Breakdown rates, nutrient concentrations, and macroinvertebrate colonization of bluejoint grass litter in headwater streams of the Kenai Peninsula, Alaska

Author(s): Rebecca S. Shaftel, Ryan S. King, and Jeffrey A. Back

Breakdown rates, nutrient concentrations, and macroinvertebrate colonization of bluejoint grass litter in headwater streams of the Kenai Peninsula, Alaska

Rebecca S. Shaftel[1], Ryan S. King[2], AND Jeffrey A. Back[3]

*Department of Biology, Center for Reservoir and Aquatic Systems Research, Baylor University,
One Bear Place #97388, Waco, Texas 76798 USA*

Abstract. Grass litter can be a dominant detritus type in many streams. However, use of this C source in stream food webs often is viewed as insignificant because of its relatively slow breakdown rates and low nutritional quality. We deployed leaf packs containing senesced bluejoint grass (*Calamagrostis canadensis*) across a natural nutrient gradient of 6 salmon-rearing headwater streams on the lower Kenai Peninsula, Alaska. We hypothesized that litter-colonizing microbes would use dissolved stream nutrients and enhance breakdown rates, litter nutrient concentrations, and densities of macroinvertebrates across streams. Leaf-pack mass and nutrient concentrations were measured on the material at 0 (predeployment), 2, 4, 6, and 8 wk in all streams. Breakdown rates were calculated from the mass measurements with an exponential decay model. Macroinvertebrate composition and abundance were measured at 8 wk in all streams and every 2 wk in 1 stream. Breakdown rates of bluejoint litter were relatively low (20–30% mass loss over 2 mo), but similar to rates found in previous studies of senesced grass litter. Weighted regressions showed that bluejoint breakdown rates in the 6 streams were significantly ($p < 0.05$) related to dissolved stream nutrient concentrations ($r^2 = 0.94$ and 0.67 for dissolved inorganic N and PO$_4$-P, respectively), litter nutrient concentration ($r^2 = 0.72$ and 0.96 for leaf % N and % P, respectively), total macroinvertebrates/g ($r^2 = 0.73$), and nonmetric multidimensional scaling-axis-1 scores of macroinvertebrate community structure ($r^2 = 0.80$). Litter nutrients changed after just 2 wk and were increasingly and significantly related to stream nutrient concentrations over time. NMS ordination showed that succession of macroinvertebrates on leaf packs from one stream followed a distinct direction over time, and a large shift in macroinvertebrate community structure occurred between weeks 6 and 8, a result potentially indicating a consumer response to microbial conditioning. The abundance and diversity of macroinvertebrate taxa using bluejoint litter provide evidence that it is an important habitat and energy pathway for consumers in headwater streams of the Kenai Peninsula. In addition, climate change has the potential to change terrestrial vegetation assemblages, which drive differences in stream nutrient concentrations in this region. If N-fixing shrubs become more abundant in the future, litter-decomposition rates will be positively affected by increases in both stream and leaf-litter nutrient concentrations.

Key words: leaf decomposition, food quality, nitrogen, phosphorus, juvenile salmonids, riparian wetlands, *Alnus*.

Energy inputs to headwater streams are dominated by allochthonous sources because of their narrow channels and overhanging vegetation (Benfield 1997, Richardson and Danehy 2007). These inputs are an important C source for microbial and macroinvertebrate consumers that use leaf litter directly (Cummins et al. 1989, Graça 2001, Findlay 2010) and for higher trophic levels, such as macroinvertebrate predators

and fish (Junger and Planas 1994, Doucett et al. 1996, Perry et al. 2003). Most studies in which the fate of terrestrial litter inputs in headwater streams have been examined focused on deciduous shrub and tree leaves (Wipfli et al. 2007, Tank et al. 2010), although other organic matter inputs, such as woody debris, mosses, and grasses, also may contribute to the organic matter budget in small streams (McTammany et al. 2008, Leberfinger and Bohman 2010).

Grasses have received little attention as an allochthonous resource, most likely because of conclusions from several studies that their low nutrient

concentration makes them a poor food resource for macroinvertebrate consumers (e.g., Webster and Benfield 1986, Menninger and Palmer 2007). However, many streams, including large grassland streams (Huryn et al. 2001, Zeug and Winemiller 2008), agricultural streams with deforested riparian areas (Menninger and Palmer 2007), or small open-canopied streams (Niyogi et al. 2003, Leberfinger and Bohman 2010), receive substantial inputs of allochthonous grass litter. No consensus currently exists regarding the importance of grasses to stream consumers. Results of some studies suggest that grasses are a poor food resource or habitat (Scarsbrook and Townsend 1994) or are minimally consumed by macroinvertebrates relative to deciduous-tree litter (Leberfinger and Bohman 2010), but other results suggest that grass litter can be an important C source, contributing a large proportion of the energy used in biomass formation by macroinvertebrates (Huryn et al. 2001) and fish (Zeug and Winemiller 2008). Despite their poor nutritional quality, grasses may be an important energy resource when they dominate the riparian communities of stream ecosystems.

Litter nutrient concentrations play an important role in initial colonization by microbes (Bärlocher 1985) and subsequent consumption by macroinvertebrates (Haapala et al. 2001, Hladyz et al. 2009). Low-nutrient litter tends to break down slowly (Gessner and Chauvet 1994, Richardson et al. 2004), but rates can be enhanced by dissolved nutrients in the stream water (Suberkropp and Chauvet 1995). Experimental nutrient additions of N and P can increase decomposition rates (Robinson and Gessner 2000, Gulis and Suberkropp 2003) and increase macroinvertebrate (Robinson and Gessner 2000), bacterial (Gulis and Suberkropp 2003), and fungal biomass (Gulis and Suberkropp 2003). Breakdown rates of nutrient-poor C sources, such as grass, may be particularly enhanced by dissolved nutrient subsidies (Ferreira et al. 2006, Greenwood et al. 2007). Thus, dissolved nutrient concentrations in streams may be an important factor driving use of grasses as a C source to microbes and higher tropic levels.

Our study was conducted in 6 small, 1st-order streams on the lower Kenai Peninsula, Alaska (USA). Headwater streams in this region are frequently open-canopied and bordered by extensive riparian wetlands dominated by bluejoint grass (*Calamagrostis canadensis*). Because of their small size, these streams receive little to no subsidies of marine-derived nutrients or C from adult salmon. However, they support juvenile salmonids, particularly coho salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus*

malma) that disperse upstream from spawning areas in larger reaches downstream. Grass is the dominant riparian plant species and a potential source of terrestrial organic matter, so it could be an important energy source for macroinvertebrate consumers and the juvenile salmonids that feed on them.

The 6 streams spanned a nutrient gradient caused mostly by differences in alder cover, a N-fixing shrub that contributes most of the dissolved NO_3 to streams in this region (Shaftel et al. 2010). The objectives of our study were to: 1) estimate breakdown rates of bluejoint grass, 2) contrast breakdown rates and nutrient concentrations of litter across a nutrient gradient spanning the 6 streams, and 3) evaluate macroinvertebrate colonization and temporal succession of community structure on leaf packs. We hypothesized that bluejoint breakdown rate, litter nutrient concentrations, and macroinvertebrate abundance would be positively associated with higher stream nutrient concentrations.

Methods

Study area

Headwater streams of the lower Kenai Peninsula are part of 5 major watersheds that flow westerly into Cook Inlet: Ninilchik River, Deep Creek, Stariski Creek, and the North and South Forks of the Anchor River. The lower Kenai Peninsula is largely undeveloped. The region has 2 small cities (population ~5000 in 2005 census estimates), and <1% of its area is in agricultural land (2007 Census of Agriculture; http://www.agcensus.usda.gov/index.asp). The closest weather station to the study area is the Homer Airport, where total precipitation from 1932 to 2005 averaged 63 cm annually, ~13 to 18 cm of which were snow. The average maximum temperature occurs in July at 16.1°C, and the minimum occurs in January at −8.5°C (Western Region Climate Center; http://www.wrcc.dri.edu/summary/climsmak.html).

The headwater streams included in our study are in the interior of the lower Kenai Peninsula and probably experience warmer temperatures and more precipitation in the form of snow than Homer, which is on the coast. Vegetation consists of mixed forests dominated by lutz spruce (*Picea lutzii*), white spruce (*Picea glauca*), and paper birch (*Betula papyrifera*), interspersed with willow (*Salix* spp.) and alder (*Alnus* spp.) thickets and meadows dominated by bluejoint grass and fireweed (*Chamerion angustifolium*) (Reynolds 1990, Viereck et al. 1992). Wetlands cover 43% of the area (Gracz et al. 2004). Terrestrial P originates from volcanic ash layers deposited in soils (Dugdale and Dugdale 1961, Ping and Michaelson 1986).

TABLE 1. Watershed characteristics and stream water chemistry for 6 streams in the lower Kenai Peninsula, Alaska (USA). Stream water chemistry and discharge are means (SE) for samples taken over the course of the leaf decomposition experiment (n = 5). Current velocity is an average of 4 measurements taken at each of the 5 racks in each stream measured at initial deployment (1–6 June 2009). Streams are arranged in order of decreasing dissolved inorganic N (DIN) concentrations. NO_x-N = NO_3 + NO_2, TN = total N, TP = total P, DOC = dissolved organic C.

Stream number	22	1203	44	619	545	171
Watershed	Stariski	Anchor	Anchor	Ninilchik	Ninilchik	Stariski
Location (lat °N, long °W)	59.91, 151.49	59.78, 151.55	59.86, 151.66	60.05, 151.34	60.05, 151.63	59.84, 151.78
Area (km^2)	3.5	3.3	8.2	11.9	9.8	4.1
Mean elevation (m)	377	411	156	439	71	84
Current velocity (m/s)	0.34 (0.03)	0.21 (0.03)	0.36 (0.03)	0.29 (0.02)	0.32 (0.03)	0.31 (0.03)
Discharge (m^3/s)	0.02 (0.004)	0.02 (0.001)	0.09 (0.013)	0.07 (0.009)	0.05 (0.009)	0.04 (0.01)
NH$_4$-N (µg/L)	7.1 (2.4)	6.1 (2.1)	20.7 (3.7)	3.4 (0.6)	8.1 (3)	2.9 (0.2)
NO$_x$-N (µg/L)	331.7 (37.9)	323.2 (32.2)	26.3 (2.4)	39.7 (4.8)	26.9 (5.1)	9 (1)
DIN (µg/L)	338.8 (37.4)	329.3 (33.4)	47 (4.1)	43.1 (5.3)	35 (7.9)	11.9 (1.1)
TN (µg/L)	488 (46.3)	511 (109)	335.7 (66.9)	205.6 (24)	344.2 (57.7)	285.6 (26.2)
PO$_4$-P (µg/L)	40.2 (3.2)	52.5 (1.9)	37.9 (4.6)	28.2 (3.3)	26.0 (5)	18.8 (2.1)
TP (µg/L)	54.4 (5.3)	59.3 (4)	82.5 (8.7)	43.7 (2.8)	49.8 (6.3)	50.8 (6.7)
DOC (mg/L)	4.1 (0.3)	2.1 (0.1)	6.3 (0.4)	2.9 (0.3)	6.3 (0.4)	6.7 (0.2)
Temperature (°C)	4.5 (0.2)	7.3 (0.2)	7.9 (0.2)	7.1 (0.2)	11.1 (0.2)	11.9 (0.2)
Conductivity (µS/cm)	53.3 (5.5)	72.8 (5.3)	68.3 (8.6)	75.7 (6.5)	76.5 (9.4)	85.5 (11.4)
pH	7.6 (0.2)	7.8 (0.2)	7.3 (0.1)	7.9 (0.1)	7.6 (0.1)	7.1 (0.1)

Terrestrial N sources include several genera of N-fixing plants (for example, *Myrica, Shepherdia*, and *Dryas*), but primarily *Alnus* spp. Atmospheric N deposition in Alaska is low, averaging 0.58 kg ha^{-1} y^{-1} (sum of NH$_4$-N and NO$_3$-N deposition for Denali National Park; National Trends Network; http://nadp.sws.uiuc.edu/NTN/).

The streams selected for our study were all 1st-order streams of similar size. Watershed area ranged from 3.3 to 11.9 km^2, and streams were between 71 and 439 m in elevation (Table 1). Instantaneous discharge measured during the 8-wk study ranged from 0.02 to 0.09 m^3/s. The riffles within and among streams were selected so that depths and velocities experienced by deployed leaf packs were similar to minimize differences in breakdown caused by physical processing. At leaf-pack deployment, 4 velocity measurements were made at each rack in front of each pair of leaf packs (see *Leaf packs* for a description of the experimental setup). The mean current velocity for the 5 racks within each of the 6 streams ranged from 0.21 to 0.34 m/s. Riparian vegetation was dominated by bluejoint grass in most of the streams (Fig. 1A, B), but both willow and alder also grew in the riparian areas of some streams. Tree species that occurred at low densities in the riparian area included white spruce and birch.

Leaf packs

Senesced bluejoint grass (*Calamagrostis canadensis*) was collected in May from a single location in the riparian zone of stream 44, a stream with relatively low dissolved nutrient concentrations. The leaf material collected was dead from the previous year and would have entered the stream during the following spring snowmelt, which probably represents the largest litter pulse of the year (Huryn et al. 2001).

The leaf material was air-dry at collection time and was stored <2 wk prior to deployment. A sample was analyzed for initial C, N, and P content (see below). Leaf material was assembled into leaf packs consisting of 5.0 g ($\pm$0.1 g) of air-dry material, which was the equivalent of 4.06 g ash-free dry mass (AFDM; see below for method).

Forty leaf packs were assembled for each of 6 streams. In each stream, 8 leaf packs were attached to each of 5 wire-mesh racks deployed in separate riffles ≥10 m apart in early June. The wire-mesh racks were placed across the stream bed and anchored with rebar and rocks. Leaf packs were moistened with deionized water before deployment to minimize breakage losses and were attached to the racks with zip ties. A set of 5 leaf packs was deployed in stream 545 and retrieved immediately to determine handling losses (Hauer and Lamberti 2006). The oven-dry mass (65°C, 24 h) of the handling-loss leaf packs was averaged to determine the initial starting mass of the leaf packs for mass-loss calculations.

Leaf packs were incubated for a maximum of 8 wk. Ten bags (2 from each rack) were randomly collected every 2 wk and placed in individual Ziploc® bags to avoid loss during transport. Upon return to the lab, each leaf pack was rinsed over 2 nested sieves, 1 mm
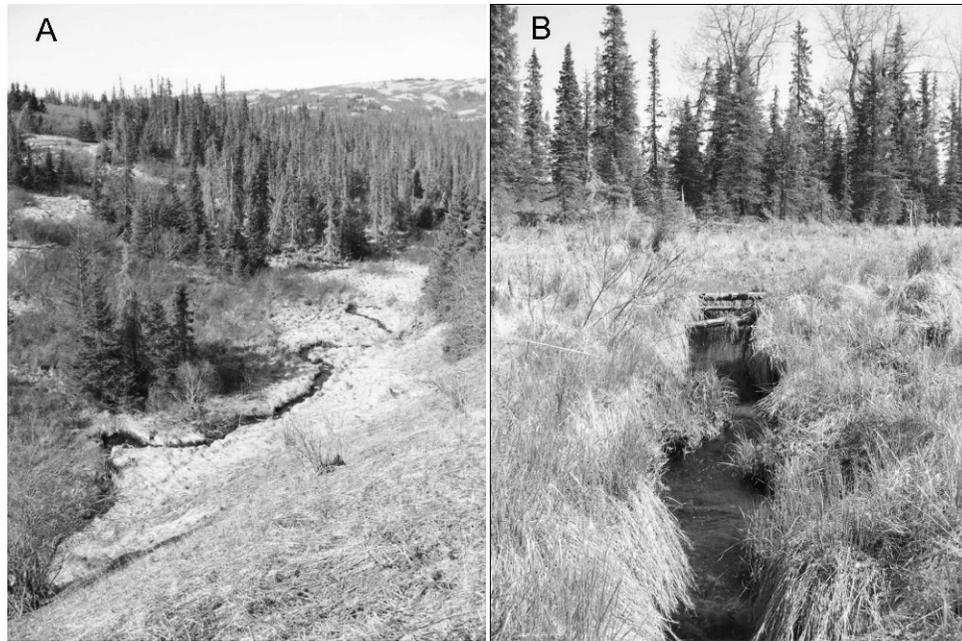
FIG. 1. Headwater stream valley bottom (A) and study reach (B). Bluejoint grass is a dominant riparian vegetation species, and dead litter reaches streams through lateral transport or from overhanging banks.

and 250 μm, to remove adhering debris and macroinvertebrates. Leaf material collected from the 1-mm sieve consisted of coarse particulate organic matter (CPOM; ≥1 mm) that had not yet decomposed to fine particulate organic matter (FPOM; <1 mm). CPOM was transferred from the 1-mm sieve to a plastic boat, dried at 65°C for 24 h, placed in a desiccator to cool, and weighed to obtain oven-dry mass. Large macroinvertebrates picked from the 1-mm sieve, and all organic material and organisms in the 250-μm sieve were preserved in 10% buffered formalin.

Oven-dried leaf material was homogenized initially in a coffee grinder. A subsample was subjected to secondary homogenization to a powder in a Mini-Beadbeater™ (Biospec Products, Bartlesville, Oklahoma). Subsamples of powdered leaf material (20–600 mg depending on amount of leaf material remaining) were placed in aluminum weigh pans, dried at 60°C overnight, placed in a desiccator to cool, and weighed to obtain an initial sample mass for AFDM calculations. Samples were then ignited at 550°C for 2 h and weighed again (Heiri et al. 2001). The proportion of AFDM was calculated for each subsample by subtracting the final mass (ash) from the initial sample mass and dividing by the initial sample mass. To calculate final AFDM, the oven-dry mass for each leaf pack was multiplied by the proportion of AFDM. Percentage remaining leaf mass was calculated by dividing the final AFDM by the initial AFDM. Approximately 6 to 8 mg of powdered

leaf material were weighed into 5 × 9-mm aluminum tins and % C and % N were estimated on a ThermoQuest Flash EATM 1112 elemental analyzer (CE Instruments, Hindley Green, UK). Percent P was estimated from digestions of 1 to 3 mg of material on a QuikChem 8500 flow-injection autoanalyzer (Lachat Instruments, Loveland, Colorado) with the molybdate colorimetric method (Faerovig and Hessen 2003).

Preserved macroinvertebrates were identified and counted from all leaf packs collected at 8 wk and from leaf packs collected from stream 1203 at 2, 4, and 6 wk. Stream 1203 was selected for evaluation of macroinvertebrate colonization because its high nutrient concentrations were expected to stimulate high diversity and abundance of macroinvertebrates on the leaf packs. Macroinvertebrates in most insect orders were identified to genus, except for Chironomidae (subfamily), Simuliidae (family), and early instars that could not be identified below order or family, with keys in Wiederholm 1983, Wiggins 1996, and Merritt et al. 2008. The remaining macroinvertebrates were identified to class or order (e.g., bivalves, gastropods, hydracaranids; Thorp and Covich 2001, Voshell 2002). Taxonomic references also were used to assign feeding habits for the macroinvertebrate taxa.

Stream physical and chemical variables

Water-temperature data loggers (HOBO® Pro v2; Onset Corporation, Bourne, Massachusetts) deployed

in each stream recorded temperature every 15 min for the duration of the decomposition study. In addition, water samples were collected for nutrient analysis, and in-situ water chemistry and stream discharge were measured simultaneously with leaf pack deployment and retrieval. A YSI 556 Multiprobe System (Yellow Springs Instruments, Yellow Springs, Ohio) was calibrated before each biweekly field event and was used to measure pH and conductivity. Instantaneous discharge was measured using a Marsh–McBirney Flo-Mate^{TM} flow meter and a top-setting wading rod (Marsh–McBirney, Frederick, Maryland). Water samples were analyzed for total N (TN), $NO_3 + NO_2$ (NO_x-N), NH_4-N, total P (TP), orthophosphate (PO_4-P), and dissolved organic C (DOC). Samples for dissolved nutrients were filtered in the field with a 0.45-µm filter and syringe. All water samples except for DOC were analyzed according to standard methods (APHA 2005) on a flow-injection autoanalyzer (Lachat QuikChem 8500 and Series 520 XYZ Autosampler). Analysis for NO_x-N followed the cadmium-reduction method. NH_4-N was analyzed using the phenelate method. TN was digested in persulfate and sodium hydroxide, buffered in boric acid, and run as above for NO_x-N. Stream NO_x-N and NH_4-N were summed to determine dissolved inorganic N (DIN). Water samples were analyzed for PO_4-P using the ammonium-molybdate method. TP samples were digested in persulfate and analyzed as above for PO_4-P. DOC samples were acidified using 50 µL of 6N HCl and analyzed with the high-temperature combustion method on a Shimadzu TOC-VCSH Analyzer and ASI-V Autosampler (Shimadzu, Kyoto, Japan) (APHA 2005).

Data analysis

All leaf decomposition endpoints (leaf mass, % C, % N, % P, and macroinvertebrate abundances) were averaged for the 2 leaf packs collected from each rack for a single time period. This procedure simplified the data set to 5 replicates each in 6 streams for every biweekly sampling period. Mass loss was approximated using an exponential decay model: $M_t = M_0 e^{-kt}$, where M_t is the mass at time t, M_0 is the initial mass, and k is the exponential decay coefficient (Graça et al. 2005). Decay coefficients were calculated as a function of time in days and degree days. Degree days were calculated by summing the average daily temperature for each incubation period in the individual streams.

Mean leaf % N and % P were compared to dissolved stream nutrient concentrations (DIN and PO_4-P) for each sampling period (2, 4, 6, and 8 wk) to examine the relationship between dissolved nutrient availability and microbial colonization (Bärlocher 1985). To determine whether changes in litter nutrient concentrations were the result of microbial immobilization of dissolved nutrients or leaching of C compounds, changes in the mass of nutrients also were evaluated (Findlay 2010). DIN was $log(x)$-transformed to improve normality. Stream nutrient concentrations were means of the samples collected before the sampling period (e.g., mean of 0 and 2 wk for the 2-wk regression, mean of 0, 2, and 4 wk for the 4-wk regression). A weighted regression model was used with stream nutrient concentrations predicting leaf % N and % P for each sampling period. The mean leaf % N and % P were weighted by $1/s^2$. Variance was based on the 5 racks in each stream.

Weighted regression also was used to examine the importance of stream nutrient concentrations, leaf nutrient concentrations, and macroinvertebrate indices (total no./g and total taxa/leaf pack) as predictors of the breakdown rate for all 6 streams. Means over the 8-wk study were used for stream nutrient concentrations and leaf nutrient concentrations. Macroinvertebrate indices were based on data from week 8.

Individual taxon abundances counted on each leaf pack at week 8 were standardized to numbers/mass remaining (g AFDM) and $log(x + 1)$-transformed. Nonmetric multidimensional scaling (NMS) was used to ordinate the multivariate macroinvertebrate community abundance data for the 5 racks in each of the 6 streams at 8 wk. The Bray–Curtis distance measure was used to transform the species matrix. The ordination was rotated to match the breakdown rate. The arrangement of sites along the 2nd axis was strongly driven by unique taxa present in 1 site. Therefore, NMS axis-1 scores were used to describe differences in macroinvertebrate community structure among the 6 streams in remaining analyses. The NMS axis-1 scores were used to predict the breakdown rate in a weighted regression to examine the relationship between macroinvertebrates and leaf decomposition. In addition, weighted averages were calculated from the NMS ordination for the 27 taxa that occurred in ≥1 stream. The weighted-average scores from NMS axis 1 were used to examine species locations along the stream gradient.

NMS was run (as described above) on the taxon abundances for the 2-, 4-, 6-, and 8-wk sampling periods to evaluate macroinvertebrate community succession over time on the leaf packs in stream 1203. Successional vectors showed the change in direction and magnitude of colonization from 2 to 8 wk. A multivariate permutation procedure was used to assess differences in community composition

between time periods. Indicator species analysis (ISA) was used to evaluate taxa significantly associated with each time period. ISA combines the relative abundance (concentration of abundance into a particular group) and relative frequency (proportion of sites in each group that contain the species) to calculate an indicator value for each species (McCune and Grace 2002). A species is assigned to the group for which it has the highest indicator value, and a permutation test ($n = 500$) is run to evaluate the probability that the indicator value is higher than would be obtained by chance.

All data analyses were done in the R statistical program (version 2.10.1; R Development Core Team, Vienna, Austria). The nlme library was used for the mixed models (Pinheiro et al. 2009), vegan and ecodist libraries were used for the multivariate macroinvertebrate analysis (Goslee and Urban 2007, Oksanen et al. 2009), labdsv was used for ISA (Roberts 2010), and plotrix and stringr were used for graphical functions (Lemon et al. 2009, Wickham 2010).

Results

Stream water chemistry

Mean stream DIN concentrations ranged from 11.9 to 338.8 µg/L, and PO_4-P concentrations ranged from 18.8 to 52.5 µg/L among streams (Table 1). Stream DIN was correlated with stream PO_4-P ($r^2 = 0.79$, $p = 0.02$). DOC concentrations were relatively high in all streams and ranged from 2.1 to 6.7 mg/L. DOC was not correlated with DIN or PO_4-P ($p > 0.05$). Average daily stream temperatures ranged from 4.5 to 11.9°C. Velocity was similar among streams.

Leaf-pack breakdown rates among streams

The amount of leaf material remaining among the 6 streams ranged from 71 to 82% at the end of the 8-wk study (Fig. 2A, B). Total degree days for the 6 streams ranged from 260 to 670. Breakdown rates per day (d^{-1}) ranged from 0.0035 to 0.0060 (Table 2), whereas rates per degree day (dd^{-1}) ranged from 0.0003 to 0.0009.

Stream nutrient concentrations were strongly related to the leaf breakdown rate (dd^{-1}). DIN explained more variance in leaf breakdown than did PO_4-P ($r^2 = 0.94$, $p = 0.003$ and $r^2 = 0.67$, $p = 0.03$, respectively; Fig. 3A, B). Week-8 leaf nutrient concentrations and macroinvertebrate indices were both positively associated with leaf breakdown rates. Leaf % P explained more variance in leaf breakdown rates than did leaf % N ($r^2 = 0.96$, $p = 0.02$ and $r^2 = 0.72$, $p < 0.001$, respectively; Fig. 3C, D). Total macroinvertebrates (no./g) and the NMS axis-1 scores were both good
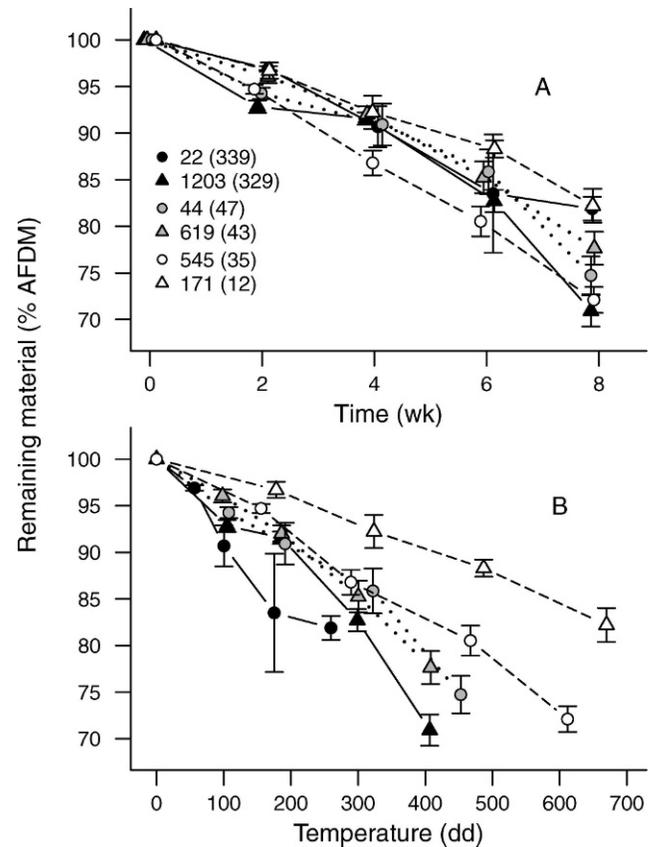
FIG. 2. Mean (± 1 SE; $n = 5$) remaining material (% ash-free dry mass [AFDM]) as a function of time (A) and temperature (in degree days [dd]) (B) for the same period in 6 streams in the Kenai Peninsula, Alaska. Numbers in key to symbol are stream identifiers, with dissolved inorganic N concentrations (µg/L) in parentheses.

predictors of leaf breakdown and explained 73% and 80% of the variance in the breakdown rate, respectively ($p = 0.02$ for both). Total macroinvertebrate taxa (no./leaf pack) was not strongly related to leaf breakdown ($r^2 = 0.41$, $p = 0.09$).

Litter nutrient concentration

The N content of senesced bluejoint leaves collected in early May was 0.38%. At the end of the 8-wk study, leaf N in the 6 streams ranged from 0.45 to 0.78% (Fig. 4A). The average mass of N in the leaf packs for the 6 streams increased from 0.015 g initially to 0.022 g at 2 wk, a result indicating that immobilization of nutrients in the leaf packs led to increasing nutrient concentrations. Leaf P was 0.08% at the start of the study and ranged from 0.07 to 0.12% by week 8 (Fig. 4B). The average mass of P in the leaf packs for the 6 streams increased from 0.0032 g initially to 0.0035 g by 2 wk. The amount of variation explained

TABLE 2. Mean (SE; $n = 5$) leaf breakdown rates (k) per day and degree day (dd) for 6 streams arranged in order of decreasing dissolved inorganic N (DIN) concentrations.

Stream	DIN (µg/L)	k (d^{-1})	R^2	k (dd^{-1})	R^2
22	339	0.0041 (0.0009)	0.47	0.0009 (0.00019)	0.46
1203	329	0.0060 (0.0005)	0.88	0.0008 (0.00006)	0.89
44	47	0.0048 (0.0005)	0.80	0.0006 (0.00006)	0.82
619	43	0.0044 (0.0004)	0.87	0.0006 (0.00004)	0.88
545	35	0.0059 (0.0003)	0.93	0.0005 (0.00003)	0.93
171	12	0.0035 (0.0003)	0.83	0.0003 (0.00003)	0.84

(r^2) in the weighted regressions between stream nutrient concentrations and leaf nutrient concentrations increased strongly from 2 to 6 wk and remained high at 8 wk (Fig. 5). The amount of variation explained in the weighted regressions for leaf nutrient concentrations at 8 wk as a function of mean stream nutrient concentrations over the 8-wk study ranged from $r^2 = 0.65$ to 0.92 (Fig. 6A–D).

Colonization of litter by macroinvertebrates

Total macroinvertebrate abundance (no./g) at week 8 ranged from 41 to 82 in the 6 streams (Table 3). The number of taxa on each leaf pack ranged from 13 to 18. Of the 44 total taxa, 12 occurred in all 6 streams. The 3 most-abundant taxa were Orthocladinae (Diptera, dominated by *Brillia* sp., a shredder), *Zapada* sp. (Plecoptera, shredder), and Ostracoda (Table 4). Oth-

er common taxa that occurred in ≥2 streams included several shredders (Limnephilidae and *Psychoglypha* sp.), scrapers (Diamesinae, *Baetis* sp.), and predators (Tanypodinae, *Dicranota* sp., *Rhyacophila* sp.).

The NMS ordination of the macroinvertebrate communities on leaf packs over time from Stream 1203 indicated a consistent colonization pattern across all 5 racks (Fig. 7). Communities changed in the same
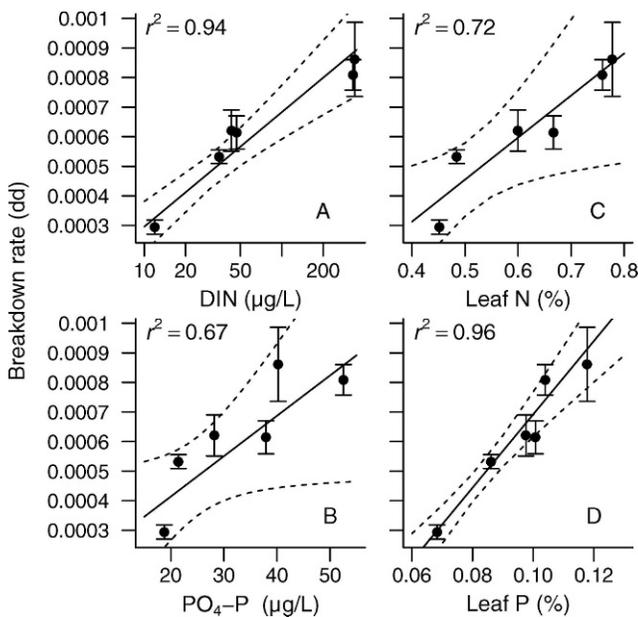
FIG. 3. Mean (±1 SE; $n = 5$) leaf breakdown rates (in degree days [dd]) predicted by stream dissolved inorganic N (DIN) (axis log-transformed) concentrations (A), stream PO$_4$-P concentrations (B), leaf % N at 8 wk (C), and leaf % P at 8 wk (D). Dashed curves show 95% confidence intervals.
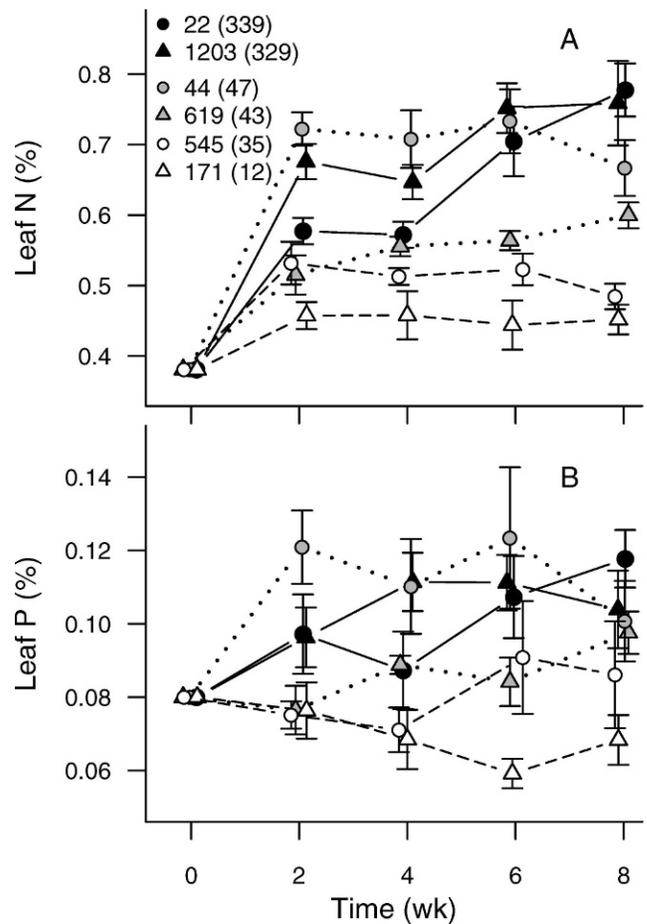
FIG. 4. Mean (±1 SE; $n = 5$) N (A) and P (B) content of bluejoint grass litter decomposing over 8 wk in 6 streams. Numbers in key to symbol are stream identifiers, with dissolved inorganic N concentrations (µg/L) in parentheses.
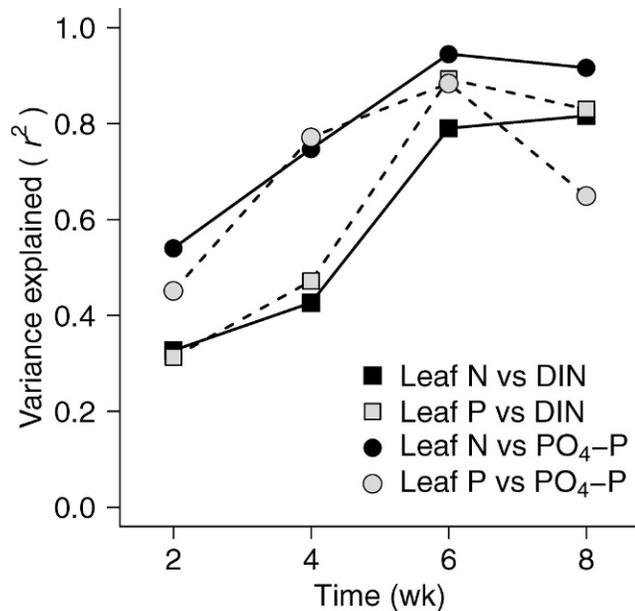
FIG. 5. r^2 values over time for weighted regressions for litter nutrient concentrations as functions of stream nutrient concentrations.

FIG. 6. Mean (± 1 SE; $n = 5$) leaf % N (A, B) and % P (C, D) at 8 wk predicted by stream dissolved inorganic N (DIN) (axis log-transformed) (A, C) and stream PO_4-P (B, D) concentrations. Dashed curves show 95% confidence intervals.

direction (increasing along the 1st axis) except for 1 rack from week 2 to week 4. The magnitude of the shift increased slightly from week 2 to week 6, but shifted substantially more between week 6 and week 8. The multivariate permutation test showed that groups were significantly different between time periods ($p = 0.002$). ISA results identified 11 significant taxa associated with the leaf packs at 8 wk and only 1 significant taxon at 2 and 6 wk (Table 5). Taxa that were strongly associated with leaf packs collected at 8 wk included the shredders *Psychoglypha* and *Zapada*, collector-gatherers (*Ecclisomyia* sp., *Pericoma* sp., and Chironominae), and predators (*Dicranota* and *Rhyacophila*). Diamesinae and Tanytarsini colonized leaf packs at 2 and 6 wk, respectively. Both are collector-gatherers as well as filterers and scrapers.

Discussion

Bluejoint grass is a dominant riparian species along headwater streams of the Kenai Peninsula, but little is known of its contribution to total productivity in these systems. Breakdown rates measured for 6 headwater streams showed that bluejoint grass decomposes slowly, a result that is consistent with data on grass decomposition in other streams (Webster and Benfield 1986, Young et al. 1994). The slow breakdown rate of bluejoint grass in our streams (20–30% mass loss over 2 mo) can be explained by its low initial nutrient concentration and low stream temperatures.

More than 1 growing season may be required for complete breakdown of bluejoint litter in the streams of the Kenai Peninsula.

The nutrient concentrations of riparian bluejoint grass may be higher in watersheds where flow paths draining upland alder stands provide dissolved N to plant roots. Several studies have shown that the N concentration of leaf litter is positively associated with the breakdown rate (Richardson et al. 2004, Hladyz et al. 2009). Bluejoint grass collected from watersheds with high alder cover may decompose more rapidly than the bluejoint grass used in our study.

Dissolved nutrients in stream water positively affected litter decomposition and, therefore, nutrient cycling in our study streams. Dissolved nutrients can be assimilated by decomposers. This assimilation may be especially important for substrates, such as bluejoint grass, that have low nutrient concentrations. Litter nutrient concentrations also increased along the stream nutrient gradient, a result indicating that dissolved nutrients were limiting to decomposers colonizing the bluejoint grass. Other correlative studies have provided evidence for increased leaf decomposition along stream nutrient gradients (Young et al. 1994, Suberkropp and Chauvet 1995), but differences are often related to anthropogenic activities, and other variables can confound the relationship between decomposition and nutrients (Niyogi et al. 2003, Chadwick et al. 2006). In our study

TABLE 3. Mean (SE; $n = 5$) total macroinvertebrates per g of leaf litter remaining and total taxa after 8 wk in bluejoint leaf packs. Streams are arranged in order of decreasing dissolved inorganic N (DIN) concentrations.

Stream	Total macroinvertebrates/g leaf litter remaining	Total taxa
22	67 (10)	16 (0.8)
1203	82 (13)	18 (0.9)
44	48 (11)	14 (1.5)
619	73 (3)	15 (0.4)
545	76 (5)	18 (1.4)
171	41 (8)	13 (0.6)

system, differences in stream N concentrations are driven by alder cover in the watershed (Shaftel et al. 2010). Cover by N-fixing alder reaches up to 28% in 1st-order watersheds on the lower Kenai Peninsula and explains 75 to 96% of the variation in stream NO_x-N concentrations. N fixed by alder reaches streams through leaching and lateral transport of surface and groundwater from riparian zones and upland alder stands (Compton et al. 2003, Cairns and Lajtha 2005).

DIN explained more variation in the breakdown rate than did PO_4-P, a result indicating that DIN may be the nutrient most limiting to the stream heterotrophic community. PO_4-P concentrations were relatively high because of deposition of P-rich volcanic ash and was well above levels typically associated with P limitation for all 6 streams. Accordingly, DIN:PO_4-P ratios were quite low in all streams (0.6–8.4), further evidence that stream production is N limited. Thus, the significant increases in % P on leaf packs in high DIN streams probably were related to reduced N limitation, which allowed greater uptake of P (Cross et al. 2003, Ferreira et al. 2006).

Litter nutrient concentrations, macroinvertebrate densities, and macroinvertebrate composition all were associated with bluejoint grass breakdown rates. In low-order streams, the breakdown of leaf litter is attributed to shredding invertebrates (Graça et al. 2001, Hieber and Gessner 2002). The dominant shredding macroinvertebrates (either *Zapada* or limnephilid caddisflies) were found in all 6 streams. Their distribution along NMS axis 1 indicates that they probably contributed to the breakdown of bluejoint litter across the nutrient gradient. The strong association between litter nutrient concentrations and the bluejoint litter breakdown rate indicates that fungi and other heterotrophic microbes also played a part in the breakdown of bluejoint litter. Fine-mesh bags could be used to exclude macroinvertebrates (Chung and Suberkropp 2008) to measure the relative effects

of microbes vs shredders on the breakdown rate in these headwater ecosystems in future studies.

Despite the low nutrient concentration of bluejoint litter, macroinvertebrate densities in bluejoint litter packs 8 wk after deployment were similar to densities reported in decomposition studies of other grasses and lower than low-quality tree litter. Macroinvertebrate densities ranged from <10 to >50/g tussock grass litter in litter packs placed in 6 small streams along a nutrient gradient (Young et al. 1994). In our study, total macroinvertebrates/g of leaf pack in our high-nutrient streams exceeded the densities reported by Young et al. (1994) for tussock grass litter packs and were lower than densities found in birch litter packs (125 macroinvertebrates/g dry mass). Birch is a relatively low-quality deciduous tree litter (leaf % N = 0.7–0.8; Haapala et al. 2001).

Bluejoint litter supported a relatively diverse macroinvertebrate assemblage. Macroinvertebrate compositional information has not been reported in other studies from the lower Kenai Peninsula, but an average of 12 genera per pack was reported in an extensive decomposition study in 119 streams in British Columbia (Sylvestre and Bailey 2005). A mean of 16 taxa were recorded per pack in our study, and this number would have been much higher had chironomid subfamilies been keyed to genus. In addition to shredders, other frequent taxa, such as *Baetis* mayflies, probably used the bluejoint litter as a food resource by scraping microbes from the conditioned leaf litter (Merritt et al. 2008). Leaf packs also could have been used as habitat by filterers or collectors (chironomid midges and simuliid black flies) and as potential sources of prey by predators (*Dicranota* craneflies and *Rhyacophila* caddisflies) (Merritt et al. 2008). The diversity of macroinvertebrate taxa found in the bluejoint litter packs provides evidence that bluejoint litter is an important food resource and habitat in headwater stream ecosystems.

The colonization pattern of the leaf packs in stream 1203 and the high number of indicator taxa at 8 wk indicated that microbial conditioning was important to macroinvertebrates. Fungi and bacteria improve the palatability of leaf litter by providing a high-nutrient food resource and via enzymatic breakdown of structural compounds (Cummins and Klug 1979, Cummins et al. 1989, Graça 2001). In our study, stream nutrient concentrations positively affected litter nutrient concentrations (probably associated with microbial colonization) on the bluejoint litter. The increase in mass of N and P in the leaf packs at 2 wk and the strong relationship between stream nutrient concentrations and litter nutrient concentrations at 6 and 8 wk provide inferential evidence that

TABLE 4. Macroinvertebrate abundances, frequencies, nonmetric multidimensional scaling (NMS) scores, and feeding habits for taxa that occurred in ≥2 streams. Taxa are sorted in order of descending NMS scores. Freq = frequency, C-G = collector-gatherer, C-F = collector-filterer, D = detritivore, H = herbivore, P = predator, Sc = scraper.

Taxon	NMS scores	Stream abundance (no./g)						Freq (%)	Mean no./g	Feeding habit
		22	1203	44	619	545	171			
Heptageniidae (Ephemeroptera)	0.470	0.16	0.07	0.00	0.00	0.03	0.00	50	0.04	Generally Sc, C-G
Chironominae (Diptera)	0.270	0.36	0.44	0.00	0.00	0.00	0.00	33	0.13	Generally C-G and C-F
Podonominae (Diptera)	0.237	0.07	0.10	0.00	0.00	0.00	0.00	33	0.03	Generally C-G, Sc
Simuliidae (Diptera)	0.232	0.38	0.00	2.12	1.55	1.51	0.00	67	0.93	Generally C-F
Baetis (Ephemeroptera)	0.225	11.31	0.39	4.19	0.45	3.15	0.31	100	3.30	C-G (diatoms, detritus), Sc
Isoperla (Plecoptera)	0.206	0.10	0.00	0.00	0.00	0.24	0.00	33	0.06	P (engulfers), facultative C-G
Rhyacophila (Trichoptera)	0.204	1.57	2.16	0.00	2.32	0.07	0.00	67	1.02	P (engulfers), Sc, C-G, Sh-H (chewers)
Zapada (Plecoptera)	0.140	17.42	20.20	0.13	15.28	17.63	1.64	100	12.05	Sh-D (leaf litter) -H (moss)
Probezzia (Diptera)	0.123	0.00	0.04	0.00	0.00	0.24	0.00	33	0.05	P (engulfers)
Turbellaria	0.092	0.26	7.90	0.04	4.75	1.52	0.03	100	2.42	Generally P (engulfers and piercers), C-G
Pericoma (Diptera)	0.086	0.00	0.57	0.07	0.06	0.57	0.00	67	0.21	C-G
Diamesinae (Diptera)	0.081	1.47	6.27	12.74	0.16	1.75	0.09	100	3.75	Generally C-G, Sc
Ecclisomyia (Trichoptera)	0.064	0.00	1.05	0.00	1.95	0.07	0.06	67	0.52	C-G, Sc
Chelifera (Diptera)	0.055	0.03	0.68	0.16	0.51	0.03	0.03	100	0.24	Unknown
Orthocladiinae (Diptera)	0.029	28.55	25.24	17.99	26.18	27.91	10.91	100	22.80	Generally C-G, Sc
Limnephilidae (Trichoptera)	0.020	0.19	0.27	0.66	0.27	0.44	0.06	100	0.32	Generally Sh-D (chewers), C-G, Sc
Ephemerella (Ephemeroptera)	0.019	0.00	0.00	0.07	0.00	1.86	0.00	33	0.32	C-G, Sc
Dicranota (Diptera)	0.012	0.15	0.29	0.89	0.59	0.30	0.39	100	0.43	P (engulfers)
Clinocera (Diptera)	−0.011	0.03	0.18	0.00	0.07	0.06	0.06	83	0.07	Unknown
Hydrachnida	−0.013	0.30	3.28	0.56	1.38	4.63	1.03	100	1.86	Generally P (piercers), parasites, C-G, H (piercers)
Oligochaeta	−0.070	0.55	6.18	1.20	0.71	1.79	1.97	100	2.07	Generally C-G, P (engulfers)
Ostracoda	−0.080	2.38	5.13	0.68	16.05	9.45	14.17	100	7.98	H (algae), D
Psychoglypha (Trichoptera)	−0.273	0.00	0.24	3.17	0.00	1.09	1.47	67	0.99	C-G, Sh-D (chewers, including scavengers)
Tanypodinae (Diptera)	−0.337	0.03	0.84	0.42	0.31	1.14	4.49	100	1.21	Generally P (engulfers and piercers)
Tanytarsini (Diptera)	−0.362	1.05	0.40	0.00	0.03	0.00	3.11	67	0.76	Generally C-F and G
Grensia (Trichoptera)	−0.365	0.00	0.00	0.95	0.00	0.00	0.03	33	0.16	Unknown
Pisidium	−0.889	0.00	0.00	0.03	0.00	0.00	0.06	33	0.01	C-F
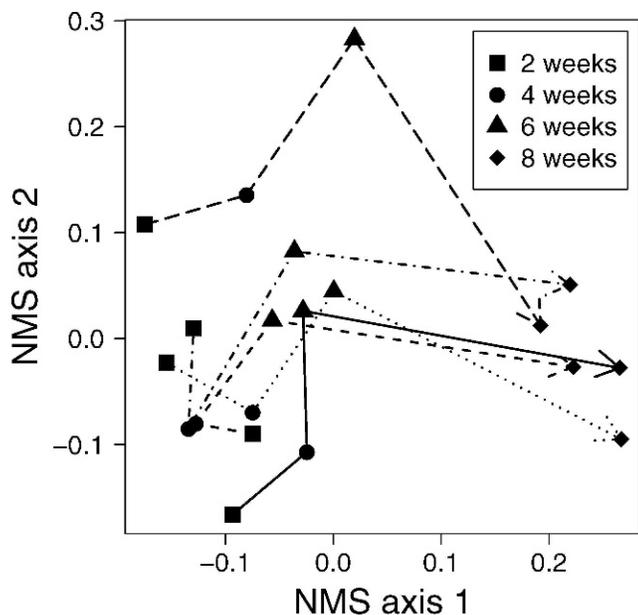
FIG. 7. Nonmetric multidimensional scaling (NMS) ordination for leaf packs arranged on 5 racks and decomposing over 8 wk in Stream 1203. Lines connect values for a single rack and arrows show the direction of change over time.

TABLE 5. Indicator species analysis (ISA) results for taxa in leaf packs over time in Stream 1203. Indicator value combines frequency and abundance of an individual taxon to show affinity for a specific group (time). Significance of group assignments was determined with a permutation test ($n = 500$).

| | | Indicator | |
Taxon name	Weeks	value	p-value
Diamesinae (Diptera)	2	0.34	0.006
Tanytarsini (Diptera)	6	0.44	0.020
Ecclisomyia (Trichoptera)	8	1.00	0.002
Pericoma (Diptera)	8	0.73	0.004
Psychoglypha (Trichoptera)	8	0.71	0.006
Dicranota (Diptera)	8	0.65	0.006
Ostracoda	8	0.63	0.002
Chironominae (Diptera)	8	0.55	0.038
Oligochaeta	8	0.52	0.002
Rhyacophila (Trichoptera)	8	0.42	0.002
Turbellaria	8	0.41	0.002
Zapada (Plecoptera)	8	0.35	0.002
Hydrachnida	8	0.34	0.026

microbes were using dissolved nutrients and colonizing the leaf litter. The conditioning period for bluejoint took ~6 wk and was followed by a dramatic change in macroinvertebrate community composition. Macroinvertebrates can become food resources for juvenile salmonids when they enter the drift, either accidentally or during emergence (Nielsen 1992). Because of the slow breakdown rate of bluejoint litter, longer deployments would be helpful for further examination of the role of taxa observed at 8 wk. In addition, either stable-isotope or gut-content analysis could be used to measure directly the importance of bluejoint litter to macroinvertebrates in stream food webs.

Alder cover in these watersheds drives stream N concentrations and may affect litter decomposition. Increased temperatures resulting from climate change in southcentral Alaska are associated with higher incidences of insect outbreaks and forest fires (Soja et al. 2007). The decrease in forest canopy cover after large-scale disturbances may allow increased alder cover either initially or during forest succession (Werner et al. 2006). In addition, warmer temperatures on the Kenai Peninsula over the last 50 y have been linked to expansion of woody vegetation into drying wetlands (Klein et al. 2005). Should any of these drivers increase alder cover, litter nutrient concentrations and stream N concentrations might

increase and positively affect the rate at which allochthonous material decomposes in headwater streams.

Literature Cited

APHA (AMERICAN PUBLIC HEALTH ASSOCIATION). 2005. Standard methods for the examination of water and wastewater. 21st edition. American Public Health Association, American Water Works Association, and Water Environment Federation, Washington, DC.

BÄRLOCHER, F. 1985. The role of fungi in the nutrition of stream invertebrates. Botanical Journal of the Linnean Society 91:83–94.

BENFIELD, E. F. 1997. Comparison of litterfall input to streams. Journal of the North American Benthological Society 16:104–108.

CAIRNS, M. A., AND K. LAJTHA. 2005. Effects of succession on nitrogen export in the west-central Cascades, Oregon. Ecosystems 8:583–601.

CHADWICK, M. A., D. R. DOBBERFUHL, A. C. BENKE, A. D. HURYN, K. SUBERKROPP, AND J. E. THIELE. 2006. Urbanization affects stream ecosystem function by altering hydrology, chemistry, and biotic richness. Ecological Applications 16:1796–1807.

CHUNG, N., AND K. SUBERKROPP. 2008. Influence of shredder feeding and nutrients on fungal activity and community structure in headwater streams. Fundamental and Applied Limnology 173:35–46.

COMPTON, J. E., M. R. CHURCH, S. T. LARNED, AND W. E. HOGSETT. 2003. Nitrogen export from forested watersheds in the Oregon Coast Range: the role of N_2-fixing red alder. Ecosystems 6:773–785.

CROSS, W. F., J. P. BENSTEAD, A. D. ROSEMOND, AND J. B. WALLACE. 2003. Consumer-resource stoichiometry in detritus-based streams. Ecology Letters 6:721–732.

CUMMINS, K. W., AND M. J. KLUG. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics 10:147–172.

CUMMINS, K. W., M. A. WILZBACH, D. M. GATES, J. B. PERRY, AND W. B. TALIAFERRO. 1989. Shredders and riparian vegetation. BioScience 39:24–30.

DOUCETT, R. R., G. POWER, D. R. BARTON, R. J. DRIMMIE, AND R. A. CUNJAK. 1996. Stable isotope analysis of nutrient pathways leading to Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences 53:2058–2066.

DUGDALE, R. C., AND V. A. DUGDALE. 1961. Sources of phosphorus and nitrogen for lakes on Afognak Island. Limnology and Oceanography 6:13–23.

FAERØVIG, P. J., AND D. O. HESSEN. 2003. Allocation strategies in crustacean stoichiometry: the potential role of phosphorus in the limitation of reproduction. Freshwater Biology 48:1782–1792.

FERREIRA, V., V. GULIS, AND M. A. S. GRAÇA. 2006. Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. Oecologia (Berlin) 149:718–729.

FINDLAY, S. 2010. Stream microbial ecology. Journal of the North American Benthological Society 29:170–181.

GESSNER, M. O., AND E. CHAUVET. 1994. Importance of stream microfungi in controlling breakdown rates of leaf litter. Ecology 75:1807–1817.

GOSLEE, S. C., AND D. L. URBAN. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22:1–19.

GRAÇA, M. A. S. 2001. The role of invertebrates on leaf litter decomposition in streams – a review. International Review of Hydrobiology 86:383–393.

GRAÇA, M. A. S., F. BÄRLOCHER, AND M. O. GESSNER (EDITORS). 2005. Methods to study litter decomposition. Springer, Dordrecht, The Netherlands.

GRAÇA, M. A. S., R. C. F. FERREIRA, AND C. N. COIMBRA. 2001. Litter processing along a stream gradient: the role of invertebrates and decomposers. Journal of the North American Benthological Society 20:408–420.

GRACZ, M., P. NORTH, K. NOYES, G. TANDE, AND D. VAN PATTEN. 2004. Wetlands of the Kenai Lowlands: a landscape-level wetland management tool. Kenai Watershed Forum, Fritz Creek, Alaska. (Available from: http://www.kenaiwetlands.net/)

GREENWOOD, J. L., A. D. ROSEMOND, J. B. WALLACE, W. F. CROSS, AND H. S. WEYERS. 2007. Nutrients stimulate leaf breakdown rates and detritivore biomass: bottom-up effects via heterotrophic pathways. Oecologia (Berlin) 151:637–649.

GULIS, V., AND K. SUBERKROPP. 2003. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. Freshwater Biology 48:123–134.

HAAPALA, A., T. MUOTKA, AND A. MARKKOLA. 2001. Breakdown and macroinvertebrate and fungal colonization of alder, birch, and willow leaves in a boreal forest stream. Journal of the North American Benthological Society 20:395–407.

HAUER, R. F., AND G. A. LAMBERTI (EDITORS). 2006. Methods in stream ecology. 2nd edition. Academic Press, San Diego, California.

HEIRI, O., A. F. LOTTER, AND G. LEMCKE. 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of Paleolimnology 25:101–110.

HIEBER, M., AND M. O. GESSNER. 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. Ecology 83:1026–1038.

HLADYZ, S., M. O. GESSNER, P. S. GILLER, J. POZO, AND G. WOODWARD. 2009. Resource quality and stoichiometric constraints on stream ecosystem functioning. Freshwater Biology 54:957–970.

HURYN, A. D., R. H. RILEY, R. G. YOUNG, C. J. ARBUCKLE, K. PEACOCK, AND G. LYON. 2001. Temporal shift in contribution of terrestrial organic matter to consumer production in a grassland river. Freshwater Biology 46:213–226.

JUNGER, M., AND D. PLANAS. 1994. Quantitative use of stable carbon-isotope analysis to determine the trophic base of invertebrate communities in a boreal forest lotic system. Canadian Journal of Fisheries and Aquatic Sciences 51:52–61.

KLEIN, E., E. E. BERG, AND R. DIAL. 2005. Wetland drying and succession across the Kenai Peninsula Lowlands, south-central Alaska. Canadian Journal of Forest Resources 35:1931–1941.

LEBERFINGER, K., AND I. BOHMAN. 2010. Grass, mosses, algae, or leaves? Food preference among shredders from open-canopy streams. Aquatic Ecology 44:195–203.

LEMON, J., B. BOLKER, S. OOM, E. KLEIN, B. ROWLINGSON, H. WICKHAM, A. TYAGI, O. ETERRADOSSI, G. GROTHENDIECK, AND M. TOEWS. 2009. plotrix: various plotting functions. R package version 2.7-2. R Project for Statistical Computing, Vienna, Austria.

MCCUNE, B., AND J. B. GRACE. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

MCTAMMANY, M. E., E. F. BENFIELD, AND J. R. WEBSTER. 2008. Effects of agriculture on wood breakdown and microbial biofilm respiration in southern Appalachian streams. Freshwater Biology 53:842–854.

MENNINGER, H. L., AND M. A. PALMER. 2007. Herbs and grasses as an allochthonous resource in open-canopy headwater streams. Freshwater Biology 52:1689–1699.

Merritt, R. W., K. W. Cummins, and M. B. Berg (editors). 2008. An introduction to the aquatic insects of North America. 4th edition. Kendall/Hunt, Dubuque, Iowa.

Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121:617–634.

Niyogi, D. K., K. S. Simon, and C. R. Townsend. 2003. Breakdown of tussock grass in streams along a gradient of agricultural development in New Zealand. Freshwater Biology 48:1698–1708.

Oksanen, J., K. Roeland, P. Legendre, B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2009. vegan: community ecology package. R package version 1.15-4. R Project for Statistical Computing, Vienna, Austria.

Perry, R. W., M. J. Bradford, and J. A. Grout. 2003. Effects of disturbance on contribution of energy sources to growth of juvenile chinook salmon (Oncorhynchus tshawytscha) in boreal streams. Canadian Journal of Fisheries and Aquatic Sciences 60:390–400.

Ping, C. L., and G. J. Michaelson. 1986. Phosphorus sorption by major agricultural soils of Alaska. Communications in Soil Science and Plant Analysis 17:299–320.

Pinheiro, J., D. Bates, S. Debroy, S. Deepayan, R Core Team. 2009. nlme: linear and nonlinear mixed effects models. R package version 3.1-96. R Project for Statistical Computing, Vienna, Austria.

Reynolds, K. M. 1990. Preliminary classification of forest vegetation of the Kenai Peninsula, Alaska. Research Paper PNW-RP-424. Pacific Northwest Research Station, US Department of Agriculture Forest Service, Portland, Oregon. (Available from: http://www.fs.fed.us/pnw/pubs/pnw_rp424)

Richardson, J. S., and R. J. Danehy. 2007. A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. Forest Science 53:131–147.

Richardson, J. S., C. R. Shaughnessy, and P. G. Harrison. 2004. Litter breakdown and invertebrate association with three types of leaves in a temperate rainforest stream. Archiv für Hydrobiologie 159:309–325.

Roberts, D. W. 2010. labdsv: ordination and multivariate analysis for ecology. R package version 1.4-1. R Project for Statistical Computing, Vienna, Austria.

Robinson, C. T., and M. O. Gessner. 2000. Nutrient addition accelerates leaf breakdown in an alpine springbrook. Oecologia (Berlin) 122:258–263.

Scarsbrook, M. R., and C. R. Townsend. 1994. The roles of grass leaf litter in streams draining tussock grassland in New Zealand: retention, food supply and substrate stabilization. Freshwater Biology 32:429–443.

Shaftel, R. S., R. S. King, and J. A. Back. 2010. Alder cover drives nitrogen availability in Kenai lowland headwater streams, Alaska. Biogeochemistry doi:10.1007/s10533-010-9541-3

Soja, A. J., N. M. Tchebakova, N. H. F. French, M. D. Flannigan, H. H. Shugart, B. J. Stocks, A. I. Sukhinin, E. I. Parfenova, F. S. Chapin, and P. W. Stackhouse. 2007. Climate-induced boreal forest change: predictions versus current observations. Global and Planetary Change 56:274–296.

Suberkropp, K., and E. Chauvet. 1995. Regulation of leaf breakdown by fungi in streams: influences of water chemistry. Ecology 76:1433–1445.

Sylvestre, S., and R. C. Bailey. 2005. Ecology of leaf pack macroinvertebrate communities in streams of the Fraser River Basin, British Columbia. Freshwater Biology 50:1094–1104.

Tank, J. L., E. J. Rosi-Marshall, N. A. Griffiths, S. A. Entrekin, and M. L. Stephen. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. Journal of the North American Benthological Society 29:118–146.

Thorp, J. H., and A. P. Covich (editors). 2001. Ecology and classification of North American freshwater invertebrates. 2nd edition. Academic Press, San Diego, California.

Viereck, L. A., C. T. Dyrness, A. R. Batten, and K. J. Wenzlick. 1992. The Alaska vegetation classification. General Technical Report PNW-GTR-286. Pacific Northwest Research Station, US Department of Agriculture Forest Service, Portland, Oregon. (Available from: http://www.fs.fed.us/pnw/publications/pnw_gtr286/)

Voshell, J. R. 2002. A guide to common freshwater invertebrates of North America. McDonald and Woodward Publishing Company, Blacksburg, Virginia.

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

Werner, R. A., E. H. Holsten, S. M. Matsuoka, and R. E. Burnside. 2006. Spruce beetles and forest ecosystems in south-central Alaska: a review of 30 years of research. Forest Ecology and Management 227:195–206.

Wickham, H. 2010. stringr: make it easier to work with strings. R package version 0.3. R package version 1.15-4. R Project for Statistical Computing, Vienna, Austria.

Wiederholm, T. (editor). 1983, Chironomidae of the Holarctic Region. Keys and diagnoses. Part 1. Larvae. Entomologica Scandinavica Supplement 19.

Wiggins, G. B. 1996. Larvae of the North American caddisfly genera (Trichoptera). 2nd edition. University of Toronto Press, Toronto, Ontario.

Wipfli, M. S., J. S. Richardson, and R. J. Naiman. 2007. Ecological linkages between headwaters and downstream ecosystems: transport of organic matter, invertebrates, and wood down headwater channels. Journal of the American Water Resources Association 43:72–85.

Young, R. G., A. D. Huryn, and C. R. Townsend. 1994. Effects of agricultural development on processing of tussock leaf litter in high country New Zealand streams. Freshwater Biology 32:413–427.

Zeug, S. C., and K. O. Winemiller. 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89:1733–1743.