of litter were lower at the natural flood site compared to the other three sites, which did not differ from each other. Values are the average ash-free dry-weight of all organic matter above mineral soil (n = 10 samples per collection) for April (A) and September (S); vertical bars indicate standard errors.

t = 2.70, p = 0.015; April 1992: t = 3.42, p = 0.005; September 1992: t = 2.12, p = 0.048) but did not differ between sites during the remaining years (Fig. 5). This was due to a decrease in litter estimated at reference 1 rather than a change at the experimental flood site and probably reflects the high spatial variation in litter accumulations. In contrast, when all four sites were compared for 1995, the accumulation of forest-floor litter was significantly lower at the natural flood site than at the other three sites during both collections (ANOVA; April: $F_{3,36} = 11.54$, p < 0.0001; September: $F_{3,35} = 29.35$, p < 0.0001; Fig. 5). Multiple *t* tests indicated no differences among the other three sites.

Leaf Decomposition

Prior to experimental flooding, there was no apparent difference in leaf decomposition between the experimental flood and reference 1 sites. Overwinter weight loss by leaves in decomposition bags did not differ between the sites for any year, nor did sites differ in the extent of weight loss between the June and final November collections in 1991–1992, when both sites remained dry (Table 1). However, overwinter weight loss at both sites did vary significantly among years (Table 1; Fig. 6), which probably reflected variation in winter

Table 1. Results of analysis of variance for experimental leaf decomposition, evaluating the effect of year, collection period, and flood treatment (site) in the weight of leaves in decomposition bags for four years.*

Source	df	MS	F	р
Initial (November) and post-winter (April) collections, all				
years $(n = 80)$				
Site	1	0.1	3.46	0.07
Year	3	0.8	24.03	0.0001
Collection	1	10.6	333.99	0.0001
Site \times year	3	0.1	1.84	0.15
Site \times collection	1	0.1	3.14	0.08
Year $ imes$ collection	3	0.6	20.28	0.0001
Error	67	0.03		
Final two collections in 1991–1992, with no flooding $(n = 20)$				
Site	1	0.1	1.65	0.22
Collection	1	0.7	10.07	0.006
Site $ imes$ collection	1	0.2	3.27	0.09
Error	16	0.07		
Final two collections	during y	ears of floo	oding ($n = 60$)
Site	1	26.2	1216.55	0.0001
Year	2	0.02	0.96	0.39
Collection	1	0.2	10.47	0.0022
Site \times year	2	1.0	46.69	0.0001
Site \times collection	1	0.5	21.98	0.0001
Year $ imes$ collection	2	0.06	2.85	0.07
Error	50	0.02		

*1991–1992, 1992–1993, 1993–1994, 1994–1995. Site differences correspond to the presence (experimental flood site) or absence (reference 1) of flooding during 1992–1993, 1993–1994, and 1994–1995 post-flood comparisons.



Figure 6. Decomposition of cottonwood leaves increased significantly during flooding. There were no differences in weight loss between the experimental flood and reference 1 sites during overwinter periods (November to April) each year, or for the remaining collections during 1991–1992 (a). Weight loss was significant during flooding at the experimental flood site but differed among years, reflecting the extent of winter precipitation (b–d). Leaf weights for the natural flood and reference 2 sites (d) show patterns similar to those of the experimental flood and reference 1 sites, respectively. Values are the mean ash-free dry-weight of leaves from five decomposition bags for each collection at each site; vertical bars are standard error.

precipitation. Overwinter loss was greatest during the moist conditions of 1991–1992 and lowest during the relatively dry winter of 1993–1994 (Fig. 2).

Experimental flooding accelerated leaf decomposition. Leaves remaining in decomposition bags at the experimental flood site weighed significantly less than leaves at reference 1 after flooding each year (Table 1; Fig. 6). This difference between sites varied among years and was greatest during the dry winter of 1993–1994, when overwinter decomposition was low. Differences in decomposition at the natural flood and reference 2 sites were similar to those seen at the experimental flood and reference 1 sites: decomposition was greater at the

flooded site and occurred primarily during the period of inundation (Fig. 6). Even with a longer period of inundation, decomposition of leaves at the natural flood site was similar to that seen at the experimental flood site (Fig. 6).

Wood Decomposition

Three seasons of flooding slightly increased wood decay rates at the experimental flood site over those at reference 1 (Fig. 7). Although the trend suggests that differences in wood decomposition would be significant after additional flooding, this cannot be confirmed because remaining logs at the experimental flood site were completely destroyed in a fire during June 1996. Prior to flooding, decay rates averaged 0.003 and 0.004 per year for logs at the experimental flood and reference 1 sites, respectively, predicting half-lives of over 200 years. The overall decay rate for logs at reference 1 for the entire 1991–1995 period was 0.010 per year, reflecting some annual differences due to precipitation. This predicts a half-life of 69.3 years. The average decay rate for logs at the experimental flood site between 1993 and 1995 increased to 0.065 year, which predicts a halflife of 10.6 years.

Litter Production

Although flooding did not produce a clearly significant effect on litter production, observations suggest a possible benefit to litter production after several years. Total leaf fall differed between the experimental flood and reference 1 sites only in 1993–1994 ($F_{(1,22)} = 13.99$, p = 0.001), but interannual variation suggests that this difference may not reflect flooding (Fig. 8). Leaf fall at ref-



Figure 7. The decay rate of logs at the experimental flood site was slightly greater than at reference 1 during 1993–1995 (Z = -1.87, p = 0.06), while pre-flood (1991–1993) rates did not differ between the sites (Z = -0.15, p = 0.88). Values are the average ash-free dry-weight of four logs for each collection at each site; vertical bars are standard errors.



Figure 8. Total annual leaf fall was significantly lower at the experimental flood site than at reference 1 during 1993–1994 but not during other years. Leaf fall increased significantly at both sites during the final season over that of the first four years. Considering all four sites during the final two seasons indicated greater leaf fall at the natural flood site than at the experimental flood site during 1994–1995 but not during 1995–1996, while leaf fall was higher at the natural flood site in the final year than at the two reference sites. Values are the mean total dry weight (g/m²) of cottonwood leaves within each site (n = 12 litter traps per collection per site); vertical bars are standard error.

erence 1 was more variable among years, while leaf fall at the experimental flood site showed a slight linear decline across the first four seasons; leaf fall at both sites increased significantly during the final year compared to other years ($F_{(1,22)} = 30.03$, p = 0.0001). A profile analysis for all four sites during the final two seasons indicated significantly greater leaf fall at the natural flood sit than at the experimental flood site during 1994–1995 but not during 1995–1996, while during the last year leaf fall was significantly higher at the natural flood site than at the two reference sites. See Table 2 for overall MANOVA results for both tests. Pairwise comparisons not listed were not significantly different.

Discussion

Three years of flooding was not long enough to reduce the substantial build-up of litter on the forest floor, but lower quantities of leaf litter at the natural flood site suggest that repeated flooding would eventually decrease the quantity of organic litter. Other studies confirm the reduction of forest-floor litter at flooded riparian sites (Bell & Sipp 1975; Peterson & Rolfe 1982). Since woody biomass was not measured before experimental flooding, we cannot determine possible changes in quantities of wood resulting from 3 years of flooding. Increased wood decomposition rates indicate that a decade or more of flooding will be needed to see this **Table 2.** Results of profile analysis (MANOVA) for leafcollections, evaluating effects of year and flood treatment(site) on total leaf fall for five seasons at the experimentalflood and reference 1 sites (a) and for all four sites during thefinal two seasons (b).*

a. Comparison between experimental flood and reference 1 sites across 5 seasons:

		Betweer	n Sites	
Source Site Error	MS 7361.9 8908.9	df 1 22	F 0.83	<i>p</i> > <i>F</i> 0.37
		Within	Sites	
Source Year Year × site	F 19.49 7.44	Num df 4 4	Den df 19 19	p > F 0.0001 0.0009

b. Comparison of all four sites during final two seasons:

		Between	n Sites	
Source Site Error	MS 14658.9 4450.3	df 3 44	F 3.29	<i>p</i> > <i>F</i> 0.03
		Within	Sites	
Source Year Year × site	F 90.47 2.98	Num df 1 3	Den df 44 44	<i>p</i> > <i>F</i> 0.0001 0.04

*The *F* statistics for all four MANOVA test criteria were identical for all treatment combinations. Num df and Den df are numerator and denominator degrees of freedom, respectively.

change, which is supported by comparisons of woody debris at the natural flood site.

Litter accumulation is determined by the balance among four processes: in situ litter production, deposition of litter from outside the system, litter destruction, and removal of litter (Facelli & Pickett 1991). Flooding and moisture availability can influence all of these processes.

Three points suggest that moisture availability plays a key role in regulating both the amount and timing of leaf decomposition in this system. First, overwinter weight loss varied among years, with the greatest decomposition occurring during the wettest winter. Second, rapid weight loss coincided with flooding, with large changes in leaf weight between the April and June collections. Leaves at the experimental flood site lost 30–50% of their initial weight during flooding, while leaves at reference 1 lost 1–5% during the same period. Third, weight loss during flooding varied inversely with overwinter decomposition; the greatest weight loss occurred during flooding following the driest winter. This resulted in the greatest differences between sites that year.

Early summer flooding thus increases the breakdown of leaves and consequently the release of essential nutrients within the ecosystem at a time critical for plant growth, which may increase primary production. In sites that remain dry throughout the early growing season, and especially during years with low winter precipitation, nutrients remain bound in dry, dead leaf tissue. Without early summer flooding, most decomposition follows late-summer thunderstorms, thereby delaying nutrient release until after the peak of the growing season. Other studies have reported similar increases in leaf decomposition rates with flooding (Bell et al. 1978; Peterson & Rolfe 1982; Shure et al. 1986). This study shows that such benefits can be at least partially restored with artificial flooding.

Similar weight loss by leaves subjected to 1 month of flooding at the experimental flood site and those submerged for 2.5 months at the natural flood site suggests that most loss of mass during flooding was due to leaching. Leaves of deciduous trees may lose up to 30% of their weight during the first 24-48 hours after immersion (Cummins 1974; Webster & Benfield 1986; Bärlocher 1992). This leaching increases rates of decomposition (Peterson & Rolfe 1982; Day 1983; Shure et al. 1986), with mass loss beyond about 35% probably reflecting fungal and microbial respiration (Harmon et al. 1986). Although flood waters may carry nutrients leached from forestfloor litter out of the forest, vegetative demand for dissolved nutrients may greatly reduce nutrient loads of groundwater passing through riparian zones (Gregory et al. 1991). Whether a floodplain site acts as a source or sink for dissolved compounds may vary among nutrients and with other factors such as flooding cycle and vegetative cover (Junk et al. 1989). In chemical analyses associated with this study, more nitrogen entered the site in surface water than left, with over 85% consumed locally (Minckley 1997). This indicates high retention within the local system.

Wood decomposition is influenced by microbial and fungal activity (Harmon et al. 1986), which in turn are affected by temperature, moisture, and aeration (Rayner & Todd 1979; Marra & Edmonds 1994). Excessive moisture may decrease aeration essential to obligate aerobic fungi (Harmon & Hua 1991), suggesting that fungi may be relatively inactive during periods of inundation. Residual moisture retained in wetted logs may provide conditions favoring bacterial and fungal growth, and thus intermittent wetting of riparian soils combined with water draw-downs to increase aeration may enhance potential decomposition even more than extended periods of inundation. Forest-floor respiration increased dramatically during experimental flooding but was lower at the natural flood site, possibly reflecting a process of ecosystem reorganization as large accumulations of organic matter were broken down at the previously disconnected sites (Molles et al. 1998).

Silt deposition may bury surface litter, which may increase (Shure et al. 1986) or decrease (Chauvet 1988)

rates of leaf decay depending on environmental conditions such as aeration. Preliminary litter samples collected in September 1994 at the natural flood site revealed layers of leaves intermixed with sediment and an indistinct mineral-layer transition. Subsurface layering was less evident in 1995, indicating high decomposition rates of buried leaves. Experimentally measured silt deposition was greater at the natural flood site than at the experimental flood site (measured per unit area per day; unpublished data), suggesting that the import of sediment may have been a more widespread and significant factor during historic flooding. This sediment may represent a significant input of nutrients to the system (Junk et al. 1989). Canal water used for the experimental floods may not have carried sediment inputs equivalent to flood water directly from the river.

Physical transport of wood and leaf litter into or out of a site may be a minor factor in low-intensity backwater floods such as that simulated by our experimental flooding, but it may be more important during highintensity scouring floods that historically would have characterized areas immediately adjacent to the active river channel. Flow rates at the natural flood site during peak inundation in 1995 averaged only 9.6 cm per second, and wood was never seen being transported into or out of the area by floodwater. Leaves seen moving in water typically accumulated in clumps at the bases of shrubs and did not travel far. These observations suggest either that physical transport currently plays a minor role in this system or that it may be restricted to years of higher flows. Such scouring flows have been greatly diminished with river regulation.

The influence of flooding on litterfall patterns in riparian forests appears varied. Peterson and Rolfe (1982) found nearly identical rates of litter production in riparian and upland sites, while other studies report increased (Brinson et al. 1980; Gomez & Day 1982) or decreased (Bell et al. 1978; Shure & Gottschalk 1985) litter production for a wet riparian site compared to drier sites. Both rainfall and length of growing season influence litter production (Bray & Gorham 1964; Meentemeyer et al. 1982), and Greenway (1994) reported lower litterfall in a floodplain *Melaleuca* forest during a drought year than during a seasonally wet year.

We expected an initial decrease in leaf fall with the reintroduction of flooding, because trees unaccustomed to flooding would be faced with anoxic conditions for the first time. Because leaf fall at the experimental flood site declined over the first four seasons, however, we cannot determine if there was an initial negative response to flooding. We have observed a similar decline in litterfall over 8 years at three cottonwood forest sites in Albuquerque, which led us to conclude that those trees are senescing (Molles et al. 1998). This trend was reversed in the final year of this study. While leaf fall increased at all sites during the final season, the increase at the experimental flood site following four seasons of decline suggests a positive effect of repeated flooding. Leaf fall at the natural flood site was greater than at the experimental flood site during 1994-1995 but not during 1995–1996, also suggesting a greater relative increase at the experimental site. Since a large portion of the leaves that fall in a given litter season are preformed the previous year (Critchfield 1960), the initial response to flooding may have been delayed. Overall, our results suggest a positive influence of flooding on leaf fall, which provides a useful indicator of minimum levels of net primary productivity at a site (Bray & Gorham 1964). Unfortunately, a fire at the experimental flood site in 1996 prevented continued study and confirmation of any beneficial effects of flooding on litter production.

The managed floods used in this study differ from natural flooding in a number of ways. For example, canal water differed from river water in sediment load, as indicated by comparisons with the natural flood site. Our manipulated floods each lasted 1 month, compared to the 2.5-month inundation at the natural flood site in 1995. Although these differences may be reflected in differences among sites in woody debris and forestfloor litter storage, the most significant result-that flooding increases leaf and wood decomposition-was not affected by these differences. Given restrictions on access to water, this method provides a beneficial alternative to the complete lack of flooding. Water use could be decreased by pulsing floods, with an area inundated for several days and then allowed to dry for a week or more before re-flooding. In some areas, banks may be mechanically lowered to allow inundation directly from the river, or water might be diverted from stormwater runoff channels en route to the river.

Conclusions

The elimination of the annual flood pulse on the Rio Grande has significantly altered the structure and function of associated floodplain ecosystems (Molles et al. 1995; Crawford et al. 1996; Molles et al. 1998). Many changes to the riparian forest due to water management and other human impacts are irreversible, and complete restoration of either ecosystem structure or function are clearly impossible. The accumulation of organic debris resulting from regulation is important both in terms of nutrient cycling and for its role in promoting fire. We show that even limited, managed floods can increase rates of leaf and wood decomposition, suggesting an increase in nutrient cycling and thus at least partial restoration of ecosystem function. Although three seasons of experimental flooding were not enough to reduce the substantial quantity of organic litter present at the isolated site, the naturally flooded forest had significantly less wood and leaf litter on the forest floor, suggesting that repeated flooding may eventually reduce these accumulations. Thus, reestablishing the hydrological connection with the river via carefully regulated flooding will help to maintain currently established forests and prevent the complete loss of this ecosystem, which is essential for maintaining high regional biodiversity.

Acknowledgments

Many people have contributed to this study. N. Cox, F. Heinzelmann, and H. Kirchner provided invaluable technical assistance in the field and in the lab, and J. Thibault produced woody biomass measurements as part of the Research Experience for Undergraduates program funded by the National Science Foundation. The manuscript benefitted greatly from comments by J. H. Brown and two reviewers. J. Craig helped make the map, and E. Bedrick provided statistical advice. We thank P. Norton, J. Taylor, and the staff of Bosque del Apache National Wildlife Refuge for generous logistical support. Rainfall data were provided by the U.S. Fish and Wildlife Service and by the University of New Mexico Long Term Ecological Research group. The study was funded through Cooperative Agreement 14-16-0002–19–228 between the University of New Mexico and the U.S. Fish and Wildlife Service, and by a National Science Foundation Small Grant for Exploratory Research, DEB9414767.

LITERATURE CITED

- Bärlocher, F. 1992. Effects of drying and freezing autumn leaves on leaching and colonization by aquatic hyphomycetes. Freshwater Biology 28:1–7.
- Bayley, P. B. 1995. Understanding large river-floodplain ecosystems. BioScience 45:153–158.
- Bell, D. T., and S. K. Sipp. 1975. The litter stratum in a streamside forest ecosystem. Oikos 26:391–397.
- Bell, D. T., F. L. Johnson, and A. R. Gilmore. 1978. Dynamics of litter fall, decomposition, and incorporation in the streamside forest ecosystem. Oikos 30:76–82.
- Benke, A. C. 1990. A perspective on America's vanishing streams. Journal of the North American Benthological Society 9:77–88.
- Bray, J. R., and E. Gorham. 1964. Litter production in forests of the world. Advances in Ecological Research **2**:101–157.
- Brinson, M. M., H. D. Bradshaw, R. N. Holmes, and J. B. Elkins, Jr. 1980. Litterfall, streamflow, and throughfall nutrient fluxes in an alluvial swamp forest. Ecology 61:827–835.
- Brown, J. K. 1971. A planar intersect method for sampling fuel volume and surface area. Forest Science **17:**96–102.
- Brown, J. K. 1974. Handbook for inventorying downed woody material. General technical report INT-16. Intermountain Forest and Range Experiment Station, U.S. Forest Service, Ogden, Utah.

- Brown, J. K., and P. J. Roussopoulos. 1974. Eliminating biases in the planar intersect method for sampling small fuel volumes. Forest Science 20:350–356.
- Chauvet, E. 1988. Influence of environment on willow leaf litter decomposition in the alluvial corridor of the Garrone River. Archiv für Hydrobiologie **112:**371–386.
- Collier, M. P., R. H. Webb, and E. D. Andrews. 1997. Experimental flooding in Grand Canyon. Scientific American **276**:82–89.
- Crawford, C. S., A. C. Culley, R. Leutheuser, M. S. Sifuentes, L. H. White, and J. P. Wilber. 1993. Middle Rio Grande ecosystem: bosque biological management plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.
- Crawford, C. S., L. M. Ellis, and M. C. Molles, Jr. 1996. The Middle Rio Grande bosque: an endangered ecosystem. New Mexico Journal of Science **36**:276–299.
- Critchfield, W. B. 1960. Leaf dimorphism in *Populus trichocarpa*. American Journal of Botany **47**:699–711.
- Cummins, K. W. 1974. Structure and function of stream ecosystems. BioScience 24:631–641.
- Dahm, C. N., and D. I. Moore. 1994. The El Niño/Southern Oscillation phenomenon and the Sevilleta Long-Term Ecological Research site. Pages 12–30 in D. Greenland, editor. El Niño and Long-Term Ecological Research (LTER) sites. Publication no. 18. LTER Network Office, University of Washington, Seattle.
- Dahm, C. N., K. W. Cummins, H. M. Valett, and R. L. Coleman. 1995. An ecosystem view of the restoration of the Kissimmee River. Restoration Ecology 3:225–238.
- Day, F. P., 1983. Effects of flooding on leaf litter decomposition in microcosms. Oecologia 57:180–184.
- Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science **266**:753–762.
- Ellis, L. M., C. S. Crawford, and M. C. Molles, Jr. 1998. Comparison of litter dynamics in native and exotic riparian vegetation along the Middle Rio Grande of central New Mexico, U.S.A. Journal of Arid Environments **38**:283–296.
- Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. The Botanical Review **57**:1–32.
- Fenner, P. W., W. Brady, and D. R. Patton. 1985. Effects of regulated water flows on regeneration of Fremont cottonwood. Journal of Range Management 38:135–138.
- Gomez, M. M., and F. P. Day, Jr. 1982. Litter nutrient content and production in the Great Dismal Swamp. American Journal of Botany **69:**1314–1321.
- Greenway, M. 1994. Litter accumulation in a *Melaleuca quinque nervia* (Cav.) S. T. Blake wetland in south-eastern Queensland. Australian Journal of Freshwater Research **45**:1509–1519.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–551.
- Harmon, M. E., and C. Hua. 1991. Coarse woody debris dynamics in two old-growth ecosystems. BioScience **41:**604–610.
- Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15**: 133–302.
- Howe, W. H., and F. L. Knopf. 1991. On the imminent decline of the Rio Grande cottonwoods in central New Mexico. Southwestern Naturalist **36**:218–224.
- Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publication in Fisheries and Aquatic Sciences 106:110–127.
- Koebel, J. W., Jr. 1995. An historical perspective on the Kissimmee River Restoration Project. Restoration Ecology 3:149–159.
- Marra, J. L., and R. L. Edmonds. 1994. Coarse woody debris and

forest floor respiration in an old-growth coniferous forest on the Olympic Peninsula, Washington, U.S.A. Canadian Journal of Forest Research **24:**1811–1817.

- Meentemeyer, V., E. O. Box, and R. Thompson. 1982. World patterns and amount of terrestrial plant litter production. Bio-Science **32**:125–128.
- Michener, W. K., and R. A. Haeuber. 1998. Flooding: natural and managed disturbances. BioScience **48:**677–680.
- Minckley, W. L., editor. 1997. Aquatic Ecosystems Symposium: a report to the Western Water Policy Review Advisory Commission. Arizona State University, Tempe.
- Molles, M. C., Jr., C. S. Crawford, and L. M. Ellis. 1995. The effects of an experimental flood on litter dynamics in the Middle Rio Grande riparian ecosystem. Regulated Rivers: Research and Management 11:275–281.
- Molles, M. C., Jr., C. S. Crawford, L. M. Ellis, H. M. Valett, and C. N. Dahm. 1998. Managed floods: restoration of riparian forest ecosystem structure and function along the Middle Rio Grande. BioScience 48:749–756.
- National Resource Council. 1992. Restoration of aquatic ecosystems. National Academy Press, Washington, D.C.
- Nicholls, N. 1988. El Niño-Southern Oscillation and rainfall variability. Journal of Climate 1:418–421.
- Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology **44**:322–331.
- Peterson, D. L., and G. L. Rolfe. 1982. Nutrient dynamics and decomposition of litterfall in floodplain and upland forests of central Illinois. Forest Science 28:667–681.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47:769–784.
- Rayner, A. D. M., and N. K. Todd. 1979. Population and community structure and dynamics of fungi in decaying wood. Advances in Botanical Research 7:333–420.
- Reily, P. W., and W. C. Johnson. 1982. The effects of altered hydrologic regime on tree growth along the Missouri River in North Dakota. Canadian Journal of Botany 60:2410–2423.
- Rood, S. B., and S. Hinze-Milne. 1989. Abrupt downstream forest decline following river damming in southern Alberta. Canadian Journal of Botany 67:1744–1749.
- Rood, S. B., and J. M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. Environmental Management 14:451–464.
- SAS Institute, Inc. 1989. SAS/STAT user's guide, vols. 1 & 2. Version 6. Fourth edition. Cary, North Carolina.
- Shure, D. J., and M. R. Gottschalk. 1985. Litter-fall patterns within a floodplain forest. American Midland Naturalist **114**:98–111.
- Shure, D. J., M. R. Gottschalk, and K. A. Parsons. 1986. Litter decomposition processes in a floodplain forest. American Midland Naturalist 115:314–327.
- Slack, J. R., A. M. Lumb, and J. M. Landwehr. 1993. Hydro-Climatic Data Network streamflow data set, 1874–1988. Water-resources investigations report 93–4076. U.S. Geological Survey, Reston, Virginia.
- Sparks, R. E., P. B. Bayley, S. L. Kohler, and L. L. Osborne. 1990. Disturbance and recovery of large floodplain rivers. Environmental Management 14:699–709.
- Stromberg, J. C., and D. T. Patton. 1991. Instream flow requirements for cottonwoods at Bishop Creek, Inyo County, California. Rivers 2:1–11.
- Stuever, M. 1997. Fire induced mortality of Rio Grande Cottonwood. Master's thesis. University of New Mexico, Albuquerque.
- U.S. Army Corps of Engineers. 1958. Rio Grande and tributaries, New Mexico: review survey for flood control. Interim report

on main stem of the Rio Grande above Elephant Butte Dam. Serial no. 48. U.S. Army Engineer District, Albuquerque, New Mexico.

Van Wagner, C. E. 1968. The line intersect method in forest fuel sampling. Forest Science **14**:20–26.

von Ende, C. N. 1993. Repeated measures analysis: growth and

other time-dependent measures. Pages 113–137 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman & Hall, New York.

Webster, J. R., and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17:567–594.

Appendix 1. Average densities (g/cm^3) of coarse woody debris of cottonwood, saltcedar, and seepwillow used to estimate biomass in three decomposition classes.*

	Decomposition Class		
Species	1	2	3
cottonwood saltcedar seepwillow unidentified	0.522 0.604 0.529 0.557	0.515 0.557 0.519 0.529	0.306 0.423 0.455 0.386

*Mean values were used for samples for which species could not be determined. See text for definition of decomposition classes.

Appendix 2. Density values (g/cm^3) used in biomass calculations for fine woody debris.

Size Class (diameter, cm)	Density
0.0–0.5 0.51–1.0 1.01–2.0	0.485 0.532 0.506