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Authors: Nelson, S. Mark, and Andersen, Douglas C.

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VARIABLE ROLE OF AQUATIC MACROINVERTEBRATES IN INITIAL BREAKDOWN OF SEASONAL LEAF LITTER INPUTS TO A COLD-DESERT RIVER

S. MARK NELSON* AND DOUGLAS C. ANDERSEN

Bureau of Reclamation, 86-68220, P.O. Box 25007, Denver, CO 80225 (SMN)
U.S. Geological Survey, Fort Collins Science Center, c/o BOR, 86-68220, P.O. Box 25007, Denver, CO 80225 (DCA)
**Correspondent: msnelson@do.usbr.gov*

ABSTRACT—We used coarse-mesh and fine-mesh leafpacks to examine the importance of aquatic macroinvertebrates in the breakdown of floodplain tree leaf litter that seasonally entered a sand-bedded reach of the sixth-order Yampa River in semiarid Colorado. Leafpacks were positioned off the easily mobilized channel bed, mimicking litter trapped in debris piles. Organic matter (OM) loss was fastest for leaves collected from the floodplain and placed in the river in spring ($k = 0.029$/day) and slowest for leaves collected and placed in the river in winter (0.006/day). Macroinvertebrates were most abundant in winter and spring leaves, but seemed important to processing only in spring, when exclusion by fine mesh reduced OM loss by 25% and nitrogen loss by 65% in spring leaves. Macroinvertebrates seemed to have little role in processing of autumn, winter, or summer leaves over the 50-day to 104-day monitoring periods. Desiccation during bouts of low discharge and sediment deposition on leaves limited invertebrate processing in summer and autumn, whereas processing of winter leaves, which supported relatively large numbers of shredders, might have been restricted by ice formation and low water temperatures. These results were consistent with the concept that microbial processing dominates in higher-order rivers, but suggested that macroinvertebrate processing can be locally important in higher-order desert rivers in seasons or years with favorable discharge and water quality conditions.

RESUMEN—Utilizamos empaques de hojas con mallas finas y gruesas para examinar la importancia de macro invertebrados acuáticos en la descomposición de hojarasca en una zona de inundaciones que estacionalmente entra a los límites arenales de un río del sexto orden, el Río Yampa en la parte semiárida del estado de Colorado. Se colocaron empaques de hojas fuera del cauce principal del río, imitando hojarasca atrapada en pilas. La pérdida de materia orgánica fue más rápida en hojas recolectadas de la zona de inundación y colocadas en el río durante la primavera ($k = 0.029$/día), y más lenta en hojas recolectadas y colocadas en el río durante el invierno (0.006/día). Los macro invertebrados fueron más abundantes en las hojas del invierno y de la primavera, pero parecieron tener importancia en el procesamiento solamente durante la primavera, cuando la exclusión por malla fina redujo la materia orgánica en un 25% y la pérdida de nitrógeno en un 65% en hojas de la primavera. Los macro invertebrados parecieron jugar un papel pequeño en el procesamiento de hojas del otoño, invierno o verano durante los períodos de 50 a 104 días observados. La disecación durante períodos de poca descarga y el depósito de sedimentación sobre hojas limitaron el procesamiento por parte de invertebrados durante el verano y otoño, mientras que el procesamiento de hojas del invierno, que alimentaba números relativamente altos de trituradores, puede haber sido restringido por la presencia de hielo y temperaturas bajas de agua. Estos resultados fueron consistentes con el concepto de que el procesamiento microbiano domina en ríos de alto orden, pero sugirieron que el procesamiento por macro invertebrados puede ser importante localmente aún en ríos de desiertos de alto orden durante temporadas o años con condiciones favorables de descarga y calidad de agua.

The pulse of autumn leaf litter produced by floodplain trees is an important source of energy and nutrients for aquatic organisms, and can be an important determinant of invertebrate community structure and ecological functioning in streams (Wallace et al., 1997) and rivers (Thorp and Delong, 1994). The classic model of leaf processing for temperate woodland streams, where material is introduced in the autumn and processing takes place through the winter (e.g., Merritt and Lawson, 1992) might not apply to rivers in temperate semiarid or arid settings. For example, alluvial segments of rivers draining the high mountains of the interior western United States commonly feature extensive floodplain forests or woodlands whose autumn leaf drop coincides with lowest discharge. As a result, most autumn leaf litter falls onto the dry floodplain or parafluvial zone. Because of the dry conditions at discharges other than floods, this litter decays slowly (Andersen and Nelson, 2006) and serves as a reservoir from which coarse particulate organic matter (CPOM) can enter the river via lateral transport throughout the remainder of the year or through entrainment or in situ processing during large floods.

Relatively few studies have addressed litter processing in desert streams and rivers (Herbst and Reice, 1982; Reice and Herbst, 1982; Boulton et al., 1992; Pomeroy et al., 2000; Sheldon et al., 2002; Kennedy and Hobbie, 2004), and the applicability of models of lotic ecosystem function developed in mesic environments is unclear. For example, the river continuum concept (Vannote et al., 1980), based largely on knowledge gained in tropical and moist temperate regions, suggests that a predictable decline from upstream to downstream in the ratio of CPOM to fine particulate organic matter (FPOM) leads to microbes (including fungi) becoming more important, and macroinvertebrates less important, in leaf breakdown processes in higher-order river reaches (Graça et al., 2001).

Here we compare the initial breakdown rate and macroinvertebrate use of tree leaf litter entering a large, naturally functioning, cold-desert river in autumn (i.e., at or soon after leaf drop) to patterns for leaves entering the river in winter, spring, and summer. The slow loss of biomass and complex shifts in nitrogen content that accompany litter breakdown on the dry floodplain (Andersen and Nelson, 2006), the presence of large seasonal changes in river water temperature, and the river continuum concept together suggested 2 hypotheses: 1) floodplain leaf litter entering the river during different seasons will support different aquatic macroinvertebrate assemblages, and 2) microbial processing is as important or more important than processing by macroinvertebrates. We tested the first hypothesis using standardized leafpacks in an assessment repeated each season and the second hypothesis in an experiment comparing litter breakdown in the standard leafpacks to that in leafpacks from which macroinvertebrates were largely excluded.

METHODS—*Study Area*—We worked on the sixth-order Yampa River in Deerlodge Park (DLP; elevation ~1,705 m) in semiarid northwestern Colorado. Deerlodge Park is an alluvial valley within Dinosaur National Monument, with open stands of mature (80 to 200+ year old) Fremont cottonwood (*Populus deltoides* subsp. *wislizenii*) and smaller areas of dense young trees (Fig. 1). The channel-bed at DLP is primarily silt and sand. Sandbar willow (*Salix exigua*) is the dominant shrub. Mean annual precipitation is 28 cm, based on U.S. National Weather Service records for Maybell, Colorado (20 km east of DLP). Additional local precipitation and air temperature data for DLP are available from a station installed in 1998.

The Yampa River features a natural flow regime with a spring flood pulse driven by snowmelt in headwater areas in the Rocky Mountains. The mean peak flood flow at DLP (drainage area 19,840 km^2) is 368 m^3/s ($\pm$ 18.1 *SE*, $n = 74$; 1922–1995 data). Flood flows in DLP normally raise the river surface by 2 to 3 m. Discharge and water temperature data for the study period are available from U.S. Geological Survey gage number 09260050, located ~2 km downstream from our study site. The river surface at DLP probably freezes each winter, but the frequency, timing, and duration of ice cover varies among years.

Breakdown Rates and Processes—We used leafpacks to measure breakdown rates and examine macroinvertebrate use of cottonwood leaves entering the river in December (''winter leaves''), in April (''spring leaves''), in June (''summer leaves''), and in October (''autumn leaves''). We used 2 matched locations separated by 0.5 km (hereafter, ''upstream'' and ''downstream'') in the study. Both locations were in lotic habitat ~2 m from the toe of a cutbank and adjacent to a partially submerged, bark-free cottonwood snag (>75 cm diameter bole). The upstream site also featured an accumulation of smaller woody debris (Fig. 1a).

We collected litter off the DLP floodplain 2 to 5 weeks prior to starting each seasonal trial, selecting leaves from the most recent autumn cohort (Table 1). Collected leaves were immediately air dried, and assembled leafpacks were stored individually in airtight plastic bags until placed in the field.

We used 2 types of leafpacks to differentiate macroinvertebrate and microbial processing. Coarse-mesh leafpacks, intended to be accessible to all macroinvertebrates, consisted of ~5 g of air-dried leaves placed into envelopes (25 × 25 cm) made from black polypropylene mesh (0.6 × 0.8 cm openings). Fine-mesh leafpacks, intended to exclude invertebrates, had leaves first placed into 300-μm mesh Nitex (Sefar America Inc., Depew, New York) cloth bags, and then into the polypropylene envelopes. Seven to 10 coarse-mesh and 3 fine-mesh leafpacks were installed at each location for each seasonal trial. We used stainless steel wire to attach individual leafpacks to one or another of 3 metal fence posts (50 cm apart and oriented parallel to the current) installed vertically

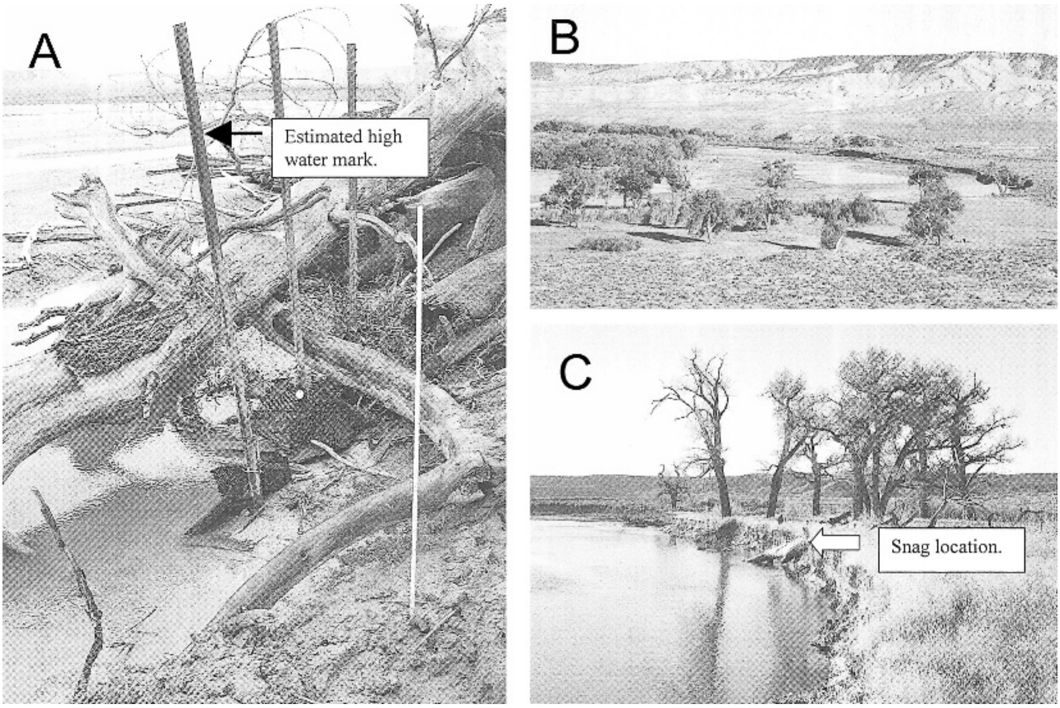

FIG. 1—A) Upstream study location at the termination of the ''summer'' trial (11 September 2002), when discharge was unusually low (~0.5 m^3/s). Note exposed leafpacks at base of fence posts. Arrow shows estimated high water level. The view is looking upstream across the exposed channel shown in panel B. B) Section of the Yampa River channel in Deerlodge Park, Dinosaur National Monument, northwestern Colorado, USA, looking upstream. Mature and young Fremont cottonwood trees (*Populus deltoides* subsp. *wislizenii*) dominate the floodplain. Image obtained 15 September 2004; discharge ~4.2 m^3/s. C) Cutbank at the upstream study location at typical autumn discharge (~5.4 m^3/s; 23 October 2003).

<1 m downstream from the snag (Fig. 1a). At installation, leafpacks were evenly mixed and distributed among the fence posts, all were submerged, and the lowest leafpacks were ~15 cm off the channel bed. The position of the leafpacks in the water column is representative of positions where leaf litter naturally accumulates (e.g., at debris piles or other flow-filtering features) on reaches with an easily mobilized bed. A previous study at the upstream location (Andersen and Nelson, 2006) demonstrated that leafpacks pinned to the channel bottom were susceptible to rapid burial under bed material, a condition that favored microbial processing.

Seasonal trials were conducted sequentially, and exposure periods did not overlap. Thus, the fence posts supported only one kind of leaf material at a time. Exposure times varied among the seasonal trials (Table 1) because of safety and logistical constraints. Each leafpack, upon retrieval, was placed in a plastic bag, packed in ice, and returned to the laboratory to be frozen.

We processed a leafpack by first thawing it and classifying the quantity of sediment accumulated on and within it as small, moderate, or large based on appearance and heft. We determined the oven-dry (100°C) mass of sediment removed from a sample of the leafpacks placed in each of these categories to quantify sediment accumulations. We then washed leafpacks with water over a 600-μm mesh screen and, under 10× magnification, hand-picked macroinvertebrates from collected debris and remaining leaf material.

Organic matter (OM) content of the initial and retrieved litter was calculated as ash-free oven-dry (60°C) biomass (AFDM). Ash content was determined as loss on ignition (450°C for ~18 h). The initial AFDM/air-dry mass conversion for each collection of litter was determined from a subset of leafpacks. Nitrogen (N) content was calculated as the product of OM mass and total Kjeldahl nitrogen (determined by acid extraction and EPA method 351.2 modified; U.S. Environmental Protection Agency, 1997). A previous study involving the same type of litter (Andersen and Nelson, 2003) showed the contribution of nitrate and nitrite to total N in initial and retrieved material to be negligible.

All collected invertebrates were identified under a stereomicroscope and counted. Each taxon was assigned to a functional feeding group by using Merritt and Cummins (1996). We looked for patterns

TABLE 1—Initial litter quality, leafpack exposure period, and breakdown rate coefficients for Fremont cottonwood (*Populus deltoides* subsp. *wislizenii*) leaf litter placed in the Yampa River in semiarid northwestern Colorado, USA. Tabulated values are means ± 1 *SE* (*n*). Column entries with the same subscript are not significantly different ($P < 0.05$).

	Litter condition when collected					Breakdown rate coefficient, *k* (per day)	
Type of leaf litter	Age (months)	OM content (%) ($n = 3$)	N content (mg/Kg OM) ($n = 3$)	Period of immersion	Exposure period (days)	Coarse mesh	Fine mesh
Winter	1	86.9 ± 0.3^{a}	4,704 ± 149^{a}	19–20 December to 2 April	103/104	0.0064 ± 0.0003 (20)^{a}	0.0064 ± 0.0005 (10)^{a}
Spring	4	90.5 ± 0.1^{b}	5,622 ± 65^{a}	2 April to 27 June*	86*	0.0291 ± 0.0022 (14)^{b}	0.0132 ± 0.0004 (6)^{b}
Summer	7	88.6 ± 0.6^{ac}	5,716 ± 255^{a}	27 June to 11 September	75	0.0128 ± 0.0020 (12)^{c}	0.0123 ± 0.0011 (6)^{b}
Autumn	0.25	89.2 ± 0.1^{bc}	5,508 ± 490^{a}	7 October to 26 November	50	0.0168 ± 0.0003 (11)^{c}	0.0161 ± 0.0003 (6)^{c}

* Four of the 14 leafpacks were retrieved 14 June, after an exposure period of only 73 d.

among aquatic macroinvertebrate assemblages with a detrended correspondence analysis (DCA; CANOCO version 4.0), using taxonomic and abundance data from the individual coarse-mesh leafpacks. We used species natural history, the season of leafpack installation, and other factors to interpret the environmental gradients represented by the ordination axes.

Andersen and Nelson (2006) documented the 48-h leaching loss for immersed autumn leaves (18% of OM) in a study undertaken at the upstream location in 2001. We estimated the analogous OM loss attributable to leaching from spring leaves in the laboratory with three 5-g batches of air-dried litter immersed in 1.4 L of river water (both leaves and water collected in March 2004) maintained at a representative early spring river temperature (~8°C). Infusions were periodically stirred, and water was replaced after 24 h. Leaves were removed from the water after 48 h and oven dried (60°C) to constant mass. Separate batches of air-dried leaves were oven dried to determine initial litter moisture content.

A portable meter was used to measure seasonal Yampa River water quality parameters in situ: dissolved oxygen (DO), temperature (°C), pH, and conductivity (µS/cm). Water samples collected for alkalinity and hardness were analyzed using titration methods (test kit, Hach Company, Loveland, Colorado), and turbidity was measured in spring and summer with a turbidimeter.

Differences in seasonal OM and N losses due to location and treatment (mesh size) were each tested with 2-way ANOVA using arcsine square-root transformed proportions. The litter breakdown rate coefficient (*k*) was determined by fitting a negative exponential model to the proportion of OM remaining (γ_{OM}) versus time of exposure (t, in days): $\gamma_{OM} = e^{-kt}$. We used ANOVA to compare rate coefficients, which are independent of exposure period length, across seasons. The coarse-mesh and fine-mesh leafpack data sets were analyzed separately. Means are presented as mean ± *SE* (*n*) unless sample size (*n*) is presented elsewhere in the text.

RESULTS—*Environmental Conditions*—Weather conditions at DLP (winter 2001 through autumn 2002) were cooler and drier than average, and river discharge was below average. Winter 2001–2002 was unusually cold (average December through February air temperature = −8.2°C) and the peak instantaneous discharge during the 2002 spring flood (108 m^3/s in early June) reached only 30% of the long-term average. Low discharge levels in summer 2002 resulted in exposure of some leafpacks containing summer leaves to drying conditions at various times and for various periods, depending on leafpack location and position on the fence post (Fig. 1a).

Yampa River water temperature at leafpack locations ranged from a low of 0.0°C (below ice) in March to a high of 25.2°C in late June. An ice augur was needed for sampling near leafpack locations in March, when ice thickness was such that free water occurred only near the river bottom.

U.S. Geological Survey gage data indicated water temperature reached a high of 32°C in July, when discharge was low ($<0.1\ m^3/s$). The ranges of DO (6.6 to 11.2 mg/L), pH (7.0 to 8.5), conductivity (462 to 876 μS/cm), alkalinity (117 to 157 mg/L), and hardness (149 to 230 mg/L) indicated water quality did not limit macroinvertebrates. Turbidity reached a high of 161 NTU in the spring (April) measurement, early in the flood pulse.

Initial Litter Condition and Leaching Losses—The 4 collections of leaf litter varied in OM content ($F = 18.53$; $df = 3, 8$; $P = 0.001$) (Table 1), but there was no significant difference in N content ($F = 2.59$; $df = 3, 8$; $P = 0.13$). The 48-h leaching study conducted on spring leaf litter indicated that $8.2 \pm 0.1\%$ ($n = 3$) of oven-dry mass was lost during immersion.

Seasonal Variation in Initial Breakdown Rate—Breakdown rate coefficients (k, calculated with locations pooled) differed significantly among the seasons in both the coarse-mesh ($F = 48.4$; $df = 3, 53$; $P < 0.001$) and fine-mesh leafpacks ($F = 52.6$; $df = 3, 24$; $P < 0.001$). Post-hoc Bonferroni pairwise comparisons among coarse-mesh leafpacks indicated that spring leaves broke down faster and winter leaves broke down slower than other leaf types (Table 1). Summer and autumn leaves broke down at the same rate. In fine-mesh leafpacks, autumn leaves broke down faster and winter leaves broke down slower than other leaf types (Table 1).

Seasonal Variation in Treatment and Location Effects—We detected an effect of mesh size in some but not all seasons. We also detected an effect from location in some seasons, but the pattern differed from that for mesh size. In the winter trial, we detected no effect due to either mesh size or location on the proportion of OM lost (Table 2), but we detected a significant location effect on N loss: the downstream site lost ~50% more N than the upstream site. In the spring trial, we detected mesh size and location effects for both OM and N loss (Table 2). There was no location-treatment interaction. Losses were consistently highest at the downstream location: 6 and 10% greater OM losses and 30 and 78% greater N losses for coarse-mesh and fine-mesh leafpacks, respectively. Enclosure in fine-mesh bags reduced litter OM loss by ~25% and N loss by ~65%.

Summer trial results were similar to those from the winter trial, in that neither mesh size nor location affected OM loss, but location did affect N loss (Table 2). However, the pattern of N loss was opposite that observed in winter. Summer litter at the downstream location showed either no change (coarse-mesh leafpacks) or a net absolute increase in N (fine-mesh leafpacks), whereas litter at the upstream location lost N. A second analysis incorporating an estimate of the total time each leafpack was submerged as a covariate produced equivalent results (data not shown). Neither mesh size nor location affected breakdown of autumn leaves (Table 2).

Sediment—The amount of sediment in leafpacks varied with season. Most leafpacks with winter (70%) or spring leaves (86%) accumulated a small amount of sediment, whereas leafpacks with summer and autumn leaves were often classified as holding moderate (42 and 25%, respectively) or large (33% in both cases) sediment amounts. Weighed sediment samples indicated that our classes of small, moderate, and large amounts of sediment corresponded to 4.7 ± 3.6 g ($n = 5$), 27.8 ± 7.4 g ($n = 12$), and 357 ± 92 g ($n = 11$) of sediment/leafpack, respectively.

Macroinvertebrate Assemblages—The DCA analysis suggested the presence of distinct groups of organisms associated with winter, spring, and summer-autumn leaves (Fig. 2). The first 2 DCA axes explained 34% of the variance in the macroinvertebrate assemblage data; the eigenvalues were 0.525 and 0.256 for Axes I and II, respectively. Plecoptera, including shredders, were more diverse in winter leaves, while ephemeropteran collector-gatherers, such as *Baetis, Choroterpes, Ephemerella, Heptagenia*, and *Tricorythodes*, were common in spring leaves. Adult stoneflies (*Oemopteryx*) were observed emerging at the downstream location in March through a narrow liquid interface between the snag and river ice. Only oligochaetes were common in summer-autumn leaves. Summer leaves also were colonized by small numbers of spiders (Lycosidae) and beetles (*Anthicus, Baulius, Bembidion, Helophorus linearis, Ochthebius lineatus, Stenolophus*) that were largely of terrestrial origin.

Collector-gatherers consistently showed the highest abundance among functional feeding

Table 2—Results of ANOVAs to test for effects of location and leafpack mesh size on the arcsine-transformed proportions of organic matter and nitrogen lost from *Populus* leaf litter immersed in the Yampa River at Deerlodge Park, Dinosaur National Monument, Colorado.

Season	Dependent variable	Source	Sum-of-squares	*df*	Mean-square	*F*-ratio	*P*
Winter	Organic matter	Location	0.013	1	0.013	2.109	0.158
		Mesh	0.000	1	0.000	0.001	0.978
		Location*Mesh	0.000	1	0.000	0.008	0.930
		Error	0.162	26	0.006		
	Nitrogen	Location	0.105	1	0.105	6.044	0.021
		Mesh	0.043	1	0.043	2.470	0.128
		Location*Mesh	0.000	1	0.000	0.000	0.986
		Error	0.454	26	0.017		
Spring	Organic matter	Location	0.034	1	0.034	5.718	0.029
		Mesh	0.325	1	0.325	55.393	0.000
		Location*Mesh	0.010	1	0.010	1.749	0.205
		Error	0.094	16	0.006		
	Nitrogen	Location	0.200	1	0.200	15.793	0.001
		Mesh	1.243	1	1.243	97.977	0.000
		Location*Mesh	0.005	1	0.005	0.392	0.540
		Error	0.203	16	0.013		
Summer	Organic matter	Location	0.023	1	0.023	0.894	0.360
		Mesh	0.001	1	0.001	0.026	0.875
		Location*Mesh	0.000	1	0.000	0.003	0.956
		Error	0.367	14	0.026		
	Nitrogen	Location	1.111	1	1.111	4.507	0.052
		Mesh	0.178	1	0.178	0.723	0.409
		Location*Mesh	0.384	1	0.384	1.559	0.232
		Error	3.450	14	0.157		
Autumn	Organic matter	Location	0.000	1	0.000	0.007	0.935
		Mesh	0.001	1	0.001	1.635	0.223
		Location*Mesh	0.000	1	0.000	0.155	0.701
		Error	0.008	13	0.001		
	Nitrogen	Location	0.000	1	0.000	0.044	0.837
		Mesh	0.001	1	0.001	0.150	0.705
		Location*Mesh	0.007	1	0.007	0.678	0.425
		Error	0.126	13	0.010		

groups (Fig. 3). Shredder abundance was highest in winter (2.4 ± 0.5 individuals/leafpack), fell slightly in spring (1.3 ± 0.4), and dropped markedly in summer (0.4 ± 0.3). No shredder was found in leafpacks containing autumn leaves. Overall invertebrate abundance (individuals/leafpack) followed a pattern similar to shredder abundance: higher in winter (103 ± 25) and spring leaves (91 ± 12) than in summer (5 ± 2) or autumn leaves (12 ± 4). Invertebrate abundance was much lower in fine-mesh bags (winter, 35 ± 7; spring, 28 ± 4; summer, 0.8 ± 0.6; autumn, 1.7 ± 1.1), indicating the fine mesh was effective in restricting macroinvertebrate access to litter.

Discussion—The DCA produced 3 groups of macroinvertebrate assemblages distinguishable by their seasonality (Fig. 2), supporting our hypothesis that seasonal litter inputs support different assemblages during the first months of breakdown. The arrangement of the macroinvertebrate groups (leafpacks) and individual taxa scores in the ordination space suggested a mix of predictable and unpredictable environmental factors were responsible for the groupings. Axis I seemed to reflect a gradient in the presence or magnitude of physical barriers to processing (e.g., levels of sediment, ice, or desiccation), with restriction increasing to the right. For example, oligochaetes (a burrowing

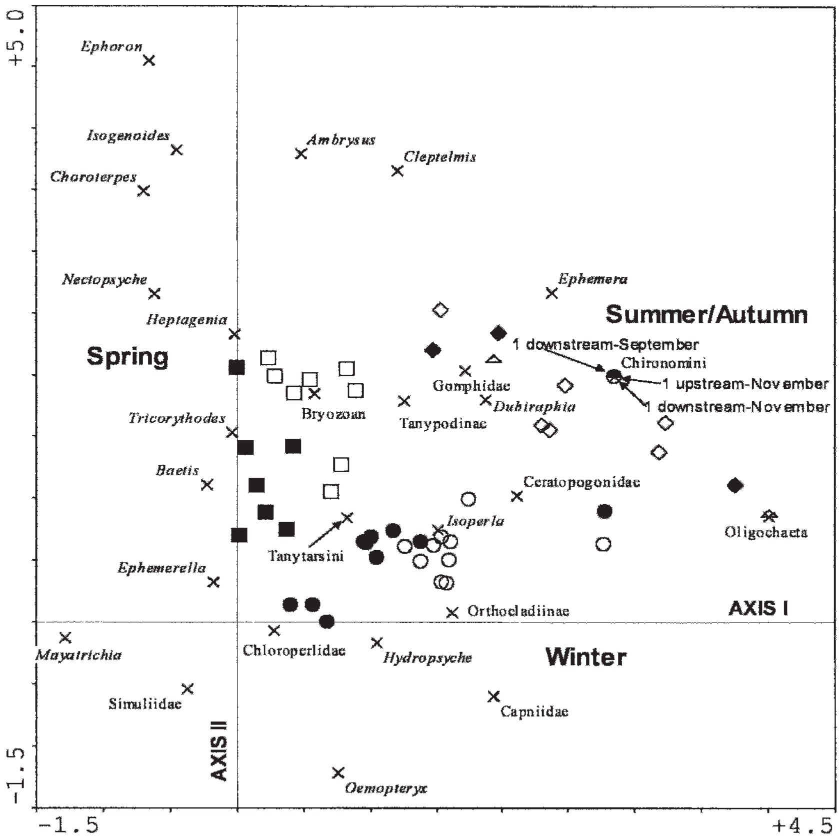

Fig. 2—Detrended correspondence analysis of kinds and numbers of macroinvertebrates collected in coarse-mesh leafpacks containing winter, spring, summer, or autumn leaves in Yampa River, Deerlodge Park, Dinosaur National Monument, in semiarid northwestern Colorado, USA. Leafpacks from the upstream location are labeled with open figures, and those from downstream sites are filled figures. Season of exposure is labeled as winter (○), spring (□), summer (△), and autumn (◇). Taxa scores can be considered an estimate of the peak of the response curve of each taxon along the ordination axes.

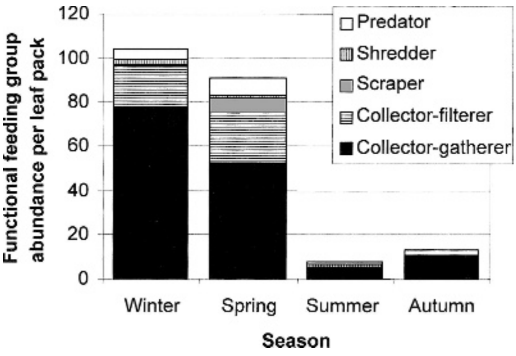

Fig. 3—Mean number per leaf pack of functional feeding groups of macroinvertebrates associated with cottonwood (*Populus deltoides* subsp. *wislizenii*) leaf litter in the Yampa River, Deerlodge Park, Dinosaur National Monument, in semiarid northwestern Colorado, USA.

collector-gatherer), which scored high on Axis I, were associated with litter inaccessible to or avoided by other taxa, e.g., litter heavily coated with sediment. Axis II likely reflected a gradient in river temperature, which can cue life-history events. For example, the plecopteran shredders *Oemopteryx* and Capniidae were absent from summer collections and scored low on Axis II. Both taxa use summer nymphal diapause to avoid high summer water temperatures (Stewart and Stark, 1988). In contrast, burrowing *Ephoron* nymphs were collected solely from spring leaves and scored high on Axis II. Eggs of some *Ephoron* species require exposure to near-freezing water temperatures followed by a rapid warming to break winter diapause (Allan, 1995: 75).

Processing by macroinvertebrates seemed to significantly contribute to litter breakdown solely during the spring, when enclosure in fine-mesh bags reduced spring litter OM loss ~25% and N loss by ~65%. Although the fine mesh likely reduced fragmentation due to physical factors (e.g., floodwater turbulence and abrasion from entrained materials), the presence of shredders and the high counts of macroinvertebrates in spring leafpacks suggest these organisms contributed significantly to the high breakdown rate (Table 1) and that at least some of the reduction in OM loss was due to their exclusion.

The disproportionately large reduction in N loss also might be from macroinvertebrate exclusion. The change in litter N is the net result of N gains and losses. Nitrogen is gained as microbial populations (including fungi) that form biofilms colonize and grow on leaf surfaces, where they assimilate N from litter and other sources. Litter N is lost through leaching, consumption, or fragmentation. Scraping macroinvertebrates process leaf litter by consuming the biofilm, which might serve as the primary food resource (Allan, 1995:193). Thus, all else being equal, a disproportionately small N loss from litter in the fine-mesh bags could result from either the mesh facilitating biofilm development or, by excluding scrapers, retarding its removal.

The apparent lack of significant macroinvertebrate processing in 3 of the 4 seasons was consistent with our hypothesis that microbial processing is as important or more important than processing by macroinvertebrates. However, the cold and drought conditions encountered in this study might have led to unusually low macroinvertebrate processing. The absence of significant macroinvertebrate processing in winter was particularly surprising, given the high shredder abundance. We speculate that the encasement of leafpacks in ice restricted shredder access and activity in winter leaves, thereby limiting the extent of their processing. Macroinvertebrates might be more important and winter breakdown rates higher during average or mild winters, when river ice would be less pervasive.

Sediment deposition also likely affected aquatic invertebrate processing. Spring flood flows kept fine sediment suspended and litter relatively sediment-free. In contrast, leafpacks containing summer or autumn leaves had large amounts of sediment and few invertebrates. Fine sediment deposition has been correlated with lower benthos abundance and changes in composition from Ephemeroptera, Plecoptera, and Trichoptera to burrowing midges and oligochaetes (Waters, 1995), as well as decreased leaf decomposition rates (Rader et al., 1994). Suspended sediment seems to have less impact on macroinvertebrates, with flow rather than sediment causing a decrease in abundance (Bond and Downes, 2003).

Microbial processing seemed to be affected primarily in winter (Table 1), presumably by low water temperatures (Webster and Benfield, 1986; Suberkropp and Chauvet, 1995). Data from fine-mesh leafpacks suggested that microbial processing was similar in spring and summer leaves. If OM losses in fresh autumn leaves are adjusted for greater leaching losses [18% (Andersen and Nelson, 2006) vs. the 8% documented here for spring leaves, and assuming 8% for winter and summer leaves], the mean *k* values for fine-mesh spring, summer, and autumn leaves become statistically indistinguishable.

The presence of seasonal differences in litter processing rates in a temperate region river like the Yampa River was not unexpected. Menéndez et al. (2003), for example, working in a Mediterranean stream, attributed the faster breakdown of *Populus alba* litter in spring-summer compared to autumn-winter to the interaction of higher temperatures and a 10-fold increase in macroinvertebrates. Numerous other freshwater studies have linked increased decomposition to increased temperatures and higher invertebrate abundances (Webster and Benfield, 1986).

Variation in breakdown rates among nearby river locations also was not unexpected, especially for habitats associated with woody debris (Palmer et al., 1996). We detected greater N loss at the downstream site in both winter and spring, but the pattern was reversed in the summer, and we found no difference in the subsequent autumn trial. This pattern might reflect the differences in woody debris at these locations. Both locations featured a downed snag, but the large amount of smaller woody debris at the upstream location likely exposed immersed leafpacks to a continuous stream of innocula from epixylic biofilms during winter and spring, leading to greater biofilm development and a lower net N loss there. During the summer, desiccation would have killed the biofilm microbes on exposed woody debris and leafpacks at the upstream location, whereas downstream conditions remained favorable, as evidenced by the net gain in litter N there. There was no location effect in net N loss in autumn leaves because the woody debris at the upstream location, although re-wetted, was not yet a major source of biofilm innocula.

The low and variable late-summer flows allowed leafpacks to be accessed by terrestrial invertebrates (mostly Coleoptera). Although low in abundance, these shredder and predator taxa might be important in linking aquatic and terrestrial food webs (e.g., Collier et al., 2002). Our earlier studies of leaf processing at this site (Andersen and Nelson, 2003; Andersen and Nelson, 2006), using hundreds of leafpacks, detected only small numbers of some of these taxa in drier portions of the floodplain, suggesting they might be largely confined to the moist river margin, where some might aid in leaf breakdown (e.g., Hutchens and Wallace, 2002). These results add to the evidence that moist river margins might be important habitats for terrestrial beetle and spider communities (Henschel et al., 2001; Sanzone et al., 2003).

The abundant sediment carried in the Yampa River and many desert rivers limits autotrophic production, and scrapers that might use algal resources were rarely collected (Fig. 3). Our feeding analysis indicated that collector-gatherers consistently made up a large proportion of the macroinvertebrates at DLP, indicating a reliance on detritus as a food source. Haden et al. (2003) indicated that terrestrial OM was the primary carbon source for macroinvertebrates in the seventh-order and eighth-order Green and Colorado rivers, downstream of DLP. Thorp and Delong (1994) suggested that floodplain litter input, both during and outside the flood pulse, is a major determinant of structure and functioning of large rivers with constricted channels, where litter retention is enhanced. Studies measuring lateral transport of floodplain litter suggest it can account for up to 10% of total annual CPOM input (Campbell et al., 1992; Benson and Pearson, 1993). Terrestrial OM availability might, in part, derive from the likelihood that litter will be continuously introduced to the system, with peaks during autumn leaf fall and in spring, with floodplain inundation. Our study suggests that deposited sediment and ice might also control availability of CPOM to macroinvertebrates.

Desert rivers whose water and sediment are derived from different parts of their watersheds, such as the Yampa River and other tributaries of the Colorado River (Andrews, 1991), are characterized by both large seasonal and large interannual variation in discharge and water quality. Long-term studies, including measurements of seasonal allochthonous inputs, are needed to fully understand the importance of terrestrial and aquatic microbial and macroinvertebrate processing in desert lotic systems. Such studies will also provide the basis for understanding how flow regime change due to river regulation, climate change, or other factors can effect litter production and processing, and thereby secondary production within desert rivers.

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