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Alder cover drives nitrogen availability in Kenai lowland headwater streams, Alaska

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Abstract Terrestrial sources of nitrogen (N), particularly N-fixing alder, may be important for sustaining production in headwater streams that typically lack substantial subsidies of marine-derived nutrients from spawning salmon yet support upstream-dispersing juvenile salmonids. However, other physiographic characteristics, such as watershed slope and topographic wetness, also control transport of nutrients to streams and may confound apparent linkages between alder and stream N. Seasonal patterns in precipitation and temperature may interact with watershed characteristics to modulate stream N availability. We empirically modeled the effect of alder cover and other watershed physiographic variables on stream N and contrasted these relationships over the growing season among 25 first-order streams from the lower Kenai Peninsula, Alaska. For each date, percent alder cover, mean topographic wetness, and mean slope were used as watershed predictors of NO_x–N concentration (nitrate + nitrite) and daily NO_x–N yield using Generalized Additive Models (GAM) and compared using Akaike's Information Criterion (AIC_c). Alder cover was the only probable model and explained 75–96% of the variation in NO_x–N concentration and 83–89% of the variation in daily NO_x–N yield. The relationship between alder and both NO_x–N concentration and daily NO_x–N yield changed from constant inputs in May across the range of alder cover (linear fit) to increasing inputs in July and September (non-linear fits) implying that high-alder watersheds were N-saturated. The strong linkage between alder and stream N coupled with the concurrent timing of maximum stream N from alder in the spring to salmon fry emergence indicates the potential importance of this subsidy to headwater stream ecosystems.

Keywords *Alnus* · Topographic wetness index · Nitrogen fixation · Watershed physiography

Introduction

Many stream ecosystems are nitrogen limited (Francoeur 2001; Dodds et al. 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 et al. 1999; Gende et al. 2002; Naiman et al. 2002). Headwater (first-order) streams may receive lower contributions of MDN because adult salmon can be limited to the lower reaches of streams with adequate gravels for spawning (Richardson and

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Danehy 2007), despite serving as rearing habitat for upstream-dispersing juvenile salmon (Bramblett et al. 2002; Bryant et al. 2004; Ebersole et al. 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 et al. 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 et al. 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 (Van Miegroet and Cole 1984; Rhoades et al. 2001; Hurd and Raynal 2004; Mitchell and Ruess 2009a) and also plant nitrogen concentrations directly beneath its canopy (Rhoades et al. 2001). Alder-fixed N (AFN) may be transported to the stream by litterfall directly to the stream, soluble nutrients from riparian zones, or leaching and lateral transport by surface and groundwater from upland alder stands (Compton et al. 2003; Stieglitz et al. 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 et al. 2002; Snyder et al. 2003; Watmough et al. 2004). Wetlands and riparian buffers in flat landscape positions with a high hydrologic residence time show increased nutrient uptake and denitrification (Hanson et al. 1994; Clement et al. 2003; Sabater et al. 2003). Topographic wetness, an index used to quantify the control of topography on hydrologic processes and predict local wetness (Sorenson et al. 2005), explained 68% of the variation in nitrate export in small, forested watersheds (Ogawa et al. 2006). Therefore, 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 (Bechtold et al. 2003; Stieglitz et al. 2003; Kane et al. 2008) and precipitation variability (Kane et al. 2008) both influence stream N through mobilization of nutrients from watersheds to streams. 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 et al. 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 et al. 2002; Golden et al. 2009). 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 during the early, middle, and late parts of the growing season. Although the contribution of AFN to stream ecosystems has been shown in one previous study (Compton et al. 2003), here we examined the relationship between alder cover and stream N in a different region, compared alder to other watershed physiographic variables known to affect the transport of terrestrial N to streams, and investigated differences in N transport to streams at different times during the growing season. The study was conducted in 25 small, salmon-rearing streams of the Lower Kenai Peninsula, Alaska; a region with relatively diverse physiography (Gracz et al. 2004) and a wide range of upland alder cover among watersheds. Alder cover was expected to be an important predictor

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	+/−

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 denitrification were expected to decrease N in streams during mid-summer (July).

Methods

Study area

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 3% of its area as agricultural land (2007 Census of Agriculture Area Profile, Kenai Peninsula Area, Alaska, http://www.agcensus.usda.gov/Publications/2007/Online_Highlights/County_Profiles/Alaska/cp02122.pdf). 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/cgi-bin/cliMAIN.pl?akhome).

The headwater streams included in this study are located between 71 and 539 m asl 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 et al. 1992). Wetlands cover 43% of the area (Gracz et al. 2004). Southcentral Alaska forests suffered from a major spruce bark beetle epidemic in the 1990s causing high mortality in mature spruce (Werner et al. 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. Stream widths ranged from 50 to 340 cm and maximum depths from 10 to 40 cm. Substrates consisted of gravels and small cobbles. 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 at 0.34 kg ha^{-1} $year^{-1}$ in 2008 (sum of ammonium and nitrate wet deposition for Denali National Park, National Trends Network, http://nadp.sws.uiuc.edu/ads/2008/AK03.pdf).

Twenty-five headwater streams (Fig. 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 (Compton et al. 2003; Ogawa et al. 2006). 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 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: $TWI = \ln(A/\tan\beta)$; A − watershed area, β − local slope (Sorenson et al. 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™. 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 et al. 2002; Gesch 2007). Other landscape variables calculated in GIS using the DEM included mean slope and mean elevation for each watershed.

Sampling and analysis

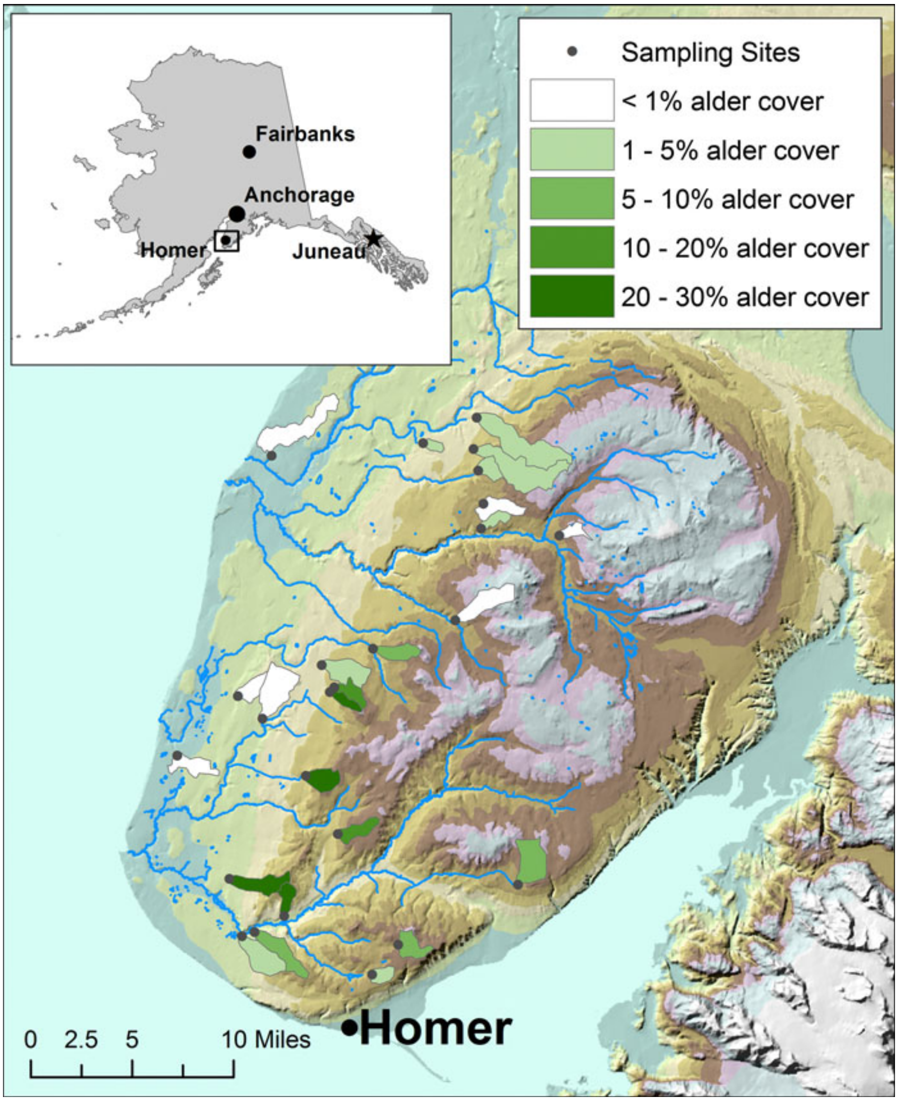
Twenty headwater streams were sampled May 18–21, July 7–10, and September 8–11, 2009 to encompass the early, middle, and late parts of the growing season; 5 additional headwater streams were only sampled in July. Water samples were collected and analyzed for total nitrogen (TN), nitrate–nitrite–N (NO_x–N), and ammonium–N (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™ 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 (Fig. 2). There are three types of alder on the Kenai Peninsula, although two are only described separately at the subspecies level: Green alder (*Alnus viridis* ssp. *fruticosa*), Sitka alder (*Alnus viridis* ssp. *sinuata*), and thin-leaf alder (*Alnus incana* ssp. *tenuifolia*). Green and Sitka alder commonly form homogenous stands on uplands, whereas thin-leaf alder occurs on wet soils next to streams and along groundwater discharge zones (Viereck and Little 2007). Both upland alder species form communities where they dominate the shrub layer with little or no forest canopy and are easily identified on color imagery for mapping purposes. Thin-leaf alder can be challenging to differentiate from other trees or shrubs due to its association with low densities of trees and willows in riparian zones. Mapped alder polygons were verified on the ground 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 used to calculate percent wetland cover for each watershed in GIS (Gracz et al. 2004).

Data analysis

The relationships between individual landscape variables (alder cover, wetland cover, mean TWI, mean

Fig. 1 Location of the 25 study streams on the Lower Kenai Peninsula. Watersheds are shaded by percent alder cover. *Inset* shows the location of the Lower Kenai Peninsula within Alaska



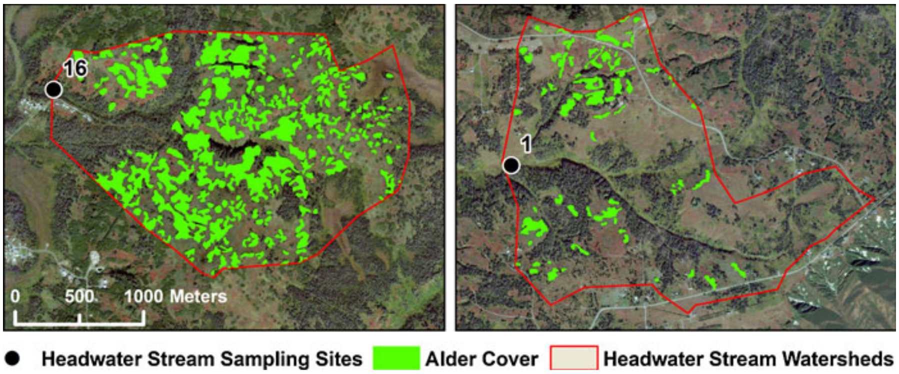


Fig. 2 Amount and spatial arrangement of alder in two headwater stream watersheds. Percent alder cover is 22 and 6 for Sites 16 (*left*) and 1 (*right*), respectively

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} day^{-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 concentration and daily 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 et al. 2009). 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 et al. 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 et al. 2005; Zuur et al. 2009). The *p*-values obtained from GAM for smoothing splines are approximate and Zuur et al. (2009) recommends that ecological significance only be attributed to smoothers with *p*-values $\leq$0.001. Significant models (*p*-values $\leq$0.001) for each response variable were compared using Akaike's Information Criterion for small-sample sizes (AIC_c) and the Akaike weights (w_i), which are the probability that a given model is the best model in the set of models considered (Anderson et al. 2000). AIC_c 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-likelihood of the model; a lower AIC_c indicates a better model. AIC_c for small sample sizes is used when the sample size divided by the number of parameters is less than 40 (Anderson et al. 2000). Fitted responses were contrasted among seasons using 95% confidence limits.

Results

Alder cover in the watersheds varied from no alder to over 28.2% cover, mean TWI ranged from 11.4 to 14.1, and mean slope ranged from 1.5 to 15.8% (Table 2). NO_x–N concentrations across streams and seasons ranged from 3 to 1560 μg L^{-1}, and NO_x–N yield varied from 0.01 to 13.11 g ha^{-1} day^{-1} (Table 3).

The GAM model outputs showed that the only explanatory variable with a significant smoother for predicting NO_x–N yield or NO_x–N concentration for all months was alder cover (Table 4, Figs. 3, 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 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 concentration 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

Table 2 Watershed characteristics of the 25 study streams on the Lower Kenai Peninsula

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] Sites were only sampled in July

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 concentration 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, Figs. 3, 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). Between May and July, NO_x–N concentrations decreased at intermediate alder cover (3–20%), but remained the same at alder cover less than 3% and above 20% (Fig. 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, Figs. 4, 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

Table 3 Discharge, flow, and dissolved nutrients of the 25 study streams on the Lower Kenai Peninsula. Minimum and maximum values are given

Site	Discharge (m^3 s^{-1})	Flow (m s^{-1})	NO_x–N (μg L^{-1})	NH_4–N (μg L^{-1})	Total nitrogen (μg L^{-1})	NO_x–N yield (g ha^{-1} day^{-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] Sites were only sampled in July

relationship was significantly nonlinear during the latter 2 months, implying a greater yield of N per unit alder at the highest cover.

Discussion

The comparison between watershed physiographic variables and alder cover in predicting stream N showed that alder cover far outweighed other predictors in explaining the variation in stream N. To our knowledge, Compton et al. (2003) is the only other study to empirically test the relationship 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. This study expands upon our understanding of AFN transport to streams by showing an impressively strong relationship between alder cover and stream N concentrations in a different geographic region during the early, middle, and late parts of the growing season. Our results are also novel because they showed that alder clearly outweighs other watershed physiographic variables in predicting stream N, which is a comparison that had not previously been made.

The range of N concentrations in the 25 headwater streams of the Kenai Peninsula (0.003–1.560 mg L^{-1}) is similar to other low order streams with alder. In 26 streams of the Oregon Coast Range, stream NO_3–N concentrations ranged from 0.074–2.429 mg L^{-1} over a 1-year sampling period (Compton et al.

Table 4 Results of GAM fits for NO_x–N concentration and daily NO_x–N yield

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

[a] Significant values at $p \leq 0.001$ (Zuur et al. 2009)

[b] 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 et al. 2009)

2003). The lower range found in the Alaskan streams is likely due to less alder cover; maximum cover in the Alaskan watersheds was 28% compared to >50% in the Oregon streams. Another study from Oregon in the west-central Cascades reported lower NO_3–N concentrations (<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 et al. 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 concentration and daily NO_x–N yield decreased from May to July and September (Fig. 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 et al. 2002; Golden et al. 2009). The summer minimum coincides with maximum N fixation rates for both green and thinleaf alder, which occur in late July and are driven by plant phenology and soil temperatures (Uliassi and Ruess 2002; Mitchell and Ruess 2009b). 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 occurred after significant rainfall in August that continued until sampling the second week of September. Terrestrial AFN may have already flushed into streams prior to the sampling in September. The maximum stream N concentrations for these streams probably 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

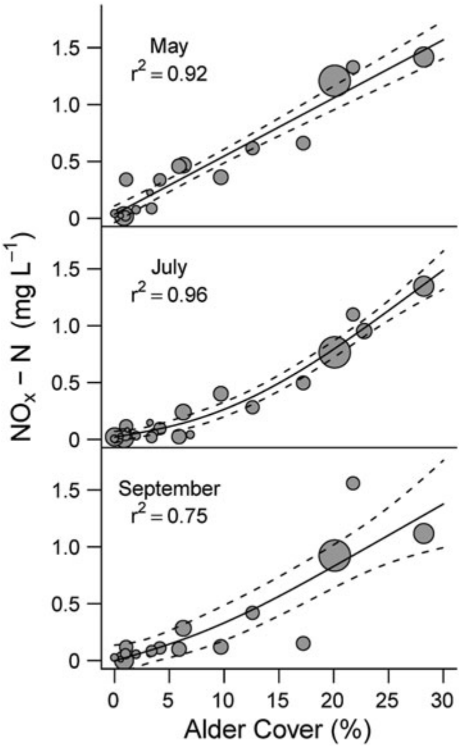


Fig. 3 Percent alder cover and NO_x–N concentrations for all months. Points are sized according to mean slope. *Dotted lines* are 95% confidence intervals

of NO_x–N from watersheds with medium alder cover and an increased export of NO_x–N in watersheds with high cover as compared to a constant export rate along the range of alder cover in May (linear fit). One hypothesis for this seasonal change may 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 (points in Figs. 3 and 4 are sized according to mean slope) nor topographic wetness (data not shown) correlate to alder cover 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.

N saturation in the watersheds with high alder cover may explain the high rates of NO_x–N export. Aber et al. (1989) define N saturation as "the availability of ammonium and nitrate in excess of

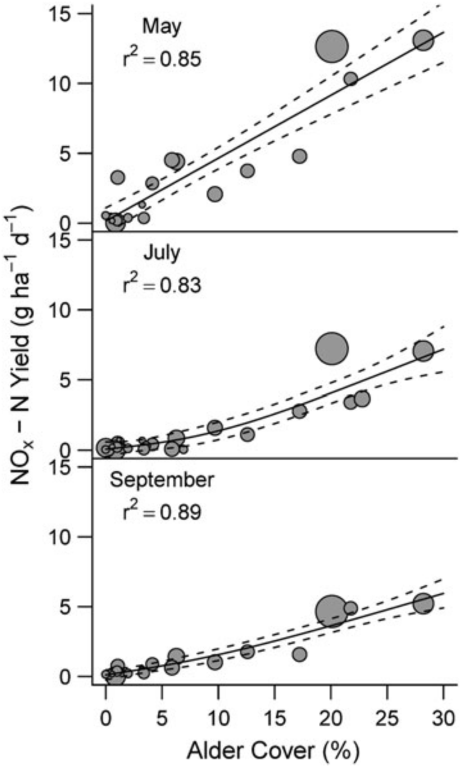


Fig. 4 Percent alder cover and daily NO_x–N yield for all months. Points are sized according to mean slope. *Dotted lines* are 95% confidence intervals

total combined plant and microbial nutritional demand". High anthropogenic N inputs to forests in the Northeastern U.S. have stimulated extensive research on N saturation and retention (Aber et al. 1998). In order to relate AFN to N saturation on the Lower Kenai Peninsula, the N inputs from the alder species in this study must be compared to the retention capabilities of the vegetation communities on the landscape. Mitchell and Ruess (2009a) report annual N inputs for green alder in interior Alaska at 6.6 kg N ha^{-1} $year^{-1}$ for late successional stands, although the authors state that rates may be much higher due to a drought during the study period suppressing N_2 fixation and an underestimate of nodule biomass. In addition, the acetylene reduction assay they used to measure N_2 fixation rates assumed a constant conversion factor between acetylene and N_2, although a large amount of variability exists for this ratio (Anderson et al. 2004). N inputs from thinleaf alder in early and mid successional stands on three rivers in Alaska using the more accurate $^{15}N_2$

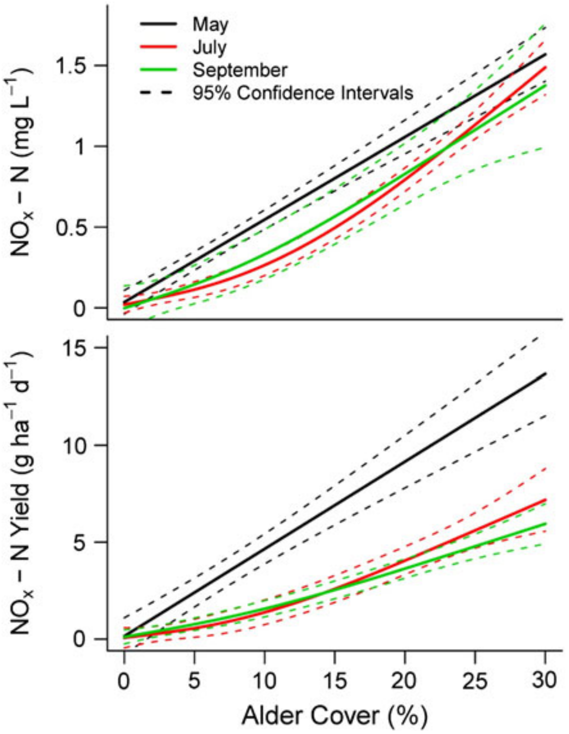


Fig. 5 Seasonal GAM fits for all 3 months for NO_x–N concentration (*top*) and daily NO_x–N yield (*bottom*)

uptake method ranged from 22–107 kg N ha^{-1} - year^{-1} (Ruess et al. 2009). Additions of NH_4NO_3 at a rate of 100 kg ha^{-1} year^{-1} in balsam poplar and white spruce forests in interior Alaska exceeded microbial and plant demand and led to leaching of NO_3–N from soils (Brenner et al. 2005). At a fertilizer plant on the Kenai Peninsula, input rates of 21 kg N ha^{-1} year^{-1} of NH_4–N resulted in N saturation indicated by high nitrification rates in soils and nutrient imbalances in vegetation close to the plant (Whytemare et al. 1997). At sites with greater than 15–20% alder cover, microbial and plant nutrient demand may not exceed export of AFN, resulting in increased NO_x–N reaching streams later in the growing season.

Alder's strong connection to stream N concentrations may have indirect effects on headwater stream biota. Headwater streams on the Lower Kenai Peninsula provide important rearing habitat for several species of juvenile salmon in addition to resident fish species. Energy inputs to headwater streams are dominated by allochthonous resources due to their narrow channels and overhanging vegetation (Richardson and Danehy 2007). These inputs provide an important carbon source for microbial and macroinvertebrate consumers that directly utilize leaf litter (Graça 2001; Findlay 2010) and also for higher trophic levels, such as macroinvertebrate predators and fish (Junger and Planas 1994; Perry et al. 2003). Whole-stream nutrient enrichment experiments have reported increased rates of leaf decomposition (Robinson and Gessner 2000; Gulis and Suberkropp 2003; Ferreira et al. 2006) and also macroinvertebrate (Robinson and Gessner 2000), bacterial (Gulis and Suberkropp 2003), and fungal biomass (Gulis and Suberkropp 2003; Ferreira et al. 2006). A study conducted concurrently to this one found rates of leaf decomposition and litter quality were strongly associated with DIN concentrations in 6 headwater streams (Shaftel, pers. comm.).

In addition, many studies of terrestrial vegetation on the Kenai Peninsula have shown that N is limiting to productivity (Laughlin et al. 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. Litter with high initial nutrient quality breaks down faster than poor quality litter in streams (Haapala et al. 2001; Hladyz et al. 2009).

Increased temperatures in Southcentral Alaska are associated with higher incidence of insect outbreaks and forest fires (Soja et al. 2007). The decrease in forest canopy cover after large-scale disturbances may allow for increased alder cover either initially or during forest succession (Werner et al. 2006). In addition, warmer temperatures on the Kenai Peninsula over the last 50 years have been tied to expansion of woody vegetation into drying wetlands (Klein et al. 2005). Should any of these drivers increase alder cover, stream N concentrations may increase, positively affecting the rate at which allochthonous material decomposes in headwater 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.

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