ABSTRACT

Alder Cover Drives Nitrogen Availability and Decomposition of Grass Litter in Salmon-Rearing Headwater Streams, Kenai Peninsula, Alaska

Rebecca S. Shaftel, M.S.

Committee Chairperson: Ryan King, Ph.D.

Terrestrial sources of nitrogen (N), such as N fixed by alder, may be important for sustaining production in headwater streams that typically lack subsidies of nutrients from spawning salmon. High nutrient concentrations in streams increase litter decomposition and can offset the low nutrient quality of grass litter. Alder cover was compared to watershed physiographic variables as predictors of stream N and contrasted over the growing season among 25 headwater streams. Leaf packs of bluejoint grass were deployed for two months across a nutrient gradient of 6 headwater streams. Alder cover explained over 75 – 96% of the variance in stream N. Bluejoint breakdown rates were related to dissolved stream nutrient concentrations and litter quality. A diversity of macroinvertebrate consumers utilized bluejoint for habitat and food. Alder drives stream N concentrations and the breakdown rate of bluejoint, which is an important consumer resource during the summer months when deciduous litter inputs are low.

Alder Cover Drives Nitrogen Availability and Decomposition of Grass Litter in Salmon-Rearing Headwater Streams, Kenai Peninsula, Alaska

by

Rebecca S. Shaftel, B.S.

A Thesis

Approved by the Department of Biology

Robert D. Doyle, Ph.D., Chairperson

Submitted to the Graduate Faculty of
Baylor University in Partial Fulfillment of the
Requirements for the Degree
of
Master of Science

Approved by the Thesis Committee

Ryan S. King, Ph.D., Chairperson

Robert D. Doyle, Ph.D.

Sascha Usenko, Ph.D.

Accepted by the Graduate School
August 2010

J. Larry Lyon, Ph.D., Dean

Page bearing signatures is kept on file in the Graduate School.

TABLE OF CONTENTS

LIST OF FIGURES v
LIST OF TABLES vii
ACKNOWLEDGMENTS viii
CHAPTER ONE 1
  Introduction 1

CHAPTER TWO 2
  Does Alder or Watershed Physiography Drive Nitrogen Availability in Salmon-Rearing Headwater Streams? 2
    Introduction 2
    Methods 5
      Site Description 5
      Sampling and Analysis 9
      Data Analysis 11
    Results 12
    Discussion 14

CHAPTER THREE 24
  Breakdown Rates, Nutrient Quality, and Macroinvertebrate Colonization of Bluejoint Grass Litter in Headwater Streams 24
    Introduction 24
    Methods 27
      Study Area 27
      Leaf Packs 28
      Stream Physical and Chemical Parameters 33
      Data Analysis 34
    Results 36

Stream Water Chemistry 36
Leaf Pack Breakdown Rates among Streams 37
Litter Quality 37
Colonization of Litter by Macroinvertebrates 38
Discussion 47

CHAPTER FOUR 51
Conclusions 51

LITERATURE CITED 53

LIST OF FIGURES

Figure 1. Location map showing headwater stream sampling sites on the Lower Kenai Peninsula. Watersheds are shaded by percent of alder cover. Inset shows the location of the Lower Kenai Peninsula within Alaska. 8

Figure 2. Amount and spatial arrangement of alder in two headwater stream watersheds. Alder cover is 22% and 6% for Sites 16 (left) and 1 (right), respectively. 10

Figure 3. Percent alder cover and NO_x-N for all months. Points are sized according to mean slope. 18

Figure 4. Percent alder cover and daily NO_x-N yield for all months. Points are sized according to mean slope. 19

Figure 5. Seasonal GAM fits for all three months for NO_x-N concentration (top) and daily NO_x-N yield (bottom). 20

Figure 6. Headwater stream valley bottom (left) and stream reach (right). Bluejoint is a dominant riparian vegetation species and dead litter reaches streams through lateral transport or from overhanging banks. 30

Figure 7. Percent of leaf material remaining over days (top) and temperature degree days (bottom) for the 8 week study. 39

Figure 8. Leaf decay rates predicted by stream DIN concentrations (top left), stream PO4-P concentrations (bottom left), leaf % N at 8 weeks (top right), and leaf % P at 8 weeks (bottom right). The axis for DIN is log-transformed. 40

Figure 9. Litter quality (leaf % N, top and leaf % P, bottom) for the 8 week study. 41

Figure 10. Relationship between stream nutrient concentrations and litter quality over time. The amount of variation explained in the weighted regressions increased from 2 to 6 weeks and remained strong at 8 weeks indicating that microbes are utilizing dissolved nutrients in the stream to enhance colonization. Legend: response variable ~ predictor variable. 42

Figure 11. Leaf % N (top) and % P (bottom) predicted by stream DIN concentrations (left) and stream PO_4-P concentrations (right). The axis for DIN is log-transformed. 43

Figure 12. NMDS ordination for 5 racks over time in Stream 1203. Macroinvertebrate communities generally shifted from left to right for all 5 racks as leaf decomposition progressed with a large consistent change between weeks 6 and 8. 46

LIST OF TABLES

Table 1. Landscape variables and effects on stream nitrogen. 6

Table 2. Watershed characteristics. 15

Table 3. Stream discharge, flow, and nutrient concentrations. 16

Table 4. Results of GAM fits for NO_x-N and daily NO_x-N yield. 17

Table 5. Watershed characteristics and stream water chemistry for 6 streams. Stream water chemistry and discharge are means (SE) for samples taken over the course of the leaf decomposition experiment (*n* = 5). Stream 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...29

Table 6. Leaf decay rates per day and degree day for 6 streams ordered from high to low stream DIN concentrations. Values are means (SE) for 5 racks in each stream. .39

Table 7. Total macroinvertebrates per g of leaf litter remaining and total taxa at the end of 8 weeks on bluejoint leaf packs in 6 streams listed in descending order of dissolved nutrient concentrations. Values are means (SE)................................43

Table 8. Macroinvertebrate abundances, frequencies, NMDS scores, and feeding habits for taxa that occurred in 2 or more streams. Taxa are sorted from high NMDS scores to low scores...44

Table 9. Indicator species analysis results for taxa associated with leaf packs over time in Stream 1203. Indicator value combines frequency and abundance of an individual taxon to a specific group (time period). Significance of group assignments were determined with a permutation test (*n* = 500)..46

ACKNOWLEDGMENTS

The Kachemak Bay Research Reserve (KBRR) made this research possible by providing necessary lab space and equipment while in Alaska. I am extremely grateful to Coowe Walker and Steve Baird with KBRR who helped me in the field and with logistics in Homer. Katie Zychowski, an undergraduate at Baylor, helped me with all of the leaf pack field and lab work while in Homer and was a hard worker and great companion the entire summer. My mother, Harriet Shaftel, drove with me to all of my water sampling sites in May and September when field partners were hard to find. My advisor, Dr. Ryan King, helped tremendously in setting up the leaf decomposition experiment over two weeks in early June. Ryan also spent a great amount of time helping me to revise both of my chapters. Dr. Doyle and Dr. Usenko both provided helpful comments on my proposal and feedback on my thesis. Financial support was provided by the C. Gus Glasscock, Jr. Endowed Fund for Excellence in Environmental Sciences and the Jack G. and Norma Jean Folmar Research Fund.

CHAPTER ONE

Introduction

Nitrogen (N) limitation is common in streams, but can be mitigated by marine-derived nutrients from spawning salmon (Naiman and others 2002). Headwater streams that support upstream-dispersing juvenile salmon typically lack nutrient subsidies from adult salmon (Bryant, Zymonas, Wright 2004). Terrestrial inputs, such as from N-fixing alder, may be important for fueling production in these ecosystems (Compton and others 2003). Watershed topography and seasonal changes in precipitation and temperature are also related to N export from the landscape (Schiff and others 2002; Kane and others 2008) and may confound linkages between alder and stream N concentrations. Alder cover was compared with watershed physiographic variables as drivers of the gradient in stream N concentrations in headwater streams of the Lower Kenai Peninsula, Alaska.

Litter inputs to headwater streams are an important basal resource that supports microbial and macroinvertebrate consumers (Cummins and others 1989; Findlay 2010). Low quality litters, such as grass, break down more slowly than deciduous tree litter (Webster and Benfield 1986). Dissolved stream nutrients that are utilized by microbes can offset the low nutrient quality of the litter (Suberkropp and Chauvet 1995). Decomposition of bluejoint grass, a dominant riparian plant species in Kenai lowland headwater streams, was examined among 6 streams that spanned a nutrient gradient to assess its breakdown rate, litter quality, and importance as habitat or food to macroinvertebrate consumers.

CHAPTER TWO

Does Alder or Watershed Physiography Drive Nitrogen Availability in Salmon-Rearing Headwater Streams?

Introduction

Many stream ecosystems are nitrogen limited (Francoeur 2001; Dodds, Smith, Lohman 2002; Tank and Dodds 2003). In streams with significant numbers of spawning salmon, marine-derived nutrients (MDN) can be a significant source of nitrogen and an important driver of primary and secondary production (Wipfli and others 1999; Gende and others 2002; Naiman and others 2002). Headwater (first-order) streams may receive lower contributions of MDN because adult salmon can be limited to the lower reaches and only in streams with adequate gravels for spawning (Richardson and Danehy 2007), despite serving as rearing habitat for upstream-dispersing juvenile salmon (Bramblett and others 2002; Bryant, Zymonas, Wright 2004; Ebersole and others 2006). Therefore, nitrogen (N) contributions from the surrounding landscape may be critical for enhancing nutritional quality and quantity of basal food resources that sustain juvenile salmon populations (Melillo, Aber, Muratore 1982; Suberkropp and Chauvet 1995; Chadwick and Huryn 2003).

Alder (*Alnus* spp.) may increase N availability by contributing fixed N to the stream nutrient budget (Dugdale and Dugdale 1961; Stottlemyer and Toczydlowski 1999; Compton and others 2003). Alder receives its N from a symbiotic relationship with bacteria of the genus *Frankia* that convert atmospheric N_2 to NH_3 for uptake by the plant. Alder has been shown to increase both ammonium (Stottlemyer and Toczydlowski 1999) and nitrate soil concentrations (Rhoades and others 2001; Hurd and Raynal 2004; Mitchell and Ruess 2009) and also plant nitrogen concentrations directly beneath its canopy (Rhoades and others 2001). There are several possible mechanisms through which alder-fixed N (AFN) may be transported to the stream: litterfall in riparian zones, soluble nutrients from riparian zones, or leaching and lateral transport by surface and groundwater from upland alder (Compton and others 2003; Stieglitz and others 2003; Cairns and Lajtha 2005). Thus, streams located in watersheds with relatively high proportions of alder cover may experience greater N availability, potentially reducing N limitation of stream ecosystem processes.

Watershed physiographic characteristics may indirectly affect the amount of terrestrial N reaching streams. Watershed slope has been shown to affect the transport of terrestrial nutrients to streams by reducing flow path length and hydrologic residence time (Schiff and others 2002; Snyder and others 2003; Watmough and others 2004). Wetlands and riparian buffers in flat landscape positions with a high hydrologic residence time show increased nutrient uptake and denitrification (Hanson, Groffman, Gold 1994; Clement and others 2003; Sabater and others 2003). For example, topographic wetness, an index used to quantify the control of topography on hydrologic processes and predict local wetness (Sorenson, Zinko, Seibert 2005), explained 68% of the variation in nitrate export in small, forested watersheds (Ogawa and others 2006). Low watershed slopes, higher proportions of wetlands, and other physiographic attributes that increase transport time along biologically active surface flow paths are likely to reduce stream N concentrations because of increased uptake and denitrification.

Seasonal changes in precipitation and temperature may also interact with physiography to control terrestrial N inputs to streams. Studies examining seasonal changes in stream N concentrations have found that precipitation (Stieglitz and others 2003; Kane and others 2008) and precipitation variability (Kane and others 2008) both influence stream N through mobilization of nutrients from watersheds to streams. Similarly, watershed area and discharge are also related to increased stream N as larger watersheds experiencing larger flow regimes can more easily transport terrestrial nutrients (Creed and Band 1998; Schaefer, Hollibaugh, Alber 2009). In regions with winter snowfall, a distinct pattern has emerged: spring flushing due to snowmelt coincides with maximum stream N whereas increased temperatures in summer months leads to nutrient uptake and denitrification and minimum stream N (Stottlemyer and Toczydlowski 1999; Schiff and others 2002; Golden and others 2009). The spring peak has been attributed to high net N mineralization rates from decreased immobilization in unfrozen soil layers under an insulating snowpack (Stottlemyer and Toczydlowski 1999). Thus, the prediction of N availability in streams may be complicated by seasonal variations in precipitation, discharge, and temperature. In addition, temporal variation in N inputs could limit basal resource production during critical periods for juvenile salmon growth, particularly during summer.

The objectives of this study were to (1) empirically model the effect of alder cover on stream N concentrations, (2) evaluate the relative influence of other watershed physiographic variables that may confound the relationship between alder and stream N, and (3) contrast the relationship between the watershed predictors and stream N over three seasons. The study was conducted in 25 small, salmon-rearing streams of the

Lower Kenai Peninsula, Alaska; a region with relatively diverse physiography (Gracz and others 2004) and a wide range of upland alder cover among watersheds. Alder cover was expected to be an important predictor of stream N, but other physiographic variables such as watershed slope, wetland cover, topographic wetness, watershed area, elevation, and stream discharge were hypothesized to modulate or possibly confound this relationship due to the tendency of alder to occur more frequently on steep uplands (Table 1). N concentrations were expected to peak early (May) and late (September) during the growing season due to snowmelt and precipitation, respectively, transporting terrestrial nutrients to streams, whereas increased nutrient uptake and denitification were expected to decrease N in streams during mid-summer (July).

Methods

Site Description

Headwater streams of the Lower Kenai Peninsula are part of five 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, with two small cities (population ~ 5,000 in 2005 census estimates) and less than 1% of its area 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 1932-2005 averages 63 cm (rain plus water equivalent of snow); approximately 13 – 18 cm of which are snow. The average maximum temperature occurs in July at 16.1° C, and the minimum occurs in January

Table 1. Landscape variables and effects on stream nitrogen.

Landscape variables	Hypothesized effect on stream nitrogen	Correlation to stream N (+ or –)
Alder cover	More alder in a watershed will lead to more alder-fixed N	+
Watershed slope	Higher mean slope indicates shorter flowpaths and residence time to stream, reducing the opportunity for uptake and denitrification	+
Topographic wetness index	Higher mean TWI will correspond to longer hydrologic residence time increasing nutrient uptake and denitrification	–
Wetland cover	Wetlands are located between uplands and streams in flat topographic positions with high hydrologic residence time increasing opportunity for uptake and denitrification	–
Watershed area	Larger watersheds may cause dilution from increased discharge and longer flowpaths may provide for increased uptake	–
Watershed elevation	Higher mean elevation related to colder streams with shorter growing season and high precipitation decreasing uptake and denitrification and increasing flushing	+
Stream discharge	Higher flows mobilize stream nutrients especially during rising limb of hydrograph, but may be related to dilution if sampling occurs after initial flush	+ / –

at -8.5° C (Western Region Climate Center, http://www.wrcc.dri.edu/summary/climsmak.html).

The headwater streams included in this study are located between 71 and 539 m in elevation in the interior of the Lower Kenai Peninsula and likely experience warmer temperatures and more precipitation in the form of snow as compared to 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 reedgrass (*Calamagrostis canadendis*) and fireweed (*Chamerion angustifolium*) (Reynolds 1990; Viereck and others 1992). Wetlands cover 43% of the area (Gracz and others 2004). Southcentral Alaska forests suffered from a major spruce bark beetle epidemic in the 1990s causing high mortality in mature spruce (Werner and others 2006). Some areas have been logged allowing light penetration and domination by bluejoint reedgrass, while others contain a high percentage of standing dead spruce in the forest overstory. Terrestrial phosphorus originates from volcanic ash layers deposited in soils (Dugdale and Dugdale 1961; Ping and Michaelson 1986). Terrestrial nitrogen sources include several genera of N-fixing plants (for example, *Myrica, Shepherdia*, and *Dryas*), but primarily *Alnus* spp. Atmospheric nitrogen deposition in Alaska is low, averaging 0.58 kg ha^{-1} yr^{-1} (sum of ammonium and nitrate deposition for Denali National Park, National Trends Network, http://nadp.sws.uiuc.edu/NTN/).

Twenty-five headwater streams (Figure 1) were sampled in 2009 to evaluate the effect of alder and other landscape variables on stream N concentrations. ESRI® ArcMap™ 9.3 GIS software was used to locate accessible streams with a range of alder cover and mean topographic wetness indices (TWI), since both factors have been shown to affect stream N concentrations. The streams layer originated from the United States Geological Survey's Digital Line Graph hydrography files, which are digital representations of 1:63,360 map features. Map boundary lines were removed and streams were merged to create a complete streams dataset for the study area. A roads layer developed by the Alaska Center for the Environment, which includes small logging roads, was used to select streams located within ¼ mile of a road. The mean TWI for

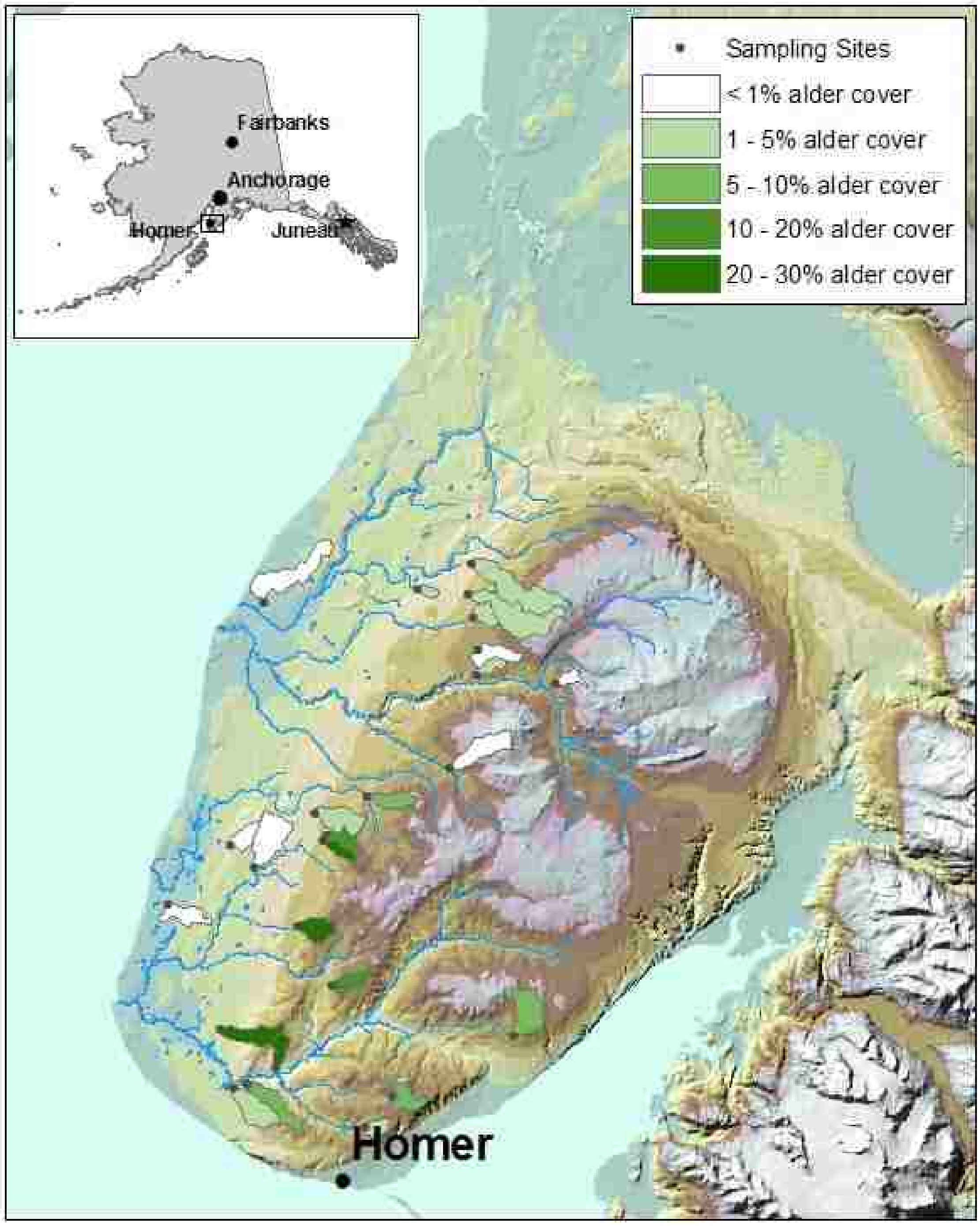

Figure 1. Location map showing headwater stream sampling sites on the Lower Kenai Peninsula. Watersheds are shaded by percent of alder cover. Inset shows the location of the Lower Kenai Peninsula within Alaska.

each headwater stream pixel was calculated based on all pixels in the watershed with a higher elevation than the sampling site. The TWI calculation is based on both watershed area and local slope: TWI = ln(A/tanβ); A – watershed area, β – local slope (Sorenson, Zinko, Seibert 2005). Watershed area and local slope were calculated using a 60 m digital elevation model (DEM) and tools from the Spatial Analyst extension in ArcMap^{TM}. The 60 m DEM was the best available elevation data for the area and originates from the United States Geological Survey's National Elevation Dataset (Gesch and others 2002; Gesch 2007). Other landscape variables calculated in GIS using the DEM included mean slope and mean elevation for each watershed.

Sampling and Analysis

Twenty headwater streams were sampled May 18-21, July 7-10, and September 8-11, 2009 to encompass the early, middle, and late parts of the growing season. An additional 5 headwater streams were sampled in July that were not reached in May and September due to logistical constraints during those field events. Water samples were collected and analyzed for total nitrogen (TN), nitrate-nitrite-N (NO_x-N), and ammonium (NH_4-N). Samples for dissolved nutrients were filtered in the field using a 0.45 µm filter and syringe. Samples were analyzed on a flow-injection auto-analyzer (Lachat QuikChem 8500 and Series 520 XYZ Autosampler). Analysis for NO_x-N followed the cadmium reduction method (American Public Health Association 2005). NH_4-N was analyzed using the phenelate method (American Public Health Association 2005). TN was digested in persulfate and sodium hydroxide, buffered in boric acid, and run as above for NO_x-N (American Public Health Association 2005). At each stream, instantaneous discharge was measured using a Marsh-McBirney Flo-Mate^{TM} flow meter and a top-setting wading rod.

Alder cover polygons were hand-digitized in GIS for each watershed using 2003 color satellite imagery from the Ikonos and Quickbird satellites (Figure 2). Alder commonly forms communities where it is the dominant shrub cover with little or no forest canopy; these communities were selected for mapping and analysis. Ground-truthing of alder polygons was performed during stream sampling and included both riparian and upland alder in watersheds where it occurred close to site access points. Additional verification was based on field data points from the Western Kenai Soil Survey provided by the Natural Resources Conservation Service (Van Patten 2005). The Wetland Mapping and Classification was also used to calculate percent wetland cover for each watershed in GIS (Gracz and others 2004).

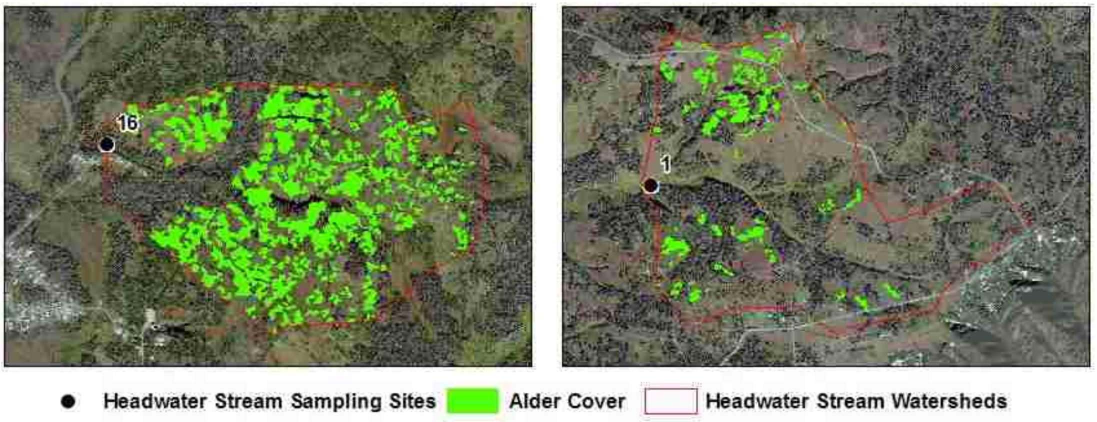

Figure 2. Amount and spatial arrangement of alder in two headwater stream watersheds. Alder cover is 22% and 6% for Sites 16 (left) and 1 (right), respectively.

Data Analysis

The relationships between individual landscape variables (alder cover, wetland cover, mean TWI, mean slope, mean elevation, instantaneous discharge, and watershed area) and stream nutrient concentrations first were examined graphically using pairwise scatterplots and bubble plots (sizing points by a second independent variable). Nutrient responses included TN, NO_x-N, NH_4-N, dissolved inorganic nitrogen (DIN = NO_x-N + NH_4-N), and daily NO_x-N yield (g ha^{-1} d^{-1}). Based on this preliminary analysis, three landscape variables were selected for modeling: alder cover, mean TWI, and mean slope. The other landscape explanatory variables under consideration revealed weak to nonexistent relationships to stream nutrient concentrations and were highly unlikely to account for the modest unexplained variance left by other predictors (see Results). In addition, NH_4-N, TN, and DIN were not included in the statistical models. No landscape explanatory variables showed any graphical relationships to NH_4-N. Both DIN and TN were strongly linearly related to NO_x-N ($r^2 = 0.99$ and 0.87, respectively); therefore, including them in further analysis was gratuitous because most of the DIN and TN was in the form of NO_x-N. Thus, only alder cover, mean TWI, and mean watershed slope were used as predictors of NO_x-N and NO_x-N yield in statistical analysis.

Each watershed predictor was fitted to each of the response variables using generalized additive models (GAM). Additive models are useful for modeling non-linear relationships when there is no a priori understanding of how the explanatory variable and response variables are related. GAMs were fit using the mgcv library in R (Wood 2008; R Development Core Team 2009), which uses splines for smoothers and cross-validation to determine the optimal amount of smoothing. In order to form the smoothers, the gradient for the explanatory variable is divided into intervals and a cubic polynomial equation is fitted to each interval. These segments are merged together to form the smoothers (Zuur and others 2009). In datasets with small sample sizes, models selected by cross validation may be over-fit. To avoid this problem, an upper limit was set on the degrees of freedom for the individual smoother in each model ($k = 4$).

Landscape variables were used individually in models for comparison because many were spatially correlated, which could lead to inaccurate attribution of variation to an explanatory variable (King and others 2005; Zuur and others 2009). The p-values obtained from GAM for smoothing splines are approximate and Zuur and others (2009) recommends that ecological significance only be attributed to smoothers with p-values ≤ 0.001. Significant models (p-values ≤ 0.001) for each response variable were compared using Akaike's Information Criterion (AIC) for small-sample sizes and the Akaike weights, which are the probability that a given model is the best model in the set of models considered (Anderson, Burnham, Thompson 2000). AIC is a model selection criterion that considers the trade-off between model precision and model complexity. It is calculated as two times the number of parameters in the model minus two times the maximum log-liklihood of the model; a lower AIC indicates a better model. AIC for small sample sizes is used when the sample size divided by the number of parameters is less than 40 (Anderson, Burnham, Thompson 2000). Fitted responses were contrasted among seasons using 95% confidence limits.

Results

Alder cover in the watersheds varied from no alder to over 28% cover (Table 2). The mean TWI for all 25 watersheds ranged from 11.4 to 14.1. Mean slope ranged from

2 to 16%. NO_x-N concentrations for all 25 streams and three seasons ranged from 2.8 to 1560 ug L^{-1} (Table 3). NO_x-N yield varied from less than 0.01 g to 13.11 g ha^{-1} d^{-1}.

The GAM model outputs showed that the only explanatory variable with a significant smoother for predicting NO_x-N yield or NO_x-N for all months was alder cover (Table 4, Figures 3 and 4). The mean slope model had a significant smoother for both nutrient responses in May and also for NO_x-N yield in July. Alder cover explained between 75 – 96% of the variation in NO_x-N and 83 – 89% of the variation in NO_x-N yield. Mean slope only explained 44% of the variation in NO_x-N in May and ~50% of the variation in NO_x-N yield in May and July. Watersheds of varying slopes were spread out along the alder gradient, and inspection of mean slope versus NO_x-N indicated that most of the correlation between slope and stream N was driven by an outlier.

A comparison of the two competing models, alder cover and mean watershed slope, using AIC_c and w_i showed that alder cover was the only probable model. The minimum ΔAIC_c for slope as the second best model was 23 and the Akaike weight (w_i) for alder (probability that it is the best model in the set of models being compared) was 100% for all comparisons (NO_x-N and NO_x-N yield in May and NO_x-N yield in July). Given the highly significant smoothers, the large amount of variation explained, and the model comparison results with the next best model (mean watershed slope), alder cover was selected as the best predictor of stream NO_x-N and NO_x-N yield.

A linear fit was the best model explaining the relationship between alder cover and stream N in May (EDF = 1, Figures 3 and 5). However, the unit effect of alder on NO_x-N concentration was disproportionately higher at the highest alder cover during July and September, resulting in a non-linear relationship (EDF > 1). NO_x-N was significantly lower in July than May at intermediate alder cover (3-20%), but was not different at levels above or below this range (Figure 5). This effect was also apparent in September, but was more variable.

NO_x-N yield was also linearly related to alder cover in May (EDF=1, Figures 4 and 5). There was a significant decrease in the amount of NO_x-N transported to the stream per unit area as a function of alder from May to July and September. This relationship was significantly nonlinear during the latter two months, implying a greater yield of N per unit alder at the highest cover.

Discussion

The comparison of watershed physiographic features and alder cover in predicting stream N showed that alder cover far outweighed other predictors in explaining the variation in stream N. Compton and others (2003) also observed a strong correlation between alder cover and stream N concentrations: broadleaf cover (composed primarily of alder) explained 65% of the variation in the flow-weighted average annual stream nitrate concentrations. Although other studies have shown that alder cover correlates to stream N concentrations, this is the first to show such an impressively strong relationship over several seasons and that alder clearly outweighs other watershed physiographic variables in predicting stream N.

The range of N concentrations in the 25 headwater streams of the Kenai Peninsula (0.002 – 1.560 mg L^{-1}) is similar to other low order streams with alder. In 26 streams of the Oregon Cascade Range, stream NO_3-N concentrations ranged from 0.074 – 2.429 mg L^{-1} over a one-year sampling period (Compton and others 2003). The lower range found in the Alaskan streams is likely due to less alder cover; maximum cover in the Alaskan

Table 2. Watershed characteristics.

Site	Major River Watershed	Area (km^2)	Mean Elevation (m)	Mean Slope (%)	Mean TWI	Alder Cover (%)	Wetland Cover (%)
0	S.F. Anchor R.	2.0	345	7.6	12.4	1.1	29.6
1	S.F. Anchor R.	3.7	421	8.7	12.1	6.3	14.7
2	S.F. Anchor R.	5.3	247	8.1	12.3	5.9	50.8
3	S.F. Anchor R.	6.3	196	7.2	12.5	4.1	56.5
4	S.F. Anchor R.	2.4	272	15.8	11.4	20.1	15.6
5	S.F. Anchor R.	5.1	235	7.5	12.4	21.8	36.9
8[a]	S.F. Anchor R.	7.0	430	5.2	12.8	6.9	57.0
10	S.F. Anchor R.	3.3	411	7.6	12.6	12.6	35.2
16	S.F. Anchor R.	4.0	344	10.6	12.0	28.2	22.7
18	Stariski Cr.	2.9	143	4.3	12.9	0.5	14.7
19	N.F. Anchor R.	2.6	332	7.7	12.4	17.2	23.3
20[a]	N.F. Anchor R.	1.8	324	8.4	12.1	22.8	22.3
21	N.F. Anchor R.	5.7	279	4.4	13.0	3.2	48.6
22	Stariski Cr.	3.5	377	8.1	12.4	9.7	22.9
25	Deep Cr.	6.4	539	10.1	12.1	0.9	33.7
28[a]	Deep Cr.	1.8	460	9.8	12.0	0.0	18.8
30	Deep Cr.	1.9	353	6.1	12.4	1.0	14.1
31	Deep Cr.	4.1	368	5.0	12.7	0.0	17.6
34[a]	Deep Cr.	2.5	338	5.6	12.8	3.6	31.0
37[a]	Ninilchik R.	1.1	188	3.5	12.9	1.2	23.0
39	Ninilchik R.	12.6	388	6.5	12.6	3.4	33.6
40	Ninilchik R.	11.9	439	5.3	12.8	2.0	27.4
42	N.F. Anchor R.	8.2	156	4.0	13.2	0.6	36.1
43	Stariski Cr.	4.1	84	1.5	13.9	0.0	70.3
44	Ninilchik R.	9.8	71	1.6	14.1	0.3	63.3

[a] Five sites were only sampled in July.

Table 3. Stream discharge, flow, and nutrient concentrations.

Site	Discharge ($m^3 s^{-1}$)	Flow ($m s^{-1}$)	NO$_x$-N ($\mu g L^{-1}$)	NH$_4$-N ($\mu g L^{-1}$)	Total Nitrogen ($\mu g L^{-1}$)	Daily NO$_x$-N Yield ($g ha^{-1}$)
0	0.01-0.023	0.18-0.24	117-342	6-31	247-420	0.51-3.28
1	0.015-0.041	0.16-0.31	241-468	17-46	374-564	0.86-4.42
2	0.022-0.06	0.26-0.41	26-459	5-17	260-552	0.1-4.53
3	0.032-0.062	0.08-0.12	98-339	10-31	266-510	0.43-2.87
4	0.014-0.029	0.1-0.3	768-1210	8-17	884-1260	4.68-12.66
5	0.018-0.046	0.15-0.52	1100-1560	2-3	1250-1650	3.43-10.34
8[a]	0.011	0.06	43	10	260	0.06
10	0.015-0.023	0.09-0.17	284-618	3-19	351-617	1.13-3.76
16	0.022-0.042	0.09-0.38	1120-1420	8-31	874-1540	5.24-13.11
18	0.017-0.035	0.13-0.24	33-63	3-10	255-578	0.22-0.51
19	0.017-0.032	0.14-0.21	152-662	7-21	528-773	1.58-4.8
20[a]	0.008	0.17	955	17	1200	3.67
21	0.031-0.056	0.09-0.17	60-226	29-63	316-539	0.51-1.32
22	0.016-0.034	0.24-0.35	123-404	6-17	311-862	1.04-2.1
25	0.011-0.014	0.1-0.12	3-19	2-5	123-179	0.01-0.04
28[a]	0.016	0.18	23	3	93	0.18
30	0.014-0.019	0.18-0.26	22-61	2-3	130-420	0.19-0.4
31	0.028-0.062	0.27-0.59	7-43	4-21	123-163	0.05-0.55
34[a]	0.016	0.10	57	19	309	0.31
37[a]	0.012	0.07	85	6	376	0.76
39	0.044-0.063	0.2-0.39	21-88	3-26	196-249	0.08-0.38
40	0.053-0.07	0.12-0.19	33-75	2-7	154-228	0.13-0.38
42	0.069-0.138	0.09-0.4	13-30	18-94	267-617	0.18-0.25
43	0.017-0.022	0.05-0.17	10-14	4-16	204-273	0.04-0.06
44	0.036-0.041	0.25-0.35	13-33	7-16	207-431	0.05-0.12

[a] Five sites were only sampled in July. Discharge, flow, and nutrient data are from July rather than ranges across three months.

Table 4. Results of GAM fits for NO_x-N and daily NO_x-N yield.

Response	Month	Predictor	Smoother p-value	R^2	EDF[a]
NOx-N	May	Alder	<<0.001	0.92	1
NOx-N	May	Mean slope	<0.001	0.44	1
NOx-N	May	Mean TWI	0.02	0.36	1.6
NOx-N	July	Alder	<<0.001	0.96	2.4
NOx-N	July	Mean slope	0.006	0.26	1
NOx-N	July	Mean TWI	0.06	0.21	1.4
NOx-N	September	Alder	<<0.001	0.75	1.7
NOx-N	September	Mean slope	0.02	0.24	1
NOx-N	September	Mean TWI	0.05	0.18	1.3
NOx-N yield	May	Alder	<<0.001	0.85	1
NOx-N yield	May	Mean slope	<0.001	0.51	1
NOx-N yield	May	Mean TWI	0.003	0.48	1.9
NOx-N yield	July	Alder	<<0.001	0.83	2
NOx-N yield	July	Mean slope	<0.001	0.50	1.8
NOx-N yield	July	Mean TWI	0.002	0.45	2.2
NOx-N yield	September	Alder	<<0.001	0.89	1.8
NOx-N yield	September	Mean slope	0.002	0.41	1
NOx-N yield	September	Mean TWI	0.01	0.36	1.7

[a] The effective degrees of freedom (EDF) represent the amount of smoothing: 1 indicates a linear fit and high values (8-10) means that a curve is highly non-linear (Zuur and others 2009).

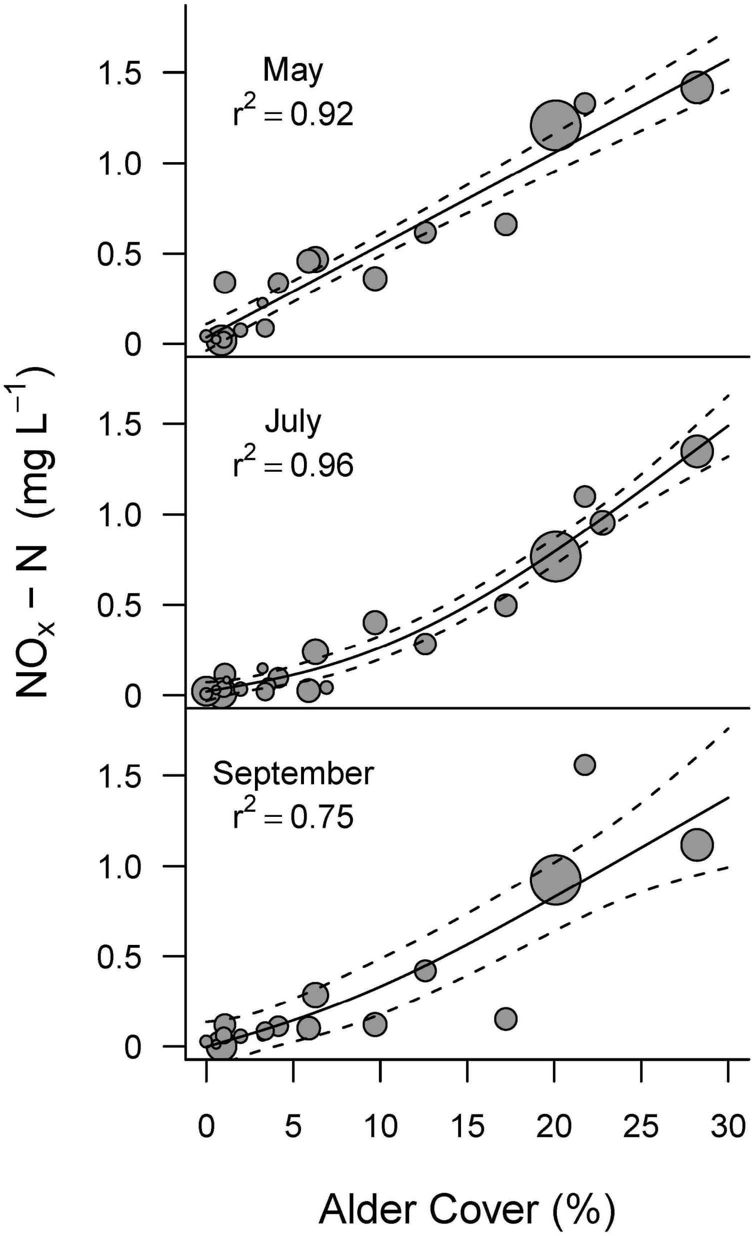

Figure 3. Percent alder cover and NO_x-N for all months. Points are sized according to mean slope.

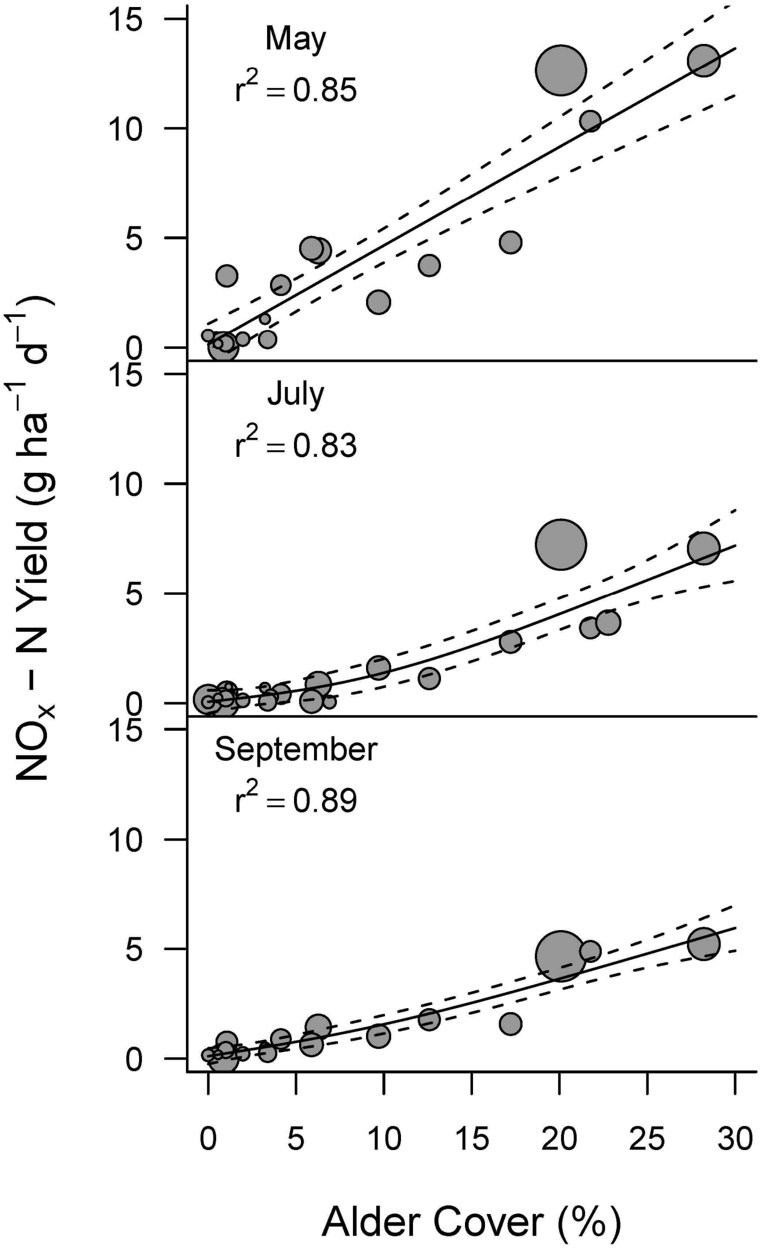

Figure 4. Percent alder cover and daily NO_x-N yield for all months. Points are sized according to mean slope.

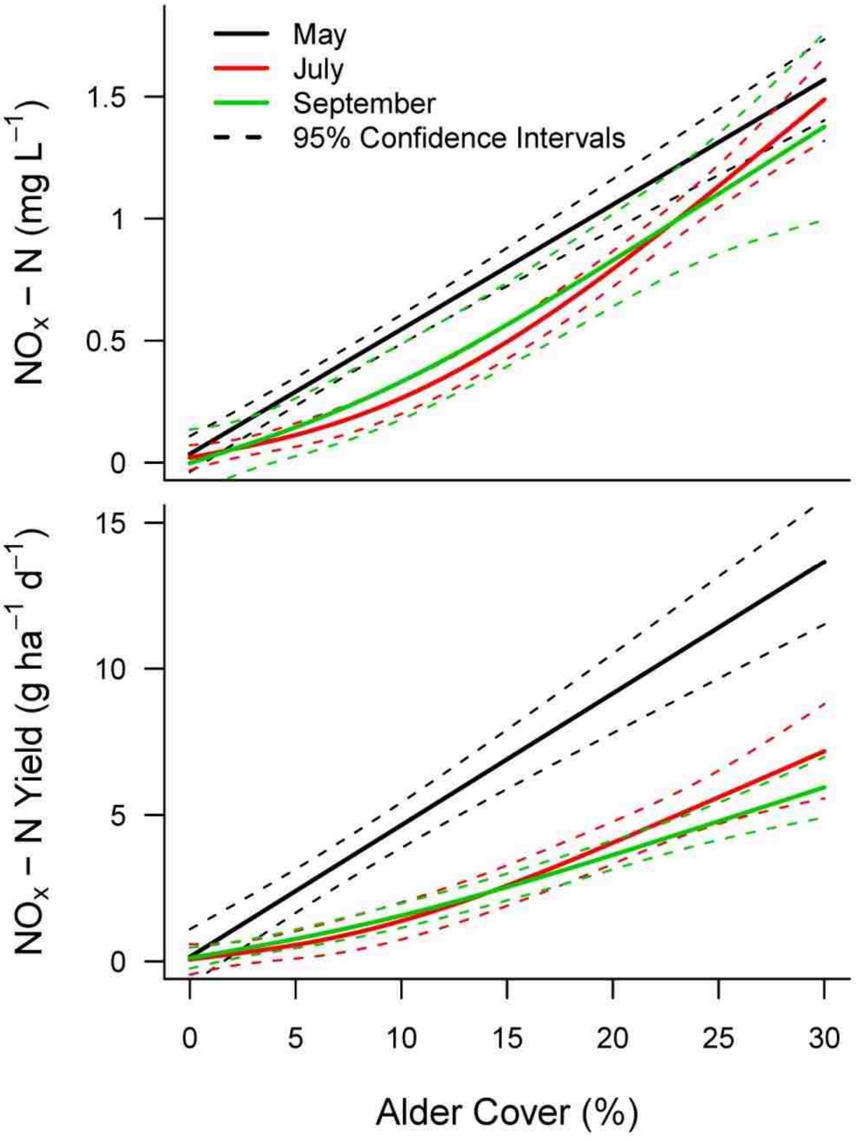

Figure 5. Seasonal GAM fits for all three months for NO$_x$-N concentration (top) and daily NO$_x$-N yield (bottom).

watersheds was 28% compared to > 50% in the Oregon streams. Another study from Oregon reported lower NO_3-N concentrations, ranging from < 0.1 – 0.35 mg L^{-1} (Cairns and Lajtha 2005). Alder cover was not examined in this study although it was listed as a potentially important factor affecting the variability in stream N. A sampling of 48 streams in Oregon during a fall storm event reported a maximum NO_3-N concentration of 10.66 mg L^{-1} with a median of 2.91 mg L^{-1} (Wigington and others 1998). NO_3-N variation in these streams was also attributed to alder cover although their vegetation characterization did not include a specific alder class.

In this study, peak stream N concentrations were observed in May for the 20 streams sampled seasonally. Both NO_x-N and daily NO_x-N yield decreased substantially for all watersheds from May to July and September (Figure 5). Other studies conducted in regions with winter snowpacks have observed a peak in nitrate exports during spring snowmelt and a summer minimum due to increased uptake and denitrification (Creed and Band 1998; Stottlemyer and Toczydlowski 1999; Schiff and others 2002; Golden and others 2009). The sampling event in the third week of May likely missed the true peak in stream N concentrations due to snowmelt as average daily temperatures in Homer were above freezing after April 10, 2009 (NCDC data summary for Homer Airport) and there was no snow remaining at the time of sampling. The September sampling event in this study occurred after significant rainfall in August that continued until sampling the second week of September. Terrestrial AFN may have already been flushed into streams prior to the sampling in September. The maximum stream N concentrations for these streams likely occurred in spring or fall and may be much higher than the concentrations observed during this study.

The non-linear fits for both stream N responses in July and September indicate a decrease in the export of NO_x-N from watersheds with medium alder cover and an increased export of NO_x-N in watersheds with high cover. One hypothesis for the seasonal change in the relationship between alder and stream NO_x-N concentrations could be that the sites with decreased export also have lower mean slope allowing for longer water residence time and increased groundwater contact with the rooting zone increasing nutrient uptake during the peak of the growing season. However, neither mean slope nor topographic wetness correlates to alder cover (Figures 3 and 4) and graphical analysis of residuals implied that most of the variance explained by slope on N was attributed to alder, but not vice-versa. Therefore, something else is contributing to the varying rates of NO_x-N export along the range of alder cover later in the growing season. Another possible explanation is that N saturation is occurring in the watersheds with high alder cover and high NO_x-N export. Pure alder stands have been shown to fix N at rates of 100-200 kg N ha^{-1} annually (Binkley, Cromack, Baker 1994). Rates well below that resulted in N saturation at a fertilizer plant on the Kenai Peninsula. Annual deposition of NH_4-N up to 21 kg N ha^{-1} correlated to high nitrification rates in soils and nutrient imbalances in vegetation close to the plant (Whytemare and others 1997). At sites with greater than 15-20% alder cover, nutrient uptake rates may not exceed export of AFN, resulting in increased NO_x-N reaching streams later in the growing season.

Headwater streams on the Lower Kenai Peninsula provide important rearing habitat for several species of juvenile salmon in addition to resident fish species. Spawning salmon are not abundant in these small, first order systems; which limits the amount of MDN available for production. This study showed that alder is strongly related to stream N, which benefits stream food webs by providing an inorganic nutrient source for heterotrophic organisms breaking down N-poor organic material. In addition, many studies of terrestrial vegetation on the Kenai Peninsula have shown that N is limiting to productivity (Laughlin, Smith, Peters 1984; Goodman and Hungate 2006). Riparian zones with alder or along flowpaths below alder may also receive N subsidies, resulting in increased litter quality and biomass immediately adjacent to streams. The timing of maximum stream N from alder in the spring and fall coincides with salmon fry emergence and plant senescence and leaf fall, respectively. Future work should focus on the importance of this N subsidy to stream food webs supporting juvenile salmon.

CHAPTER THREE

Breakdown Rates, Nutrient Quality, and Macroinvertebrate Colonization of Bluejoint Grass Litter in Headwater Streams

Introduction

Energy inputs to headwater streams are dominated by allochthonous resources due to their narrow channels and overhanging vegetation (Benfield 1997; Richardson and Danehy 2007; but see Thorp and Delong 2002). These inputs provide an important carbon source for microbial and macroinvertebrate consumers that directly utilize leaf litter (Cummins and others 1989; Graca 2001; Findlay 2010) and also for higher trophic levels, such as macroinvertebrate predators and fish (Junger and Planas 1994; Doucett and others 1996; Perry, Bradford, Grout 2003). Most studies examining the fate of terrestrial litter inputs in headwater streams have focused on deciduous shrub and tree leaves (Wipfli, Richardson, Naiman 2007; Tank and others 2010), although other organic matter inputs, such as woody debris, mosses, and grasses, may also contribute to the organic matter budget in small streams (McTammany, Benfield, Webster 2008; Leberfinger and Bohman 2010).

Grasses have received little attention as an allochthonous resource, most likely due to conclusions from several studies that their low nutrient quality makes them a poor food resource for macroinvertebrate consumers (Webster and Benfield 1986; Menninger and Palmer 2007). However, many types of stream ecosystems receive substantial inputs of allochthonous grass litter, including large grassland streams (Huryn and others 2001; Zeug and Winemiller 2008), agricultural streams with deforested riparian areas

(Menninger and Palmer 2007), or small open-canopied streams (Niyogi, Simon, Townsend 2003; Leberfinger and Bohman 2010). There have been a wide range of conclusions about the importance of grasses to stream consumers, with some studies suggesting that grasses are a poor food resource or habitat (Scarsbrook and Townsend 1994) or minimally consumed by macroinvertebrates relative to deciduous tree litter (Leberfinger and Bohman 2010). However, others studies found grass litter to be an important carbon source, contributing a large proportion of the energy used in biomass formation by macroinvertebrates (Huryn and others 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 quality plays an important role in the initial conditioning of allocththonous litter by microbes (Barlocher 1985) and subsequent consumption by macroinvertebrates (Haapala, Muotka, Markkola 2001; Hladyz and others 2009). Low nutrient litter tends to break down slowly (Gessner and Chauvet 1994; Richardson, Shaughnessy, Harrison 2004), but can be enhanced by dissolved nutrients in the surrounding stream water (Suberkropp and Chauvet 1995). Experimental nutrient additions of nitrogen and phosphorus have been shown to 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; Niyogi, Simon, Townsend 2003). Breakdown rates of nutrient-poor carbon sources such as grass may be particularly enhanced by dissolved nutrient subsidies (Ferreira, Gulis, Graca 2006; Greenwood and others 2007). Thus, dissolved nutrient concentrations in streams may be an important factor driving utilization of grasses as a carbon source to microbes and higher tropic levels.

This study was conducted in 6 small, first-order streams on the lower Kenai Peninsula, Alaska. Headwater streams in this region are frequently open canopied and bordered by extensive riparian wetlands dominated by bluejoint grass (*Calamagrostis canadensis*). Due to their small size, these streams receive little to no subsidies of marine-derived nutrients or carbon from adult salmon. But, they support juvenile salmonids, particularly coho salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*) that disperse upstream from spawning areas in larger reaches downstream. Because grass is the dominant input of terrestrial organic matter, 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 nitrogen-fixing shrub that contributes most of the dissolved nitrate to streams in this region (Shaftel, King, Back; in review). The objectives of this study were to (1) estimate breakdown rates of bluejoint grass, (2) contrast breakdown rates and nutrient quality 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 the bluejoint breakdown rate, litter nutrient quality, 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, with 2 small cities (population ~ 5,000 in 2005 census estimates) and less than 1% of its area 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 1932-2005 averages 63 cm (rain plus water equivalent of snow); approximately 13 – 18 cm of which are 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 this study are located between 71 and 439 m in elevation in the interior of the Lower Kenai Peninsula and likely experience warmer temperatures and more precipitation in the form of snow as compared to 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 (*Calamagrostis canadendis*) and fireweed (*Chamerion angustifolium*) (Reynolds 1990; Viereck and others 1992). Wetlands cover 43% of the area (Gracz and others 2004). Terrestrial phosphorus originates from volcanic ash layers deposited in soils (Dugdale and Dugdale 1961; Ping and Michaelson 1986). Terrestrial nitrogen sources include several genera of N-fixing plants (for example, *Myrica, Shepherdia*, and *Dryas*), but primarily *Alnus* spp. Atmospheric nitrogen deposition in Alaska is low, averaging 0.58 kg ha^{-1} yr^{-1} (sum of ammonium and nitrate deposition for Denali National Park, National Trends Network, http://nadp.sws.uiuc.edu/NTN/).

The streams selected for this study are all first-order streams of similar size. Watershed area ranged from 3.3 to 11.9 km^2 and streams were located between 71 and 439 m in elevation (Table 5). Instantaneous discharge measured during the 8 week 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, minimizing differences in breakdown due to 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 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 in most of the selected streams (Fig. 6), although 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

Bluejoint was collected and deployed in leaf packs in 6 streams. Senesced bluejoint was collected from the riparian zone of Stream 44, the most nutrient poor stream, in May for preparation of leaf packs. Most leaf decomposition studies collect senesced leaf material just as it falls off the tree in the fall for immediate placement into streams (Robinson and Gessner 2000; Gulis and Suberkropp 2003; Chadwick and others

Table 5. Watershed characteristics and stream water chemistry for 6 streams. Stream water chemistry and discharge are means (SE) for samples taken over the course of the leaf decomposition experiment (*n* = 5). Stream 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.

Stream Watershed	1203 Anchor	22 Stariski	619 Ninilchik	44 Anchor	171 Stariski	545 Ninilchik
Area (km^2)	3.3	3.5	11.9	8.2	4.1	9.8
Mean elevation (m)	411	377	439	156	84	71
Velocity (m/s)	0.21 (0.03)	0.34 (0.03)	0.29 (0.02)	0.36 (0.03)	0.31 (0.03)	0.32 (0.03)
Discharge (m^3/s)	0.02 (0.001)	0.02 (0.004)	0.07 (0.009)	0.09 (0.013)	0.04 (0.01)	0.05 (0.009)
NH_4-N (ug/L)	6.1 (2.1)	7.1 (2.4)	3.4 (0.6)	20.7 (3.7)	2.9 (0.2)	8.1 (3)
NO_x-N (ug/L)	323.2 (32.2)	331.7 (37.9)	39.7 (4.8)	26.3 (2.4)	9 (1)	26.9 (5.1)
DIN (ug/L)	329.3 (33.4)	338.8 (37.4)	43.1 (5.3)	47 (4.1)	11.9 (1.1)	35 (7.9)
TN (ug/L)	511 (109)	488 (46.3)	205.6 (24)	335.7 (66.9)	285.6 (26.2)	344.2 (57.7)
PO_4-P (ug/L)	52.5 (1.9)	40.2 (3.2)	28.2 (3.3)	37.9 (4.6)	18.8 (2.1)	26 (5)
TP (ug/L)	59.3 (4)	54.4 (5.3)	43.7 (2.8)	82.5 (8.7)	50.8 (6.7)	49.8 (6.3)
DOC (mg/L)	2.1 (0.1)	4.1 (0.3)	2.9 (0.3)	6.3 (0.4)	6.7 (0.2)	6.3 (0.4)
Temperature (°C)	7.27 (0.16)	4.52 (0.17)	7.05 (0.19)	7.92 (0.24)	11.87 (0.23)	11.07 (0.22)
Conductivity (µS/cm)	72.8 (5.3)	53.3 (5.5)	75.7 (6.5)	68.3 (8.6)	85.5 (11.4)	76.5 (9.4)
pH	7.8 (0.2)	7.6 (0.2)	7.9 (0.1)	7.3 (0.1)	7.1 (0.1)	7.6 (0.1)

Figure 6. Headwater stream valley bottom (left) and stream reach (right). Bluejoint is a dominant riparian vegetation species and dead litter reaches streams through lateral transport or from overhanging banks.

2006). But, several studies have also compared leaf decomposition between fall and spring and observed increased decomposition during spring, which has been attributed to warmer temperatures increasing leaching losses and microbial activity (Graca, Ferreira, Coimbra 2001) and higher nutrient content of green leaf fall during the summer (Lopez, Pardo, Felpeto 2001). The leaf material collected for this study was dead leaf litter from the previous year that enters streams the following spring snowmelt, which likely represents the largest litter pulse of the year (Huryn and others 2001).

The leaf material was air-dry at collection time and stored less than 2 weeks prior to deployment in early June. Starting leaf material was analyzed for C, N, and P to determine initial concentrations. Constructed leaf packs contained approximately 5 grams (±0.1 grams) of air-dried leaf material.

Forty leaf packs were assembled for each stream and 8 leaf packs were attached to each of 5 racks of wire mesh deployed in separate riffles at least 10 m apart in early June. The wire mesh racks were placed across the stream bed and anchored using rebar and rocks. Leaf packs were moistened with deionized water prior to deployment to minimize breakage losses and attached to the racks using zip-ties. A total of 240 leaf packs were deployed in the 6 streams. A set of 5 leaf packs were deployed in Stream 545 and retrieved immediately to determine handling losses (Hauer and Lamberti 2006). The oven-dry weight of the handling loss leaf packs was averaged to determine the initial starting weight of the leaf packs for mass loss calculations.

Leaf packs were left to incubate over 8 weeks and 10 bags (2 from each rack) were randomly collected every 2 weeks in each stream and placed into individual Ziploc bags to avoid loss during transport. Upon return to the lab, each leaf pack was rinsed over 2 nested sieves, 1 mm and 250 μm, to remove adhering debris and macroinvertebrates. Leaf material collected from the 1 mm sieve consisted of coarse particulate organic material (CPOM, ≥ 1 mm) that had not yet decomposed to fine particulate organic matter (FPOM, <1 mm). The CPOM was transferred from the 1 mm sieve to a plastic boat, dried at 65° C for 24 hours, placed into a desiccator to cool, and weighed for 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. Two leaf packs were lost during the experiment: 1 leaf pack from Stream 545 at 8 weeks and 1 leaf pack from Stream 171 at 4 weeks.

Oven-dried leaf material was initially homogenized using a coffee grinder and sub-sampled for secondary homogenization into a powder using a Mini Beadbeater™. Sub-samples of powdered leaf material (20 – 600 mg depending on amount of leaf material remaining) were placed into aluminum weigh pans, dried at 60° C overnight, placed into a desiccator to cool, and weighed to obtain an initial sample weight for ash-free dry mass (AFDM) calculations. Samples were then ignited at 550° C for 2 hours and weighed again (Heiri, Lotter, Lemcke 2001). AFDM (%) was calculated for each subsample by subtracting the final weight (ash) from the initial sample weight and dividing by the initial sample weight. The oven-dry mass for each leaf pack was multiplied by the percent AFDM to remove the effect of sediments and inorganic material on leaf mass. Approximately 6 to 8 mg of powdered leaf material was weighed into 5 by 9 mm aluminum tins and carbon (% C) and nitrogen (% N) were estimated on a ThermoQuest Flash EATM 1112 elemental analyzer. Phosphorus (% P) was estimated from digestions of 1 to 3 mg of material on a Lachat QuikChem 8500 flow-injection autoanalyzer using the molybdate colorimetric method (Faerovig and Hessen 2003).

Preserved macroinvertebrates were identified and counted for all leaf packs collected at 8 weeks and also for the leaf packs from Stream 1203 for 2, 4, and 6 weeks. Macroinvertebrates were identified to genus for most insect orders, except for Chironomidae, which were keyed to subfamily; Simuliidae, which were keyed to family; and early instars that could not be identified below order or family (Wiederholm 1983; Wiggins 1996; Merritt, Cummins, Berg 2008). The remaining macroinvertebrate classes were keyed to either class or order (e.g. bivalves, gastropods, hydracaranids, etc.; Thorp and Covich 2001; Voshell 2002). Taxonomic references were also used to review feeding habits for the macroinvertebrate taxa.

Stream Physical and Chemical Parameters

Water temperature data loggers (HOBO® Pro v2) deployed in each stream collected readings every 15 minutes for the entire decomposition study. In addition, water samples were collected for nutrient analysis, and in-situ water chemistry and stream discharge were measured simultaneously with leaf deployment and retrieval. A YSI 556 Multiprobe System was calibrated before each biweekly field event and used to measure pH and conductivity. Calibrations were checked each evening. Instantaneous discharge was measured using a Marsh-McBirney Flo-Mate^{TM} flow meter and a top-setting wading rod. Water samples were analyzed for total nitrogen (TN), nitrate-nitrite-N (NO_x-N), ammonium (NH_4-N), total phosphorus (TP), orthophosphate (PO_4-P), and dissolved organic carbon (DOC). Samples for dissolved nutrients were filtered in the field using a 0.45 μm filter and syringe. All water samples except for DOC were analyzed according to Standard Methods for Water and Wastewater (American Public Health Association 2005) on a flow-injection auto-analyzer (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 nitrogen (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 using the high temperature combustion method on a Shimadzu TOC-VCSH Analyzer and ASI-V Autosampler (American Public Health Association 2005).

Data Analysis

All leaf decomposition endpoints (leaf mass; % C, % N, and % P; and macroinvertebrate abundances) were averaged for the 2 leaf packs collected off of each rack for a single time period. This 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: $M_t = M_0e^{-kt}$; where M_t is the mass at time t, M_0 is the initial mass, k is the exponential decay coefficient, and t represents time (Graca, Barlocher, Gessner 2005). Decay coefficients were calculated as a function of time in days and temperature 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 weeks) to examine the relationship between dissolved nutrient availability and microbial colonization (as inferred by increased litter quality, Barlocher 1985). DIN was log-transformed to improve normality. Stream nutrient concentrations were means of the samples collected prior to the sampling period (e.g. mean of 0 and 2 weeks for the 2 week regression, mean of 0, 2, and 4 weeks for the 4 week regression, etc.). 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 $1/s^2$; the variance was based on the 5 racks within each stream.

Weighted regression was also used to examine the importance of stream nutrient concentrations, leaf nutrient quality (as a proxy of microbial colonization), and macroinvertebrate indices (total no./g and total taxa per leaf pack) as predictors of the breakdown rate for all 6 streams. Means over the 8 week study were used for stream nutrient concentrations and leaf nutrient quality; macroinvertebrate indices were from 8 weeks.

Individual taxa abundances counted on each leaf pack at week 8 were standardized to numbers per mass remaining in g and log-transformed (*log(x+1)*). Non-metric multidimensional scaling (NMDS) was used to ordinate the multivariate macroinvertebrate community abundance data for the 5 racks in each of the 6 streams at 8 weeks. The Bray-Curtis distance measure was used to transform the species matrix. The ordination was rotated to match the breakdown rate. Sites were sorted along the first axis and the second axis was strongly driven by unique taxa present in one site. For this reason, the NMDS axis 1 scores were used to describe differences in macroinvertebrate community structure among the 6 streams in remaining analyses. The NMDS 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 NMDS ordination for the 27 taxa that occurred in more than 1 stream. The weighted average scores from NMDS axis 1 were used to examine species locations along the stream gradient.

To evaluate macroinvertebrate community succession over time on the leaf packs in Stream 1203, NMDS was run (as described above) on the taxa abundances for the 2, 4, 6, and 8 week sampling periods. Successional vectors were used to show the direction and magnitude of colonization from 2 to 8 weeks. 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 where 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 could be obtained by chance.

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

Results

Stream Water Chemistry

Average stream DIN concentrations ranged from 15 to 384 ug/L and PO_4-P concentrations ranged from 19 to 53 ug/L among streams (Table 5). Stream DIN was correlated to stream PO_4-P ($r^2 = 0.79$, $p = 0.02$). DOC concentrations were relatively high in all streams, ranging from 2.1 to 6.7 mg/L; there was no relationship to DIN or PO_4-P ($p > 0.05$). Average daily stream temperatures ranged from 4.5 to 11.9°C. Stream velocity was similar across the 6 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 week study (Fig. 7). Total temperature degree days for the 6 streams ranged from 260 to 670. Breakdown rates (per day) ranged from 0.0035 to 0.0060 (Table 6), 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}, Fig. 8). DIN explained more variance in leaf breakdown than PO_4-P ($r^2 = 0.94$, $p = 0.003$ and $r^2 = 0.67$, $p = 0.03$, respectively). Leaf litter quality and macroinvertebrate indices were both positively associated with leaf breakdown rates. Leaf % P explained more variance in leaf breakdown rates than leaf % N ($r^2 = 0.96$, $p = 0.02$ and $r^2 = 0.72$, $p < 0.001$, respectively). Total macroinvertebrates (no./g) and the NMDS axis 1 scores were both good 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) did not have a strong relationship to leaf breakdown ($p = 0.09$, $r^2 = 0.41$).

Litter Quality

The starting % N of the senesced bluejoint collected in early May was 0.38. At the end of the 8 week study, leaf % N in the 6 streams ranged from 0.45 to 0.78 (Fig. 9). Leaf % P was 0.08 at the start of the study and ranged from 0.07 to 0.12 by week 8. The amount of variation explained (r^2) in the weighted regressions between stream nutrient concentrations and leaf nutrient quality increased dramatically from 2 to 6 weeks and remained tightly coupled at 8 weeks (Fig. 10). The weighted regressions for mean stream nutrient concentrations over the 8 week study and leaf nutrient quality at 8 weeks show the strong relationship between stream nutrient availability and microbial colonization over the two month study period (Fig. 11).

Colonization of Litter by Macroinvertebrates

The total macroinvertebrates (no./g) at week 8 ranged from 41 to 82 in the 6 streams (Table 7). The number of taxa on each leaf pack ranged from 13 to 18. Of the 44 total taxa, 12 occurred in all 6 streams and the top 3 according to abundance were Orthocladinae (Diptera, dominated by *Brillia*, a shredder), *Zapada* (Plecoptera, shredder), and Ostracoda (Table 8). Other common taxa that occurred in at least 2 streams included several shredders (Limnephilidae and *Psychoglypha*), scrapers (e.g. Diamesinae and *Baetis*), and predators (e.g. Tanypodinae, *Dicranota*, and *Rhyacophila*).

The NMDS ordination of the macroinvertebrate communities on leaf packs over time from Stream 1203 indicated a consistent colonization pattern across all 5 racks (Fig. 12). Communities changed in the same direction (increasing along the first axis) except for 1 rack from 2 to 4 weeks. The magnitude of the shift increased slightly from 2 to 6 weeks, but shifted substantially more between 6 and 8 weeks. The multivariate permutation test showed that groups were significantly different between time periods ($p = 0.002$). ISA results showed 11 significant taxa associated with the leaf packs at 8 weeks and only 1 significant taxon at 2 and 6 weeks (Table 9). Taxa that were strongly associated with leaf packs collected at 8 weeks included the shredders *Psychoglypha* and *Zapada* in addition to collector-gatherers (e.g. *Ecclisomyia*, *Pericoma,* and Chironominae), and predators (e.g. *Dicranota* and *Rhyacophila*). Diamesinae and Tanytarsini colonized leaf packs at 2 and 6 weeks, respectively, and both are collector-gatherers in addition to filtering and scraping.

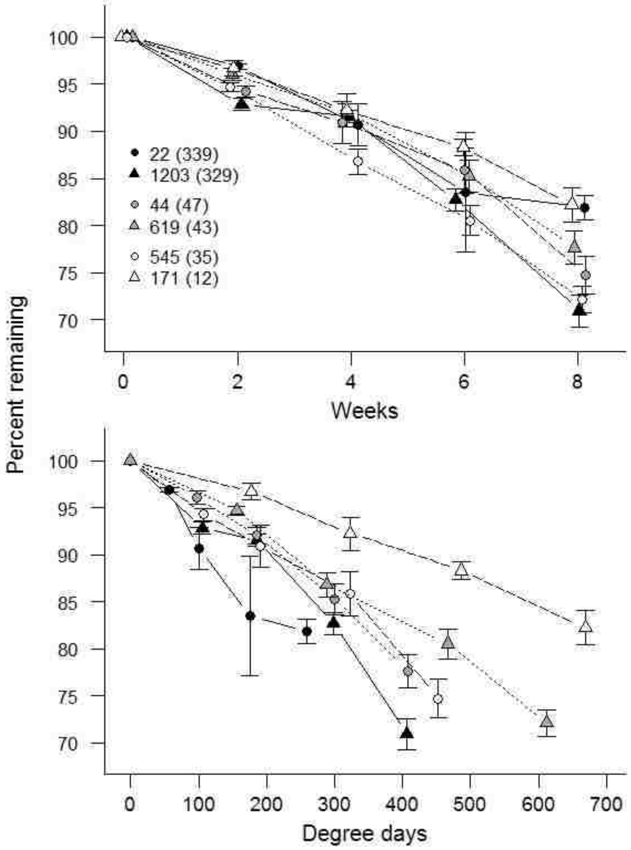

Figure 7. Percent of leaf material remaining over days (top) and temperature degree days (bottom) for the 8 week study.

Table 6. Leaf decay rates per day and degree day for 6 streams ordered from high to low stream DIN concentrations. Values are means (SE) for 5 racks in each stream.

Stream	DIN (μg/L)	*k* (day)	R^2	*k* (degree day)	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

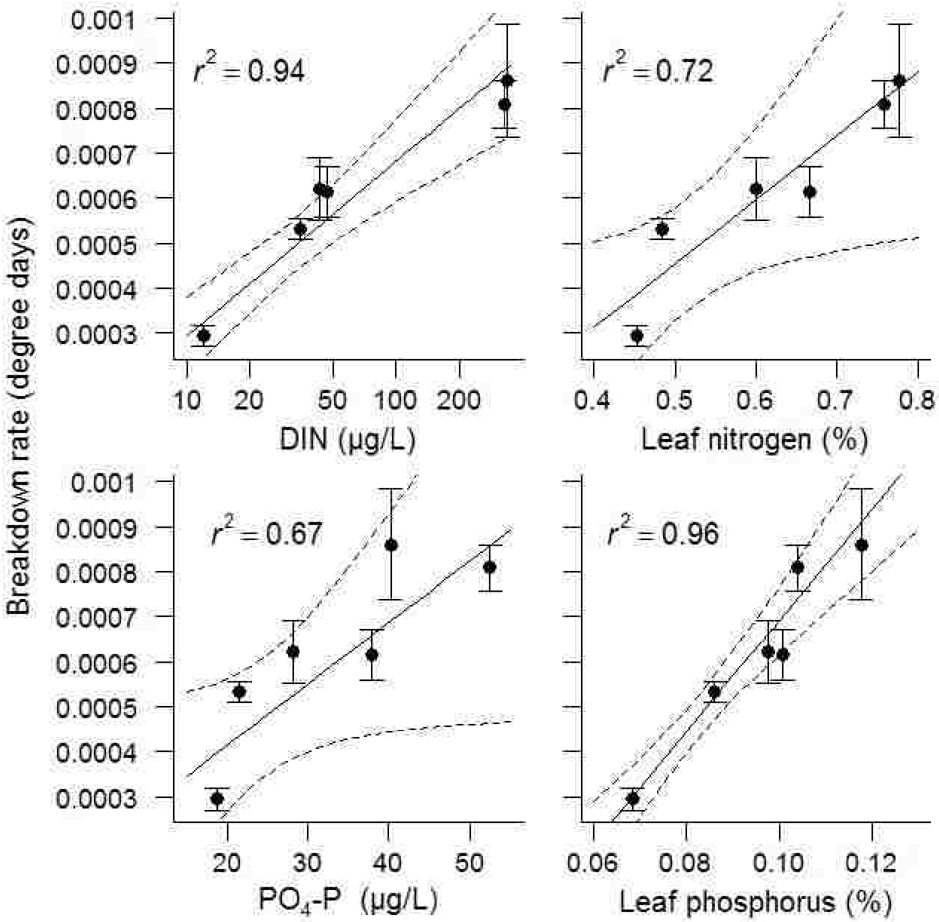

Figure 8. Leaf decay rates predicted by stream DIN concentrations (top left), stream PO4-P concentrations (bottom left), leaf % N at 8 weeks (top right), and leaf % P at 8 weeks (bottom right). The axis for DIN is log-transformed.

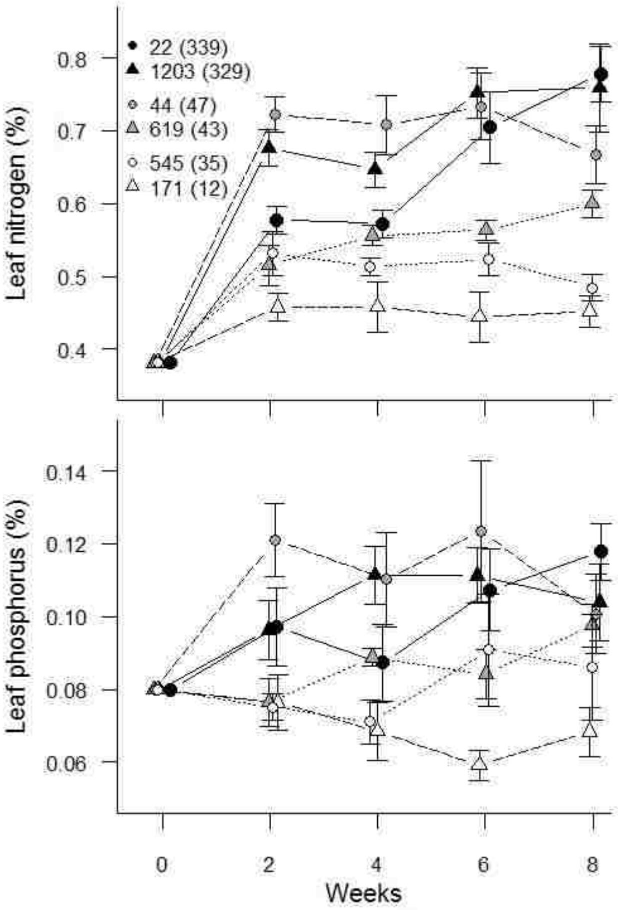

Figure 9. Litter quality (leaf % N, top and leaf % P, bottom) for the 8 week study.

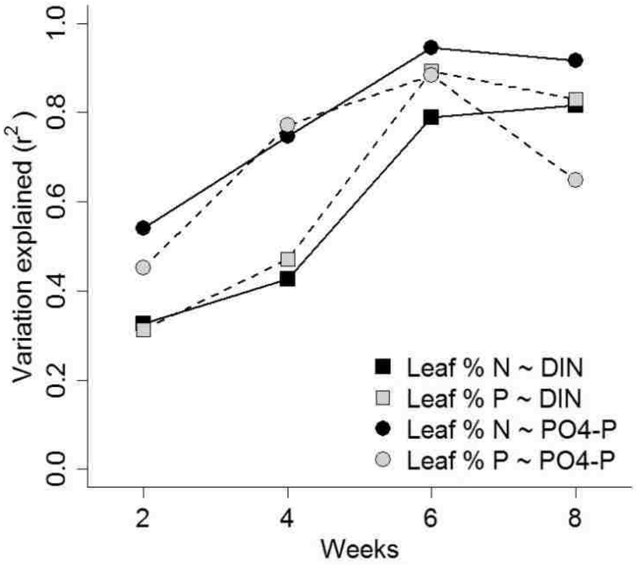

Figure 10. Relationship between stream nutrient concentrations and litter quality over time. The amount of variation explained in the weighted regressions increased from 2 to 6 weeks and remained strong at 8 weeks indicating that microbes are utilizing dissolved nutrients in the stream to enhance colonization. Legend: response variable ~ predictor variable.

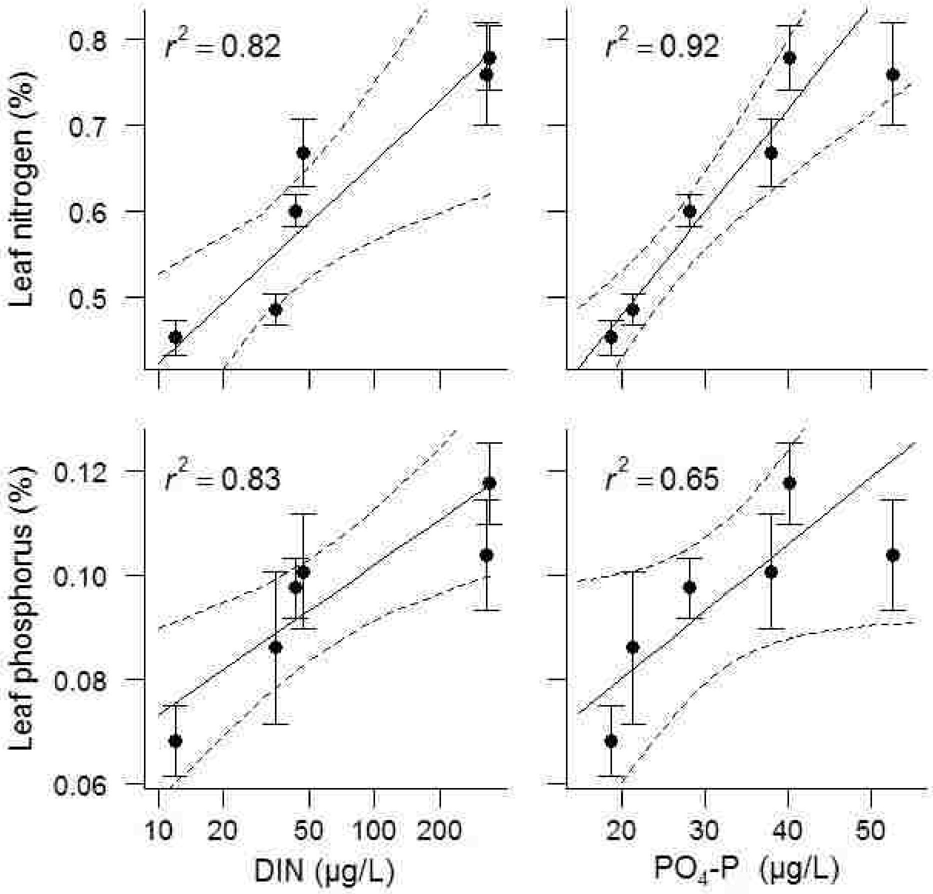

Figure 11. Leaf % N (top) and % P (bottom) predicted by stream DIN concentrations (left) and stream PO_4-P concentrations (right). The axis for DIN is log-transformed.

Table 7. Total macroinvertebrates per g of leaf litter remaining and total taxa at the end of 8 weeks on bluejoint leaf packs in 6 streams listed in descending order of dissolved nutrient concentrations. Values are means (SE).

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

Table 8. Macroinvertebrate abundances, frequencies, NMDS scores, and feeding habits for taxa that occurred in 2 or more streams. Taxa are sorted from high NMDS scores to low scores.

Taxon name	NMDS scores	Stream abundance (no./g) 22	1203	44	619	545	171	Freq. (%)	Ave. no./g	Feeding habit
Heptegeneidae (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
Orthocladinae (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

Table 8 cont.

Taxon name	NMDS scores	Stream abundance (no./g)						Freq. (%)	Ave. no./g	Feeding habit
		22	1203	44	619	545	171			
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

[a] C-collector, D-detritivore, F-filterer, G-gatherer, H-herbivore, P-predator, Sc-scraper, Sh-shredder

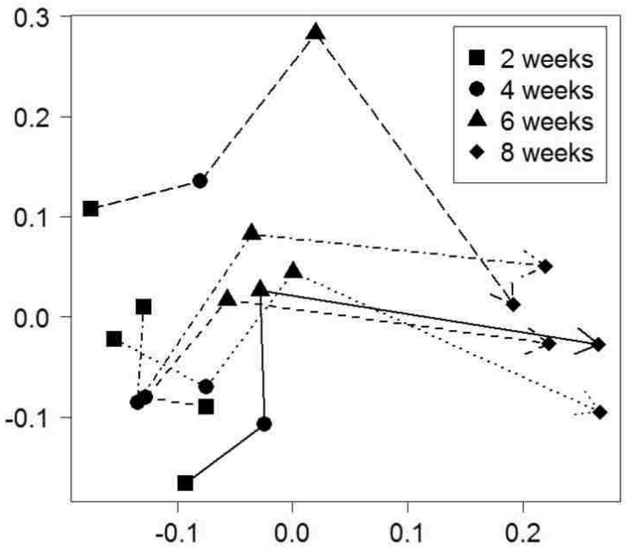

Figure 12. NMDS ordination for 5 racks over time in Stream 1203. Macroinvertebrate communities generally shifted from left to right for all 5 racks as leaf decomposition progressed with a large consistent change between weeks 6 and 8.

Table 9. Indicator species analysis results for taxa associated with leaf packs over time in Stream 1203. Indicator value combines frequency and abundance of an individual taxon to a specific group (time period). Significance of group assignments were determined with a permutation test ($n = 500$).

Taxon name	Weeks	Indicator 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

Discussion

Webster and Benfield (1986) summarized 20 studies and presented a mean decay rate in days for grasses in the family Poaceae of approximately 0.005. Although this rate represents various freshwater ecosystems and exposure techniques (bags vs. packs), it falls directly within the middle of the range of decay rates observed in the 6 streams for this study (0.0035 – 0.0060 \). More recent studies examining grass decomposition have used fresh leaf litter with a high initial % N concentration. Lopez and others (2001) reported decay rates in degree days of 0.0032 in the spring for ray grass with 3.5% leaf N. Likewise, Menninger and Palmer (2007) reported decay rates in days of 0.021 and 0.027 for 2 grass species with 1.77% and 2.33% leaf N, respectively. The decay rates of bluejoint in this study are almost an order of magnitude lower than the rates reported for fresh grass litter. In contrast, Young et al. (1994) utilized tussock grass leaves with starting leaf % N of 0.25 and reported decay rates (per day) of 0.002-0.005 for 6 streams along an agricultural gradient in New Zealand. The slow breakdown rate of bluejoint in these streams (20-30% mass loss over 2 months) compares to other studies using senesced grasses and reflects the low initial nutrient quality and cold stream temperatures, indicating it may take more than one growing season for complete breakdown.

Two lines of evidence show the importance of microbial conditioning on bluejoint decomposition. The leaf litter quality results indicate that microbial colonization occurred rapidly (< 2 weeks) and, by weeks 6 and 8, was strongly related to the stream nutrient gradient. Several studies that have shown the positive effect of increased stream nutrients on microbial colonization and breakdown of leaf litter (Suberkropp and Chauvet

1995; Gulis and Suberkropp 2003). Patterns of leaf % N reported by Young and others (1994) in their most degraded stream (NO_x-N concentrations of approximately 100 ug/L) resembled changes in litter quality over time for streams in this study: leaf % N increased to a maximum of approximately 0.6 after 28 days and remained high 5 months later. Additionally, the clear colonization pattern of the leaf packs in Stream 1203 and the high number of indicator taxa at 8 weeks shows the importance of microbial conditioning for macroinvertebrates. Fungi and bacteria improve the palatability of leaf litter by providing a high nutrient food resource and also through enzymatic breakdown of structural compounds (Cummins and others 1989; Graca 2001). Stream nutrient concentrations positively affected microbial colonization on the bluejoint litter in this study followed by a conditioning period that caused a dramatic change in macroinvertebrate community composition.

A comparison of stream nutrient concentrations, microbes, and macroinvertebrates as predictors of the bluejoint breakdown rate showed that all three affected decomposition to varying degrees. DIN explained more variation than PO_4-P, indicating it may be the nutrient most limiting to the stream heterotrophic community. Leaf litter quality, a potential indicator of microbial colonization, and the total macroinvertebrates (no./g) were comparable predictors of leaf breakdown rates. This contrasts with the general theory that shredding macroinvertebrates, rather than microbial activity, are the dominant driver of breakdown in low order streams (Graca, Ferreira, Coimbra 2001). Since the shift in the macroinvertebrate community occurred just prior to the end of the study, longer deployments may be necessary to detect a change in the breakdown rate due to macroinvertebrates.

Aggregate macroinvertebrate indices from this study compare favorably to other studies utilizing both grasses and deciduous tree litter. In a similar study evaluating decomposition of senesced tussock grass in 6 streams of varying nutrient quality, the total number of macroinvertebrates per g of leaf pack ranged from less than 10 to over 50 (Young, Huryn, Townsend 1994). In a 3rd order boreal stream in winter, the maximum number of macroinvertebrates per g of leaf pack for birch, willow, and alder were 74, 149, and 223, respectively (Haapala, Muotka, Markkola 2001). The total macroinvertebrates per g of leaf pack in streams at the high end of the nutrient gradient in this study were higher than the tussock grasses and had comparable colonization to birch, which is a relatively low quality deciduous tree litter (leaf % N of 0.7 to 0.8; Haapala, Muotka, Markkola 2001). Bluejoint also supports a diverse macroinvertebrate assemblage. Sylvestre and Bailey (2005) reported an average of 12 genera per leaf pack for 119 streams in British Columbia, which is slightly lower than the 16 mean taxa recorded for the 6 streams in this study. The mean number of taxa in this study would be even higher had chironomid subfamilies been keyed to genera. Macroinvertebrate densities on grasses are much lower than for deciduous tree litter, but diversity is high, indicating that organisms have adapted to utilize this carbon source.

The macroinvertebrate community ordination results showed that the first NMDS axis explained 80% of the variance in leaf breakdown rates and that a diversity of organisms was present along the entire stream nutrient gradient. Shredding macroinvertebrates (either *Zapada* stoneflies or limnephilid caddisflies) were found in all 6 streams. Other prevalent taxa were also utilizing the bluejoint as a food resource by scraping microbes off the conditioned leaf litter, such as *Baetis* mayflies. Additional uses of the leaf packs included habitat for filtering or collecting (chironomid midges and simuliid black flies) and also as a prey resource for predators (*Dicranota* craneflies and *Rhyacophila* caddisflies). The diversity of macroinvertebrate taxa utilizing the bluejoint in this study indicates that it comprises an important food resource and habitat in headwater stream ecosystems.

Bluejoint grass is a dominant riparian vegetation species along headwater streams of the Kenai Peninsula although little is known of its contribution to productivity in these systems. Breakdown rates measured for 6 headwater streams show that it decomposes slowly compared to other substrates of higher nutrient quality, but increases proportional to the amount of dissolved nutrients in the streams. Conditioning is an important step in breakdown and was observed to occur rapidly in these streams with a subsequent change in the macroinvertebrate community that occurred prior to 8 weeks. The macroinvertebrate community that colonized bluejoint in all 6 streams included several abundant shredder taxa along with scrapers, collector-gatherers, and predators. These macroinvertebrates may become food resources for juvenile salmonids as they enter drift, either accidentally or during emergence (Nielsen 1992). Future studies on the importance of bluejoint grass should consider longer deployments to further examine the role of macroinvertebrates, determine the time necessary for complete breakdown, and also more directly measure the importance of bluejoint to stream food webs, through either stable isotope or gut content analysis.

CHAPTER FOUR

Conclusions

In headwater streams of the Kenai lowlands, alder exerts a strong influence on stream N concentrations. Alder cover explained over 83% of the variation in NO_x-N yield in May, July, and September. The relationship between alder cover and stream N was linear in May, but changed to non-linear in July and September. Higher temperatures later in the growing season increased nutrient uptake and denitrification leading to lower export of AFN in watersheds with low alder cover. At cover greater than approximately 15%, terrestrial ecosystems may have become N saturated increasing rates of AFN reaching streams. Reported N fixation rates for alder between 100 and 200 kg ha^{-1} annually are much higher than ammonium deposition rates of 21 kg ha^{-1} annually at a fertilizer plant on the Kenai Peninsula that resulted in N saturation and nutrient imbalances in the vegetation community (Binkley, Cromack, Baker 1994; Whytemare and others 1997). Maximum stream N concentrations in the spring in Kenai lowland headwater streams coincides with fry emergence and may be an important nutrient input fueling productivity early in the growing season.

Bluejoint grass is an abundant, although low quality, terrestrial input to Kenai lowland headwater streams. After submergence in the streams, bluejoint litter quality increased rapidly and was strongly associated with stream dissolved nutrient concentrations by 6 weeks, followed by a distinct shift in the macroinvertebrate community prior to 8 weeks. The bluejoint breakdown rate (dd^{-1}) was related to the stream nutrient gradient, changes in litter quality, the total number of macroinvertebrates per g of leaf pack, and the NMDS axis scores that reflected differences in macroinvertebrate community composition among the 6 streams at 8 weeks. Longer deployments may be necessary to identify the importance of macroinvertebrate consumers on bluejoint decomposition. The total number of macroinvertebrates per g of leaf pack on bluejoint litter was much lower than abundances reported for deciduous tree litter, but diversity was high, indicating that taxa are adapted to utilize this allochthonous resource. The macroinvertebrate taxa strongly associated with bluejoint litter by 8 weeks included shredders, scrapers, collector-gathers, and predators; providing evidence that it is an important habitat and food resource during the summer months when deciduous tree litter inputs are low.

LITERATURE CITED

American Public Health Association. 2005. Standard methods for the examination of water and wastewater. 21st edition ed. Washington, D.C.: American Public Health Association, American Water Works Association, and Water Environment Federation.

Anderson DM, Burnham KP, Thompson WL. 2000. Null hypothesis testing: Problems, prevalence, and an alternative. The Journal of Wildlife Management 64:912-23.

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

Benfield EF. 1997. Comparison of litterfall input to streams. Journal of the North American Benthological Society 16:104-8.

Binkley D, Cromack K, Baker DJ. 1994. Nitrogen fixation by red alder: Biology, rates, and controls. In: The biology and management of red alder. Hibbs DE, DeBell DS,Tarrant RF, editors. Corvallis, OR: Oregon State University. 57 p.

Bramblett RG, Bryant MD, Wright BE, White RG. 2002. Seasonal use of small tributary and main-stem habitats by juvenile steelhead, coho salmon, and dolly varden in a southeastern alaska drainage basin. Trans Am Fish Soc 131(3):498-506.

Bryant MD, Zymonas ND, Wright BE. 2004. Salmonids on the fringe: Abundance, species composition, and habitat use of salmonids in high-gradient headwater streams, southeast alaska. Trans Am Fish Soc 133(6):1529-38.

Cairns MA and Lajtha K. 2005. Effects of succession on nitrogen export in the west-central cascades, oregon. Ecosystems 8(5):583-601.

Chadwick MA and Huryn AD. 2003. Effect of a whole-catchment N addition on stream detritus processing. J N Am Benthol Soc 22(2):194-206.

Chadwick MA, Dobberfuhl DR, Benke AC, Huryn AD, Suberkropp K, Thiele JE. 2006. Urbanization affects stream ecosystem function by altering hydrology, chemistry, and biotic richness. Ecol Appl 16(5):1796-807.

Clement JC, Holmes RM, Peterson BJ, Pinay G. 2003. Isotopic investigation of denitrification in a riparian ecosystem in western france. J Appl Ecol 40(6):1035-48.

Compton JE, Church MR, Larned ST, Hogsett WE. 2003. Nitrogen export from forested watersheds in the oregon coast range: The role of N-2-fixing red alder. Ecosystems 6(8):773-85.

Creed IF and Band LE. 1998. Export of nitrogen from catchments within a temperate forest: Evidence for a unifying mechanism regulated by variable source area dynamics. Water Resour Res 34(11):3105-20.

Cummins KW, Wilzbach MA, Gates DM, Perry JB, Taliaferro WB. 1989. Shredders and riparian vegetation. BioScience 39:24-30.

Dodds WK, Smith VH, Lohman K. 2002. Nitrogen and phosphorus relationships to benthic algal biomass in temperate streams. Can J Fish Aquat Sci 59(5):865-74.

Doucett RR, Power G, Barton DR, Drimmie RJ, Cunjak RA. 1996. Stable isotope analysis of nutrient pathways leading to atlantic salmon. Can J Fish Aquat Sci 53(9):2058-66.

Dugdale RC and Dugdale VA. 1961. Sources of phosphorus and nitrogen for lakes on afognak island. Limnology and Oceanography 6:13-23.

Ebersole JL, Wigington PJ, Jr., Baker JP, Cairns MA, Church MR, Hansen BP, Miller BA, LaVigne HR, Compton JE, Leibowitz SG. 2006. Juvenile coho salmon growth and survival across stream network seasonal habitats. Trans Am Fish Soc 135(6):1681-97.

Faerovig PJ and Hessen DO. 2003. Allocation strategies in crustacean stoichiometry: The potential role of phosphorus in the limitation of reproduction. Freshwat Biol 48(10):1782-92.

Ferreira V, Gulis V, Graca MAS. 2006. Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. Oecologia 149(4):718-29.

Findlay S. 2010. Stream microbial ecology. J N Am Benthol Soc 29(1):170-81.

Francoeur SN. 2001. Meta-analysis of lotic nutrient amendment experiments: Detecting and quantifying subtle responses. J N Am Benthol Soc 20(3):358-68.

Gende SM, Edwards RT, Willson MF, Wipfli MS. 2002. Pacific salmon in aquatic and terrestrial ecosystems. Bioscience 52(10):917-28.

Gesch D, Oimoen M, Greenlee S, Nelson C, Steuck M, Tyler D. 2002. The national elevation dataset. Photogrammetric Engineering and Remote Sensing 68:5-11.

Gesch DB. 2007. The national elevation dataset. In: Digital elevation model technologies and applications: The DEM users manual, 2nd edition. Maune D, editor. Bethesda, Maryland: American Society for Photogrammetry and Remote Sensing. 99 p.

Gessner MO and Chauvet E. 1994. Importance of stream microfungi in controlling breakdown rates of leaf-litter. Ecology 75(6):1807-17.

Golden HE, Boyer EW, Brown MG, Purucker ST, Germain RH. 2009. Spatial variability of nitrate concentrations under diverse conditions in tributaries to a lake watershed(1). J Am Water Resour Assoc 45(4):945-62.

Goodman LF and Hungate BA. 2006. Managing forests infested by spruce beetles in south-central alaska: Effects on nitrogen availability, understory biomass, and spruce regeneration. For Ecol Manage 227(3):267-74.

Goslee SC and Urban DL. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22:1-19.

Graca MAS. 2001. The role of invertebrates on leaf litter decomposition in streams - a review. International Review of Hydrobiology 86:383-93.

Graca MAS, Barlocher F, Gessner MO, editors. 2005. Methods to study litter decomposition. The Netherlands: Springer. 329 pages p.

Graca MAS, Ferreira RCF, Coimbra CN. 2001. Litter processing along a stream gradient: The role of invertebrates and decomposers. J N Am Benthol Soc 20(3):408-20.

Gracz M, North P, Noyes K, Tande G, Van Patten D. 2004. Wetlands of the kenai lowlands: A landscape-level wetland management tool. .

Greenwood JL, Rosemond AD, Wallace JB, Cross WF, Weyers HS. 2007. Nutrients stimulate leaf breakdown rates and detritivore biomass: Bottom-up effects via heterotrophic pathways. Oecologia 151(4):637-49.

Gulis V and Suberkropp K. 2003. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. Freshwat Biol 48(1):123-34.

Haapala A, Muotka T, Markkola A. 2001. Breakdown and macroinvertebrate and fungal colonization of alder, birch, and willow leaves in a boreal forest stream. J N Am Benthol Soc 20(3):395-407.

Hanson GC, Groffman PM, Gold AJ. 1994. Denitrification in riparian wetlands receiving high and low groundwater nitrate inputs. J Environ Qual 23(5):917-22.

Hauer RF and Lamberti GA, editors. 2006. Methods in stream ecology. 2nd edition ed. San Diego, California: Academic Press.

Heiri O, Lotter AF, Lemcke G. 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: Reproducibility and comparability of results. J Paleolimnol 25(1):101-10.

Hladyz S, Gessner MO, Giller PS, Pozo J, Woodward G. 2009. Resource quality and stoichiometric constraints on stream ecosystem functioning. Freshwat Biol 54(5):957-70.

Hurd TM and Raynal DJ. 2004. Comparison of nitrogen solute concentrations within alder (alnus incana ssp rugosa) and non-alder dominated wetlands. Hydrol Process 18(14):2681-97.

Huryn AD, Riley RH, Young RG, Arbuckle CJ, Peacock K, Lyon G. 2001. Temporal shift in contribution of terrestrial organic matter to consumer production in a grassland river. Freshwat Biol 46(2):213-26.

Junger M and Planas D. 1994. Quantitative use of stable carbon-isotope analysis to determine the trophic base of invertebrate communities in a boreal forest lotic system. Can J Fish Aquat Sci 51(1):52-61.

Kane ES, Betts EF, Burgin AJ, Clilverd HM, Crenshaw CL, Fellman JB, Myers-Smith IH, O'Donnell JA, Sobota DJ, Van Verseveld WJ, et al. 2008. Precipitation control over inorganic nitrogen import-export budgets across watersheds: A synthesis of long-term ecological research. Ecohydrology 1(2):105-17.

King RS, Baker ME, Whigham DF, Weller DE, Jordan TE, Kazyak PF, Hurd MK. 2005. Spatial considerations for linking watershed land cover to ecological indicators in streams. Ecol Appl 15(1):137-53.

Laughlin WM, Smith GR, Peters MA. 1984. Influence of N-fertilization, P-fertilization, and K-fertilization on yield and mineral-composition of native bluejoint grass on the lower kenai peninsula, alaska. Agron J 76(3):389-97.

Leberfinger K and Bohman I. 2010. Grass, mosses, algae, or leaves? food preference among shredders from open-canopy streams. Aquat Ecol 44(1):195-203.

Lemon J, Bolker B, Oom S, Klein E, Rowlingson B, Wickham H, Tyagi A, Eterradossi O, Grothendieck G, Toews M. 2009. plotrix: Various plotting functions.[computer program]. Version R package version 2.7-2. .

Lopez ES, Pardo I, Felpeto N. 2001. Seasonal differences in green leaf breakdown and nutrient content of deciduous and evergreen tree species and grass in a granitic headwater stream. Hydrobiologia 464(1-3):51-61.

McCune B and Grace JB. 2002. Analysis of ecological communities. Gleneden Beach, OR: MjM Software Design.

McTammany ME, Benfield EF, Webster JR. 2008. Effects of agriculture on wood breakdown and microbial biofilm respiration in southern appalachian streams. Freshwater Biology 53:842-54.

Melillo JM, Aber JD, Muratore JF. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63(3):621-6.

Menninger HL and Palmer MA. 2007. Herbs and grasses as an allochthonous resource in open-canopy headwater streams. Freshwat Biol 52(9):1689-99.

Merritt RW, Cummins KW, Berg MB, editors. 2008. An introduction to the aquatic insects of north america. Fourth Edition ed. Dubuque, Iowa: Kendall/Hunt Publishing Co. 1158 p.

Mitchell JS and Ruess RW. 2009. N-2 fixing alder (alnus viridis spp. fruticosa) effects on soil properties across a secondary successional chronosequence in interior alaska. Biogeochemistry 95(2-3):215-29.

Naiman RJ, Bilby RE, Schindler DE, Helfield JM. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5(4):399-417.

Nielsen JL. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transaction of the American Fisheries Society 121:617-34.

Niyogi DK, Simon KS, Townsend CR. 2003. Breakdown of tussock grass in streams along a gradient of agricultural development in new zealand. Freshwat Biol 48(9):1698-708.

Ogawa A, Shibata H, Suzuki K, Mitchell MJ, Ikegami Y. 2006. Relationship of topography to surface water chemistry with particular focus on nitrogen and organic carbon solutes within a forested watershed in hokkaido, japan. Hydrol Process 20(2):251-65.

Oksanen J, Roeland K, Legendre P, O'Hara B, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2009. vegan: Community Ecology Package [computer program]. Version R package version 1.15-4. .

Perry RW, Bradford MJ, Grout JA. 2003. Effects of disturbance on contribution of energy sources to growth of juvenile chinook salmon (oncorhynchus tshawytscha) in boreal streams. Can J Fish Aquat Sci 60(4):390-400.

Ping CL and Michaelson GJ. 1986. Phosphorus sorption by major agricultural soils of alaska. Commun Soil Sci Plant Anal 17(3):299-320.

Pinheiro J, Bates D, DebRoy S, Deepayan S, R Core Team. 2009. nlme: Linear and Nonlinear Mixed Effects Models [computer program]. Version R package version 3.1-96. .

R Development Core Team. 2009. R: A language and environment for statistical computing.[computer program]. Version R package version 2.10.1. Vienna, Austria: .

Reynolds KM. 1990. Preliminary classification of forest vegetation of the kenai peninsula, alaska. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Report nr PNW-RP-424.

Rhoades C, Oskarsson H, Binkley D, Stottlemyer B. 2001. Alder (alnus crispa) effects on soils in ecosystems of the agashashok river valley, northwest alaska. Ecoscience 8(1):89-95.

Richardson JS, Shaughnessy CR, Harrison PG. 2004. Litter breakdown and invertebrate association with three types of leaves in a temperate rainforest stream. Arch Hydrobiol 159(3):309-25.

Richardson JS and Danehy RJ. 2007. A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. For Sci 53(2):131-47.

Roberts DW. 2010. labdsv: Ordination and multivariate analysis for ecology [computer program]. Version R package version 1.4-1. .

Robinson CT and Gessner MO. 2000. Nutrient addition accelerates leaf breakdown in an alpine springbrook. Oecologia 122(2):258-63.

Sabater S, Butturini A, Clement JC, Burt T, Dowrick D, Hefting M, Maitre V, Pinay G, Postolache C, Rzepecki M, et al. 2003. Nitrogen removal by riparian buffers along a european climatic gradient: Patterns and factors of variation. Ecosystems 6(1):20-30.

Scarsbrook MR and Townsend CR. 1994. The roles of grass leaf-litter in streams draining tussock grassland in new-zealand - retention, food-supply and substrate stabilization. Freshwat Biol 32(2):429-43.

Schaefer SC, Hollibaugh JT, Alber M. 2009. Watershed nitrogen input and riverine export on the west coast of the US. Biogeochemistry 93(3):219-33.

Schiff SL, Devito KJ, Elgood RJ, McCrindle PM, Spoelstra J, Dillon P. 2002. Two adjacent forested catchments: Dramatically different NO3- export. Water Resour Res 38(12):1292.

Snyder CD, Young JA, Villella R, Lemarie DP. 2003. Influences of upland and riparian land use patterns on stream biotic integrity. Landscape Ecol 18(7):647-64.

Sorenson R, Zinko U, Seibert J. 2005.
On the calculation of the topographic wetness index: Evaluation of different methods based on field observations. Hydrol Earth Sys Sci Discuss (2):1807-34.

Stieglitz M, Shaman J, McNamara J, Engel V, Shanley J, Kling GW. 2003. An approach to understanding hydrologic connectivity on the hillslope and the implications for nutrient transport. Global Biogeochem Cycles 17(4):1105.

Stottlemyer R and Toczydlowski D. 1999. Seasonal relationships between precipitation, forest floor, and streamwater nitrogen, isle royale, michigan. Soil Sci Soc Am J 63(2):389-98.

Suberkropp K and Chauvet E. 1995. Regulation of leaf breakdown by fungi in streams - influences of water chemistry. Ecology 76(5):1433-45.

Sylvestre S and Bailey RC. 2005. Ecology of leaf pack macroinvertebrate communities in streams of the fraser river basin, british columbia. Freshwater Biology 50:1094-104.

Tank JL and Dodds WK. 2003. Nutrient limitation of epilithic and epixylic biofilms in ten north american streams. Freshwat Biol 48(6):1031-49.

Tank JL, Rosi-Marshall EJ, Griffiths NA, Entrekin SA, Stephen ML. 2010. A review of allochthonous organic matter dynamics and metabolism in streams. J N Am Benthol Soc 29(1):118-46.

Thorp JH and Covich AP, editors. 2001. Ecology and classification of north american freshwater invertebrates. 2nd Edition ed. San Diego, CA: Academic Press. 1056 p.

Thorp JH and Delong AD. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96(3):543-50.

Viereck LA, Dyrness CT, Batten AR, Wenzlick KJ. 1992. The alaska vegetation classification. Portland, OR: United States Department of Agriculture, Forest Service, Pacific Northwest Research Station. Report nr PNW-GTR-286. 278 pg.

Voshell JR. 2002. A guide to common freshwater invertebrates of north america. Blacksburg, Virginia: The McDonald and Woodward Publishing Company.

Watmough SA, Eimers MC, Aherne J, Dillon PJ. 2004. Climate effects on stream nitrate concentrations at 16 forested catchment in south central ontario. Environ Sci Technol 38:2383-8.

Webster JR and Benfield EF. 1986. Vascular plant breakdown in fresh-water ecosystems. Annu Rev Ecol Syst 17:567-94.

Werner RA, Holsten EH, Matsuoka SM, Burnside RE. 2006. Spruce beetles and forest ecosystems in south-central alaska: A review of 30 years of research. For Ecol Manage 227(3):195-206.

Whytemare AB, Edmonds RL, Aber JD, Lajtha K. 1997. Influence of excess nitrogen deposition on a white spruce (picea glauca) stand in southern alaska. Biogeochemistry 38:173-87.

Wickham H. 2010. stringr: Make it easier to work with strings [computer program]. Version R package version 0.3. .

Wiederholm T, editor. 1983. Chironomidae of the holarctic region - keys and diagnoses. part 1. larvae. Entomologica scandinavica.

Wiggins GB. 1996. Larvae of the north american caddisfly genera (trichoptera). 2nd edition ed. Buffalo, NY: University of Toronto Press.

Wigington PJ, Church MR, Strickland TC, Eshleman KN, Van Sickle J. 1998. Autumn chemistry of oregon coast range streams. J Am Water Resour Assoc 34(5):1035-49.

Wipfli MS, Richardson JS, Naiman RJ. 2007. Ecological linkages between headwaters and downstream ecosystems: Transport of organic matter, invertebrates, and wood down headwater channels. J Am Water Resour Assoc 43(1):72-85.

Wipfli MS, Hudson JP, Chaloner DT, Caouette JR. 1999. Influence of salmon spawner densities on stream productivity in southeast alaska. Can J Fish Aquat Sci 56(9):1600-11.

Wood SN. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. Journal of the Royal Statistical Society 70:495-518.

Young RG, Huryn AD, Townsend CR. 1994. Effects of agricultural-development on processing of tussock leaf-litter in high country new-zealand streams. Freshwat Biol 32(2):413-27.

Zeug SC and Winemiller KO. 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89(6):1733-43.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. New York: Springer.