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FLOOD FLOWS, LEAF BREAKDOWN, AND PLANT-AVAILABLE NITROGEN ON A DRYLAND RIVER FLOODPLAIN

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Abstract: We tested the hypothesis that decomposition in flood-inundated patches of riparian tree leaf litter results in higher plant-available nitrogen in underlying, nutrient-poor alluvium. We used leafpacks ($n = 56$) containing cottonwood (*Populus deltoides* ssp. *wislizenii*) leaf litter to mimic natural accumulations of leaves in an experiment conducted on the Yampa River floodplain in semi-arid northwestern Colorado, USA. One-half of the leafpacks were set on the sandy alluvial surface, and one-half were buried 5 cm below the surface. The presence of NO_3^- and NH_4^+ presumed to result from a leafpack's submergence during the predictable spring flood pulse was assessed using an ion-exchange resin bag (IER) placed beneath each leafpack and at control locations. Leafpacks and IERs were collected one week after flood peak (71 days total exposure) at half the stations; the remainder were collected three weeks later (93 days exposure). A multi-peaked spring flood with above-average maximum discharge inundated leafpacks for total time periods ranging from 133 to 577 hours. Litter lost from 43 to 68 percent of its initial organic matter (OM) content. Organic matter loss increased with total time inundated and total time of exposure on the floodplain. Burial retarded OM loss if the total time inundated was relatively long, and substrate texture (sand vs. silt) affected OM loss in a complex manner through interactions with total time inundated and total time of exposure. No pulse of N attributable to leaf breakdown was detected in the IERs, and leafpack litter showed no net change in the mass of nitrogen present. Patterns of leafpack and IER nitrogen levels suggested that litter removed N from floodwater and thereby reduced N availability in underlying sediment. Immobilization of floodwater-N by litter and N mineralization outside the flood period may be important components of N flux in semi-arid and arid floodplain environments.

Key Words: decomposition, floodplain, flood regime, nitrogen cycling, *Populus deltoides wislizenii*, riparian

INTRODUCTION

Patterns of nitrogen flux in the floodplains of rivers in semi-arid and arid regions are poorly understood (Fisher 1995, Schade et al. 2002). For example, the fresh deposits of sand and silt that contribute to floodplain formation along these rivers are commonly low in nitrogen (Puhakka et al. 1992, Godoy et al. 1999), and riparian plants colonizing them have been shown to be nitrogen-limited (Adair and Binkley 2002). Although nitrogen accumulation has been documented in dryland floodplain soils (Adair 2001), the sources and processes involved remain speculative. Nitrogen must be imported into floodplains lacking nitrogen-fixing plants, but the proportion of plant nitrogen that is recycled will also influence N accumulation. Flooding could be a factor in both these processes, by transporting N in floodwater onto the floodplain and by promoting decomposition and N mineralization (Lockaby et al. 1996, Xiong and Nilsson 1997, Andersen and Nelson 2003). Nitrogen mineralization associated with flood events could be especially important in dryland environments, where plant litter decomposition is controlled largely by moisture and temperature regimes (Couteaux et al. 1995). Whereas uptake of floodwater-N would benefit plants already established in nitrogen-poor substrates, germinants appearing after a flood event would have to rely on other sources of nitrogen. Litter-derived nitrogen would be available

even to species requiring bare substrate (e.g., Scott et al. 1996) through lateral transport of N during post-flood precipitation events or shallow ground-water movement, or through root extension into litter-covered zones.

Flood attributes (e.g., flood timing, magnitude, and duration) and conditions outside the flood season will interact to influence floodplain N mineralization patterns. For example, the seasonal timing of a flood event will determine how long litter is exposed to the terrestrial environment. Such exposure changes litter quality; the proportion, and in some cases the absolute amount, of N in leaf litter has been documented to increase during early phases of decomposition in both terrestrial and aquatic environments (Swift et al. 1979: 126, Webster and Benfield 1986). This change in litter quality, sometimes referred to as "conditioning," is associated with immobilization of N by microbial decomposers colonizing the litter (Baldy et al. 1995, Hobbie and Vitousek 2000). The decompositional state of floodplain litter when first inundated will thus interact with flood duration in determining the extent of N mineralization. Also, floods can bury leaf litter under sediment and thereby modify decomposition processes (Herbst 1980, Metzler and Smock 1990, Boulton and Foster 1998).

As part of a study to elucidate nitrogen dynamics on semi-arid river floodplains, we hypothesized that the spring inundation of the previous autumn's leaf litter can create a pulse of plant-available nitrogen [ammonium (NH_4^+) and nitrate (NO_3^-)] in underlying sediment. We predicted that the amount of NH_4^+ and NO_3^- (as measured by ion exchange resin bags) entering sediment under leaf litter will be positively related to both the length of inundation and the level of leaf breakdown as measured by organic matter (OM) loss. We assumed that the moisture retained in sediments following flood recession promotes additional mineralization and predicted that the total amount of plant-available nitrogen generated would be less immediately after flood recession than three weeks later, by which time growth of new seedlings is normally underway. Because sediment texture affects post-flood moisture retention, we also predicted that the additional mineralization and OM loss would be greater where sediment was fine (silt or clay) relative to where it was coarse (sand). We tested each of these predictions concerning N availability using both buried leaf litter and litter lying on the ground surface. An alternative hypothesis, that the previous autumn's leaf litter cannot furnish a pulse of plant-available N because conditioning is still underway, would be supported if we found evidence of leaf breakdown (OM loss), but no associated pulse of plant-available N and little or no loss of N from leaf litter.

STUDY AREA AND METHODS

We worked on the floodplain of the Yampa River at Deerlodge Park within Dinosaur National Monument in northwestern Colorado, USA. This river is free-flowing and, at Deerlodge Park, is a sixth-order stream with a mean annual discharge of 55 $m^3 s^{-1}$ and a large snowmelt-driven spring flood pulse (mean peak flow ≈ 350 $m^3 s^{-1}$; Cooper et al. 1999). The regional climate is semi-arid; long-term mean annual precipitation at Maybell, 20 km east of Deerlodge Park, is 28 cm. The floodplain supports an open gallery forest of Fremont cottonwood (*Populus deltoides* Marshall subsp. *wislizenii* (Watson) Eckenwalder; nomenclature follows Weber and Whittman 1996), with a well-developed herbaceous layer under the mature trees. The channel margin is irregularly bordered by dense stands of cottonwood saplings that contain few understory plants.

The study was conducted on the margin of the active channel at a site (Figure 1) where the bed has been stable or aggrading since 1997 (mean elevation increase <2 cm/yr, D. C. Andersen, unpublished data). The site is inundated during most spring floods but otherwise dry. Surface sediments are typically sand or, less commonly, silt, and microtopographic variation produces natural accumulations of cottonwood leaf litter following autumn leaf drop. Vegetation on the site was sparse. Adair (2001) reported a total nitrogen level of 0.3 mg g^{-1} or 0.03% in the upper 20 cm of freshly deposited sandy sediment along the reach, a very low value for temperate-region mineral surface soils (Post et al. 1985).

Fresh Fremont cottonwood leaf litter was collected from the ground beneath mature trees in Deerlodge Park in autumn 1999, dried (50°C), and then stored at room temperature in opaque plastic bags. Leafpacks were constructed in March 2000 by placing ~7 g of oven-dried (60°C) leaves (15–25 leaves) into ~15 × 15 cm envelopes made of polypropylene netting (~1-cm mesh). The prepared leafpacks were stored in air-tight plastic bags until installed on 28 March 2000, prior to the spring 2000 flood. With a few exceptions described below, one leafpack was placed at each of 56 stations set out at 4-m intervals along three lines oriented roughly parallel to flow. Lines were separated by at least 4 m. Each leafpack was installed ~20-cm downstream from a galvanized wire stake marking the station. Installation positions alternated along each line between (1) on the ground surface and (2) buried under 5 cm of fine sediment. To increase sample size and test for the presence of decimeter-scale spatial variation in processes, we placed a second leafpack at four stations, displaced ~40 cm toward the upland (perpendicular to flow) from the first leafpack. Surface

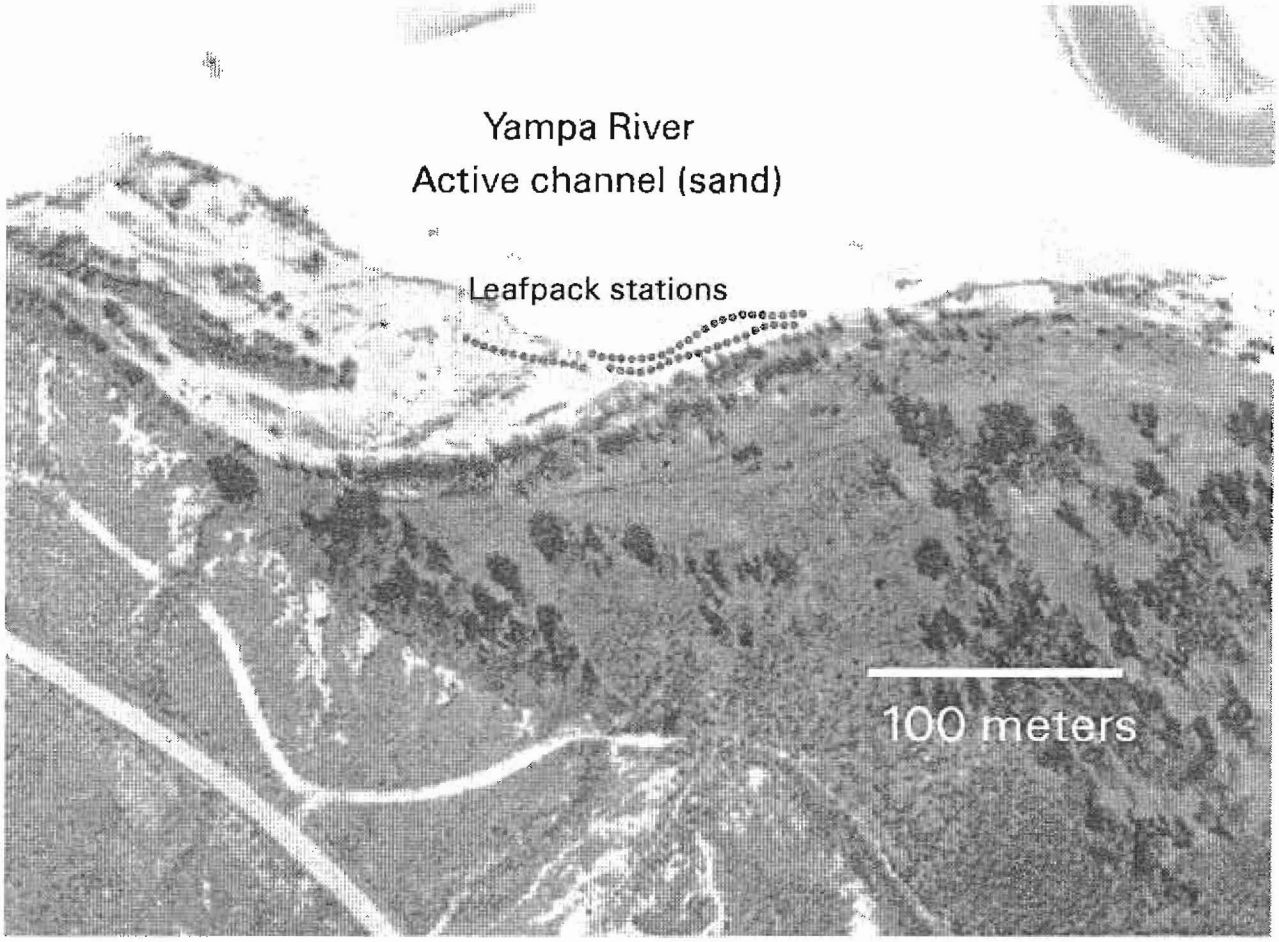

Figure 1. Rectified September 1994 aerial photograph showing the locations of the 56 leafpack stations (rows of dots just above center of image) established in 2000 on the margin of the Yampa River active channel at Deerlodge Park, Dinosaur National Monument, Colorado, USA. North is to the top of the image. The river, at low discharge, is visible in the upper right; flow is from right to left. The ribbons of young Fremont cottonwoods immediately south and downstream of the leafpack stations are inundated in most years, whereas the large, widely spaced cottonwoods (center right portion of image) are seldom inundated. A triangular section of upland containing a paved road and serpentine firebreak fills the lower left corner of the image. The variation in channel surface texture apparent in the image at the locations of the leafpack lines had disappeared by the time the study began.

leafpacks were staked down with galvanized wire pins; buried leafpacks were not staked.

We used ion-exchange resin bags (IER) to assess the relative amount of plant-available nitrogen (NH_4^+-N and NO_3^--N) entering alluvium under leafpack litter and at control locations. Each IER was constructed by placing 14 mL of anion exchange resin (with 4.2 $mmol_c$ bag^{-1}; Sybron IONAC ASB-IPOH, Sybron International, Milwaukee, WI) into the toe of a nylon stocking, sealing the end with a hot glue gun, then repeating the procedure with 14 mL of cation exchange resin (4.9 $mmol_c$ bag^{-1}, Sybron IONAC c-251 H^+) and trimming the excess stocking. The resulting 2-pouch bag was about 5 × 10 cm. One IER (hereafter, "leafpack-IER") was buried under each leafpack in a manner that ensured full contact between the IER and surrounding alluvium and resulted in ~0.5 cm of alluvium separating the upper surface of the IER from the leafpack bottom.

Two types of control IERs were installed. To assess effects from floodwater alone, IERs without an overlying leafpack ("leafless-IER") were placed on the surface (n = 2) or buried (n = 4) ~40 cm upstream from a corresponding leafpack-IER at three stations. To assess effects of time alone, five IERs were double-bagged in airtight plastic bags and buried at the site to experience similar thermal dynamics but no exposure to floodwater ("dry-IER").

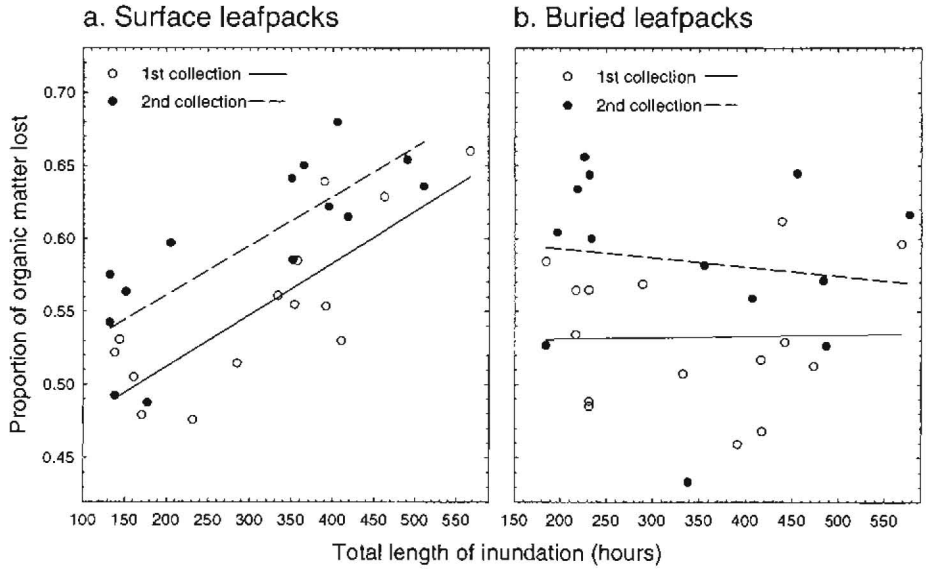

Figure 2. Relationship of the duration of submergence in floodwater (T_U) to the proportion of organic matter lost by leafpacks placed (a) on the surface or (b) buried under 5 cm of sediment in the channel of the Yampa River. Note that the graphs have the same axis scaling. Leafpacks from the 2nd collection were in place three weeks longer than those from the 1st collection. Both regressions are significant ($P < 0.05$) for the surface leafpacks, whereas neither was significant for the buried leafpacks.

The surface elevation of the river during the study period (river stage, E_R) was estimated from a stage-discharge relationship constructed from 37 stage measurements made at the study site during 1993–95. We verified the relationship's validity for the study period by determining water surface elevation five times during the experiment. We estimated discharge at the study site by summing instantaneous discharge values measured at 30-minute intervals at USGS gauges on the Yampa (Gauge 9251000; ~20 km upstream from the study site) and on the only pertinent tributary, the Little Snake River (Gauge 9260000; confluence ~10 km upstream from the study site).

The surface elevation at each station was determined by survey using an electronic total station (Sokkia® Set 3100). We estimated the total length of time each leafpack was inundated (T_U) by comparing the elevation of the leafpack (E_{LP}, = station elevation or 5 cm lower, depending on placement position) with the river stage. We tallied the number of the instantaneous stage values for which $E_R > E_{LP}$ to estimate T_U at 0.5 hr intervals during the period of exposure. We also created a categorical variable (LI) to differentiate among lengths of inundation periods. Stations were classified into LI = Short ($T_U < 200$ h), Medium ($200 \leq T_U \leq 400$), or Long ($T_U > 400$ h) inundation periods.

The stations were divided into two groups of approximately equal size based on surface elevation and leafpack position (surface or buried). Leafpacks and IERs associated with one group were retrieved immediately following the flood (Time 1: 7 June), and the others were retrieved 3-wk later (Time 2: 29–30 June) (Figure 2). At the time of collection, the minimum and maximum depths of sediment overlying each leafpack were measured and sediment texture (sand or silt) noted. We also classified the relative amount of flood-deposited surface litter present at each station as "light," "moderate," or "heavy." The dry-IER controls were collected at Time 2.

Collected leafpacks were immediately put into airtight plastic bags, placed on ice, and returned to the laboratory, where they were kept frozen until processed. Processing consisted of carefully rinsing the leaves with tapwater over a 600-micron-mesh screen and then placing the leaves in a water bath, where they were individually examined under 10-power magnification. All invertebrates associated with a leafpack were collected. Leaves were gently rubbed to remove sediment not dislodged during rinsing. The clean leaf material was dried at 60 °C, weighed, and analyzed for organic matter (OM) and nitrogen content. Organic matter content was assumed equal to ash-free oven-dry mass (AFDM), with ash content determined as loss on ignition at 450°C. Litter N was calculated as the sum of Total Kjeldahl Nitrogen (TKN) and NO_3^--N. Concentrations were determined by Perstorp autoanalyzer following H_2SO_4 digestion (with a catalyst) for TKN or after extraction with 2M KCl solution for NO_3^--N. Initial N and OM content of the cottonwood leaf litter placed on the floodplain were determined

using leaves from three leafpacks prepared as above but not placed in the field.

Collected IERs were placed in plastic bags and maintained in a cool environment until extracted with 100 mL of 2*M* KCl. The extractant was analyzed colorimetrically for NH_4^+-N and NO_3^--N on an Alpkem continuous flow autoanalyzer.

Rainfall and air temperature (~2 m height) data for the study period were collected at a station on the Deerlodge Park floodplain ~1.5 km upstream from the study site. Stream chemistry data collected by USGS (Crowfoot et al. 2001) at Deerlodge Park from March to August 2000 were used to portray N concentrations found in the Yampa River during the time that leafpacks were exposed to river water.

We used *t*-tests to compare nitrogen levels between control groups and between IERs at particular stations. We used analysis of variance (ANOVA) to test whether leafpack IER-N was affected by leafpack position (P, surface or buried), or time of collection (T, 1st or 2nd collection). We also used ANOVA to test whether these same factors influenced leaf decomposition rate (proportion of initial leafpack OM lost) and whether flood-deposited surface litter affected IER-N. Linear regression analyses were used to relate level of leaf decomposition and IER-N to total time inundated (T_U). Analyses involving proportions were performed after arcsine-square root transformation of the data. Means, calculated using untransformed data, are presented as $\bar{x} \pm$ SE (n). All statistical analyses were performed using SYSTAT® 10 software.

RESULTS

The spring 2000 flood pulse featured multiple peaks at Deerlodge Park, with the final and highest peak reached on 31 May. The maximum instantaneous discharge, 409 $m^3 s^{-1}$, was 17% greater than the long-term average. All stations had dry surface soil at the time of the first collection. Based on pre-flood surface elevations and our stage-discharge relationship, the total time a leafpack was inundated (T_U) ranged from 133 to 577 h. Inundation was not necessarily continuous; the elapsed time between first submergence and last emergence of the lowest leafpack was ~860 h. Leafpacks were exposed to 4.8 cm of precipitation during April and 1.8 cm in May. June was very dry (total rainfall < 0.5 cm) and warm (mean daily maximum air temperature = 28.7°C). Concentrations of NH_4^+ in river water were all reported as < 0.02 mg/L, whereas NO_3^- concentrations [equivalent to NO_2^- plus NO_3^- in Crowfoot et al. (2001) because NO_2^- was always below detection limits] ranged from <0.05 to 0.32 mg/L ($\bar{x}$ = 0.15 mg/L, n = 4). The average net change in station elevation due to the flood was small [mean 1.9 ± 0.47 cm (n = 56); range −5 to +14 cm]. Two leafpacks and associated IERs disappeared, presumably because of flood-induced transport downstream. Three additional leafpack-IERs disappeared, but the associated leafpack remained in place or, in one case, was recovered ~20 m downstream from its original location. One leafless-IER control disappeared. All other leafpacks and their associated IERs were considered to have remained in place during the flood. Flood-borne debris accumulated on 57% of the stations.

Cottonwood Leaf Decomposition

The Fremont cottonwood leaves placed on the floodplain had initial total N and OM contents of 0.52 ± 0.02% (AFDM basis) and 87.1 ± 0.17%, respectively. No invertebrates were found in leafpacks collected from the floodplain. Leafpack litter lost from 43 to 68% of its OM during the experiment. The mean proportions lost were 0.55 ± 0.015 (n = 14) and 0.53 ± 0.012 (n = 15) for the surface and buried leafpacks in the first collection, and 0.60 ± 0.016 (n = 14) and 0.58 ± 0.017 (n = 13) for the surface and buried leafpacks in the second collection, respectively. Results of ANOVA performed on the transformed proportions and time of collection, substrate texture, leafpack position, and length of inundation indicated a significant model effect (Table 1). Post-hoc Bonferroni tests indicated OM loss was significantly ($P < 0.05$) affected by time of collection, as well as by a 3-way interaction (time of collection × substrate × length of inundation) (Table 1). Linear regression analyses indicated that the total time inundated (T_U) had equivalent positive effects on OM loss in surface leafpacks from the 1st and 2nd collections (i.e., slopes were parallel; Figure 2a) and that greatest losses occurred in the 2nd collection leafpacks. In contrast, OM loss was unaffected by T_U in buried leafpacks (Figure 2b). The nature of the interaction between total time inundated and position suggested in the ANOVA (Table 1) was clarified in a second ANOVA testing for a position effect, but in which T_U was incorporated as a covariate. Results indicated that OM loss was significantly lower in buried leafpacks when only leafpacks inundated longest (LI = "Long") were considered ($F_{1,1,20}$ = 16.18, P = 0.001) and marginally significant when all leafpacks were considered ($F_{1,1,53}$ = 3.78, P = 0.057). The covariate was significant ($P < 0.05$) in both tests. There were significant differences in decomposition between 1st and 2nd collection leafpacks at stations either both topographically low (high T_U) and sandy (Separate Variance t = −4.81, df = 5.6, P = 0.004) or at an intermediate elevation and silty (Separate Variance t = −5.59, df = 7.4, P = 0.001). Leaf N concentration

Table 1. Results of ANOVA (first two rows) and Bonferroni post-hoc tests for effects of categorical dependent variables Initial Position (buried or surface), Time of Collection (1st or 2nd), Substrate Texture (sand or silt), and Length of Inundation (short, medium, or long) on the proportion of OM lost by leafpack cottonwood leaves (transformed data, N = 56). Only interaction terms having $P < 0.10$ are listed. ANOVA multiple R = 0.81; multiple $R^2 = 0.65$.

Source or Name of Effect	Sum-of-Squares	df	Mean-Square	F-Ratio	P
Model	0.136	22	0.006	2.84	0.003
Error	0.072	33	0.002		
Initial position (P)	0.001	1	0.001	0.471	0.497
Time of collection (T)	0.010	1	0.010	4.747	0.037
Substrate (S)	0.007	1	0.007	3.043	0.090
Length of Inundation (LI)	0.005	2	0.003	1.193	0.316
P × LI	0.012	2	0.006	2.652	0.085
T × S × LI	0.029	2	0.014	6.666	0.004

increased as OM content decreased, regardless of leafpack position (Figure 3).

Control and Leafpack IER-Nitrogen Comparisons

The mean IER-NO_3^- and IER-NH_4^+ concentrations in the dry-IER controls (never exposed to floodwaters) were 0.69 and 0.45 mg L^{-1}, respectively (Table 2). Total N concentration did not differ between leafless-IER controls placed in surface and buried positions ($t = -0.28$, $df = 3$, $P = 0.80$), and the mean concentration for the pooled group, 9.54 mg L^{-1}, was significantly higher than the mean for dry-IER controls (Separate Variance $t = -8.21$, $df = 4.2$, $P = 0.001$). Because concentrations of IER-NO_3^- were one to three orders of magnitude higher than IER-NH_4^+ concentrations in all groups other than the dry controls (Table 2), we hereafter focus on IER-NO_3^- in within-station comparisons.

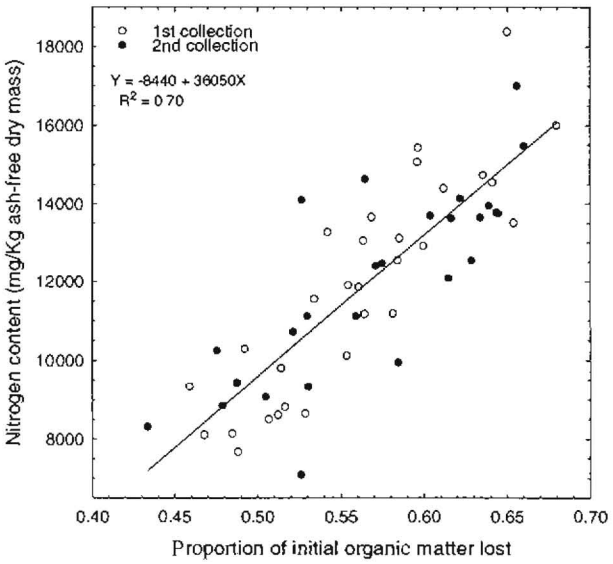

Figure 3. Relationship between nitrogen content of the remaining organic matter and the proportion of organic matter lost by Fremont cottonwood leaf litter inundated on the Yampa River floodplain during the spring 2000 flood pulse. The linear regression is for the two collections pooled.

Only one of the two "buried leafpack" stations where both leafless- and leapack-IERs were duplicated showed a significant effect from the presence of litter, but the result—a lower IER-NO_3^- level where litter was present ($t = -23.1$; df = 2; $P = 0.002$)—was contrary to our prediction. The single "surface" station containing two leafpack-IERs also had a lower mean IER-NO_3^- value for leafpack-IERs [0.055 ± 0.021 ($n = 2$) mg L^{-1}] than for the single leafless-IER present (9.87 mg L^{-1}). Because the values of T_U for the three stations were similar (buried leafpack stations: 217 and 231 h; surface leafpack station: 161 h), we also compared leafless controls and leafpack-IERs using pooled data. The reduction in IER-NO_3^- level under litter remained significant: the mean IER-NO_3^- level for the six IERs under litter was less than the mean for the five leafless-IER controls ($t = 4.631$; $df = 9$; $P = 0.001$).

Factors Affecting IER-N Levels Under Leafpacks

Total nitrogen in leafpack-IERs (IER-NO_3^- plus IER-NH_4^+) decreased as the total time a leafpack was inundated increased (linear regression on pooled treatment groups; $n = 51$, $P = 0.05$). This relationship led us to include T_U as a covariate in the ANOVA to test for effects of leafpack position and time of collection (both independent of T_U) on total IER-N. Only position had a significant effect (Table 3). This result reflects the trend in both 1st and 2nd collections for highest IER-NO_3^- levels to be associated with buried leafpacks (Table 2). There was no correlation between a station's leafpack IER-NO_3^- and IER-NH_4^+ levels at either collection period (Pearson correlation coefficient probabilities, 1st: $P = 0.97$; 2nd: $P = 0.68$), nor was there a discernable relationship between flood-borne debris accumulation and IER-N values.

Table 2. Mean levels of NO_3^-, NH_4^+, and total inorganic N (mg L^{-1}, with standard error in parentheses) in extracts from ion exchange resin bags (IERs) placed in shallow alluvium and exposed or unexposed to floodwaters during the 2000 spring flood pulse on the Yampa River. Leafless control IERs were simply placed in alluvium, whereas leafpack IERs had an overlying leafpack containing cottonwood leaf litter. Leafpacks were placed either on the floodplain surface or buried under 5 cm of alluvium. See text for details.

Treatment	Leafpack or IER Position	Collection Period	n	NO_3^-	NH_4^+	Total Inorganic N
Dry control (unexposed to floodwater)	Buried	2	5	0.69 (0.11)	0.45 (0.08)	1.14 (0.17)
Leafless control (no overlying leafpack)	Buried	1	4	9.47 (1.35)	0.07 (0.04)	9.54 (1.31)
Leafless control (no overlying leafpack)	Surface	1	1	9.87	0.03	9.90
Leafpack present	Buried	1	14	5.54 (2.16)	0.002 (0.002)	5.55 (2.16)
Leafpack present	Surface	1	11	1.79 (1.12)	0.16 (0.15)	1.95 (1.16)
Leafpack present	Buried	2	13	3.76 (1.44)	0.05 (0.02)	3.91 (1.44)
Leafpack present	Surface	2	13	2.53 (1.02)	0.08 (0.02)	2.60 (1.01)

Leafpack Nitrogen Budget

The mean mass of N in the leaves within a leafpack at installation (0.032 ± 0.0001 g) was not significantly different from the mean mass in those leaves at the end of the experiment (0.031 ± 0.0006 g; paired $t = -1.045$, $df = 47$, $P = 0.301$). Thus, despite an average loss of 56% of organic matter from a leafpack, there was no net loss of nitrogen. The proportion of initial leaf N remaining increased with OM loss (Figure 4; linear regression, $P = 0.01$), with 23 of 48 leafpacks showing absolute gains in N during the study.

DISCUSSION

Resin bags (IERs) sequester NH_4^+ and NO_3^- from the solutions to which the bags are exposed, in this case floodwaters or precipitation. The inorganic N concentration measured in the Yampa River during the 2000 flood is within the range reported for rivers moderately impacted by human activity (Allan 1995:290). We assume that observed increases in resin bag N concentrations were due primarily to exposure to floodwaters and that only minimal N was obtained from the few, small rainstorms that occurred in April, prior to floodwaters rising to the level of IERs. Support for this assumption comes from the fact that NH_4^+ and NO_3^- concentrations in rainwater had median values of 0.29 mg/L and 1.24 mg/L, respectively, at the nearest monitored locality, Douglas Pass, a 2710-m elevation site 150 km south of Deerlodge Park (Ranalli 1997). Although these values are higher than concentrations in Yampa floodwaters, the ~5 cm of April precipitation would have exposed a 5 x 10 cm resin bag to = 0.25 L of percolating rainwater. The sheltering effect of an overlying leafpack and alluvium would have further reduced that amount. In contrast, inundation exposed each resin bag to a vastly larger volume of moving, relatively N-rich floodwater.

Table 3. Results of ANOVA testing for effects of leafpack initial position (lying on the surface or buried in alluvium) and time of collection (1st or 2nd collection date) on leafpack IER-N. The latter is calculated as the sum of leafpack IER-NO_3^- and IER-NH_4^+ concentrations.

Source	Sum-of-Squares	df	Mean-Square	F-Ratio	P
Initial position (P)	172.8	1	172.8	6.32	0.015
Time of collection (T)	7.1	1	7.1	0.26	0.61
P × T	11.9	1	11.9	0.44	0.51
Covariate (T_0)	220.6	1	220.6	8.1	0.007
Error	1257.0	46	27.3		

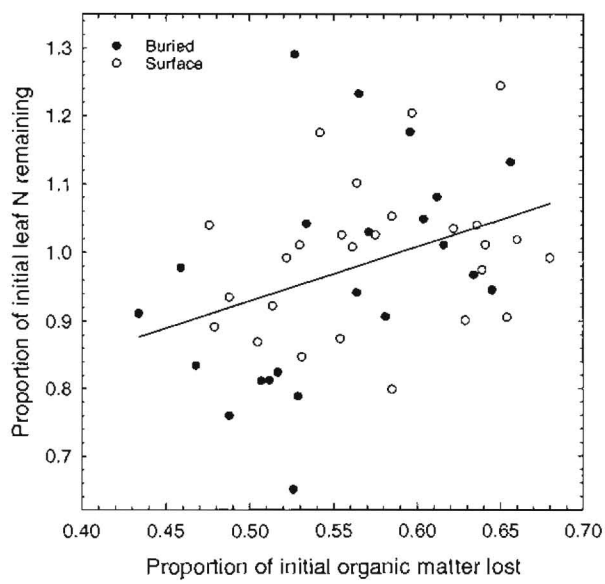

Figure 4. Relationship between the change in nitrogen content and the proportion of initial organic matter lost by Fremont cottonwood leaf litter inundated on the Yampa River floodplain during the spring 2000 flood pulse. Note that litter in both buried and surface leafpacks in some cases gained nitrogen. The linear regression is for the two groups pooled.

One week after the flood peak and ~2 months after installation, the concentration of plant-available N was higher in leafless- than in dry-IER controls, indicating that the IERs exposed to floodwater but lacking an overlying leafpack had acquired nitrogen while inundated. Contrary to our prediction, however, the nitrogen level in leafless-IER controls was also greater than that in leafpack-IERs inundated for the same length of time (Table 2). This result suggests that the presence of a leafpack reduced the amount of nitrogen reaching the underlying IER, either by removing nitrogen from the water, restricting flow over the resin bag, or both. Two lines of evidence point to immobilization of floodwater-N by decomposing litter as the mechanism involved. First, decomposition was lower in buried leafpacks than in surface leafpacks, whereas concentrations of IER-N were highest in buried leafpack-IERs. Buried leafpacks underwent less decomposition, sequestered less floodwater N, and thus made more floodwater N available to adsorb onto the resins. Second, leafpack leaves lost on average 56% of the organic matter originally present but showed no net loss of nitrogen. In fact, most leafpacks losing above-average amounts of OM actually gained N (Figure 4).

Our contention that leafpack litter removed nitrogen from floodwaters is supported by experiments demonstrating that leaf litter in a stream can reduce the nitrogen available for other heterotrophic microbial stream processes (Tank and Webster 1998). Similarly, Koechy and Wilson (1997) found IER-N levels lower for IERs with overlying litter than for those without it in a terrestrial setting. They concluded that the litter had immobilized mineral N deposited from the atmosphere. An increase in litter nitrogen concentration (Figure 3) is common during the early stages of leaf decomposition (Gurtz and Tate 1988, Mulholland 1992, Gessner and Chauvet 1994, Glazebrook and Robertson 1999, Simons and Seastedt 1999). We found no evidence of invertebrate activity in the leafpacks, corroborating Andersen and Nelson's (2003) conclusion that processing of cottonwood leaf litter on the Deerlodge Park floodplain is primarily by microbes. Based on analysis of Fremont cottonwood leaves exposed during several flood seasons at multiple sites, these authors suggested that litter N concentration started to decrease only when >60% of litter OM had been lost.

We found no effect from time of collection on leafpack IER-N concentrations. This result would be expected if the alluvium lacked sufficient interstitial water for transfer of mineralized N from litter to leafpack-IERs or if mineralization was not yet occurring in leafpacks (our alternative hypothesis). Warm, dry weather prevailed between the first and second collections, and leafpack OM loss continued only in particular environments: low, sandy sites and silty sites at intermediate elevation. River stage, which controls groundwater level on the Deerlodge floodplain (Cooper et al. 1999), fell rapidly after the flood peak, but the high soil moisture levels favoring decomposition would have been maintained longest at stations in low topographic positions and with fine textured soils. During the flood period, and perhaps through the period between collections, nitrogen lost from leafpacks in association with OM loss may have been in organic forms (e.g., microbes, their enzymes, or leaf compounds) unavailable to either plants or IERs.

Burial has been shown to reduce decomposition rates in some studies (Herbst 1980, Rounick and Winterbourn 1983, Metzler and Smock 1990) but not others (Smith and Lake 1993, Boulton and Foster 1998). Our study suggests that the effects of burial depend on the length of inundation: burial significantly decreased OM loss at high T_U (17–25 days), but the relationship weakened when low T_U leafpacks were also considered. This apparent dependency is complicated by results from a separate study conducted on the Deerlodge floodplain in which leafpacks inundated for ~35 days and naturally buried by flood-borne sediment lost more OM than did leafpacks inundated for the same period but not buried (Andersen and Nelson 2003). Herbst (1980) suggested that burial could reduce decomposition through compaction of leaves (smaller effective surface area for detritivores), decreased abrasion, reduced mechanical breakage (lack of turbulence), anaerobic conditions, or differential colonization by microbes and invertebrates. Boulton and Foster (1998) suggested that effects from burial depend in part upon whether leaves are in up- or downwelling hyporheic zones. Buried leaves are also less susceptible to recurring wet-dry cycles that can disrupt microbial populations and enhance the release of immobilized elements (Witkamp 1969, Sorenson 1974, Shure et al. 1986, but see Lockaby et al. 1996). We found little evidence of abrasion or mechanical damage to any leaves in this study but did not assess other factors.

The decrease in leafpack IER-N as the total period of inundation increased was unexpected. Giblin et al. (1994) found that IERs preloaded with nutrients lost nitrate during incubation in acidic soils and suggested the loss could be due to either microbial growth or substitution of HCO_3^- for NO_3^- on the resin beads. Another explanation is saturation of the ion exchange capacity of the IERs over time; the retention of nitrate on the resins should be very high when nitrate occupies a small proportion of the exchange capacity, but as the resins become saturated with NO_3^- ions from the floodwater solution (rather than the original OH^- saturation), retention of nitrate would drop below 100%. Yampa River floodwaters are alkaline and fea-

ture moderate bicarbonate concentrations [e.g., 66 mg L^{-1} during both the 1998 and 1999 spring floods, calculated from Deerlodge Park water quality data in Crowfoot et al. (2001)], so some substitution may have occurred. However, the level of NO_3^- in the leaflless-IER controls (Table 2) suggests that resins were saturated with only ~1.5% as NO_3^-, so NO_3^- retention should have been high. Loss of IER-N because of microbial growth during inundation seems likely. Whatever the proeess, the apparent lack of complete retention of nitrate on the resins shows that the long-term flux of nitrate may not be estimated accurately using IERs, even though the IERs can provide strong relative comparisons of treatment effects (Giblin et al. 1994). Because our tests either controlled for the relationship between IER-N and T_U or were independent of it, our conclusions are unaffected.

In contrast to the immobilization of N from river water noted in our study, Schade and Fisher (1997) reported that Fremont cottonwood leaves continuously lost nitrogen during 40 days of submergence in a Sonoran desert stream. They found no evidence of a net uptake of stream N by leaves and associated microbes. This difference could be related to differences in decomposer organisms, litter quality, or stream water quality. The rate of OM loss they report [exponential decay coefficient (k_d) = 0.0176 d^{-1}], although greater than that reported for Fremont cottonwood leaves continuously submerged in the Colorado River below Glen Canyon Dam (0.0062 d^{-1}; Pomeroy et al. 2000), produces a 20-day OM loss estimate of 70%, similar to the value of 61% derived from Figure 2a for surface leaves submerged for 20 days.

The immobilization of floodwater nitrogen by floodplain leaf litter could be an important mechanism for N retention and could explain the accumulation of N in floodplain soils. Our study showed that an above-average flood discharge inundating relatively low floodplain sites (for as long as 24 days) did not result in a net loss of N from the previous autumn's litter. Any organic N removed from the litter as OM decreased was either transported out of the local area by floodwaters or added to the local N pool. Coupled with immobilized floodwater-N, any litter-derived N added to the local pool would mean a net nitrogen gain for the site. Some retention of litter-derived N at Deerlodge Park seems likely because most floodplain locations feature flow velocities too low to move leaf litter (Andersen and Nelson 2003). Given that only the relatively rare flood that features a high stage for long-duration (i.e., many weeks) can lead to high levels of decomposition, most floods will leave behind not only the litter-derived N, but also partially decomposed ("conditioned") leaf material that will be readily susceptible to degradation and release of nutrients in subsequent periods, including winter (Taylor and Jones 1990). Dryland riparian plants may be able to immobilize nutrients rapidly following short-term soil wetting by precipitation, a trait documented for species in the adjacent upland (Bilbrough and Caldwell 1997, Cui and Caldwell 1997). Whether the N is immobilized by floodplain plants or soil organisms, the net result is a reduction in the amount of nitrogen susceptible to export. The minimal export of N, coupled with immobilization of floodwater-N, could explain the accumulation of N over time in floodplain soils.

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