

Watershed influences on the structure and function of riparian wetlands associated with headwater streams – Kenai Peninsula, Alaska

D.F. Whigham^{1,*}, C.M. Walker², J. Mauer², R.S. King³, W. Hauser^{1,4,5}, S. Baird², J.A. Keuskamp^{6,7}, P.J. Neale¹

¹Smithsonian Environmental Research Center
647 Contees Wharf Road
Edgewater, MD 21037, USA
Whigham: whighamd@si.edu
Neale: nealep@si.edu
*Corresponding author

²Kachemak Bay National Estuarine Research Reserve
University of Alaska
2181 Kachemak Drive
Homer, AK 99603, USA
Walker: cmwalker9@alaska.edu
Baird: sjbaird@alaska.edu
Mauer: jazmaurer@gmail.com

³Baylor University
Department of Biology
One Bear Place #97388
Waco, TX 76798, USA
Ryan_S_King@baylor.edu

⁴Wabash College
Biology Department
Crawfordsville, IN 47933, USA

⁵Present Address
University of Indiana
School of Public and Environmental Affairs
1315 E. Tenth Street
Bloomington, IN 47405
whauser15@wabash.edu

⁶Netherlands Institute of Ecology (NIOO-KNAW)
P.O. Box 59
6700 AB Wageningen, The Netherlands
j.keuskamp@nioo.knaw.nl

⁷Utrecht University
Institute for Environmental Biology
Padualaan 8
3584 CH Utrecht, The Netherlands

Abstract

Riparian wetlands are dynamic components of landscapes. Located between uplands and aquatic environments, riparian habitats intercept sediments and nutrients before they enter aquatic environments. They are a source of organic matter and nutrients to aquatic systems, and they provide important habitat for animals, often serving as corridors for the movement of animals between habitats in fragmented landscapes. In this project, we focused on the structure and function of riparian wetlands associated with headwater streams in Alaska that serve as nursery habitats for juvenile salmonids. We asked whether or not the structure and function of headwater wetlands differed between watersheds with and without nitrogen-fixing Alder (*Alnus* spp.). We found that the aboveground biomass of riparian vegetation was higher in the watershed with Alder, but the largest differences were in the litter layer and belowground where vegetation in the watershed with no Alder had significantly higher root biomass. Interstitial water chemistry also differed between the study sites with significantly higher inorganic N and significantly different characteristics of colored dissolved organic matter at the site with Alder on the watershed. The biomass of litter that hung over the creek bank was less at the site with Alder on the watershed and an *in situ* decomposition experiment showed significant differences between the two systems. Results of the research demonstrates that watershed characteristics can impact the ecology of headwater streams in ways that had not been previously recognized.

1. Introduction

Interactions between streams and riparian wetlands adjacent to streams have been shown to be important in tidal and non-tidal systems. Riparian zones have been linked to surface and subsurface removal of nutrients, sediments, and organic matter before they reach streams (Naiman and Décamps 1997, Sebilo et al. 2003, Rutherford and Nguyen 2004, McLaughlin et al. 2011, Sakamaki and Richardson et al. 2011), especially in systems with floodplains that are periodically inundated during overbank flooding (Brinson et al. 1984, Rybecki et al. 2015). Wetlands that are immediately adjacent to streams and floodplains that are adjacent to streams also provide important ecological services in landscapes where uplands have been highly modified, especially when areas upslope of streamside wetlands have been converted into agricultural uses (Mulholland 1992, Pinay et al. 1993, Cirimo and McDonnell 1997). Nutrients and sediments that are transported from agricultural fields are intercepted resulting in the deposition of sediments and the uptake or immobilization of nutrients (e.g., Lowrance et al. 1984, Peterjohn and Correll 1984, Jordan et al. 1993). Wetlands adjacent to streams, often categorized as riparian buffers, are especially important as sites for nitrogen removal (Peterjohn and Correll 1984).

Headwater streams, which occupy a large percentage of river networks, are closely linked with the surrounding landscape, and contribute substantially to the ecology of downstream waters (Bryant et al 2004; Alexander et al. 2007; Meyer et al 2007; Nadeau and Rains 2007; Wipfli et al 2007). Boreal stream catchments are typically nutrient poor due to recent glaciation, have cold temperatures (Callahan et al. 2014) and slow soil development. Headwater streams are also typically located above the influence of marine derived nutrients, which come in the form of salmon carcasses when salmon spawn and die, leaving behind nutrient-rich biomass. Where spawning salmon are present, riparian zones play an important role in transforming and sequestering these marine derived nutrients (Helfield and Naiman 2002, Bartz and Naiman 2005, Edmonds and Mikkelsen 2006, Nagasaka et al, 2006, O'Donnell and Jones 2006, Denton et al. 2009, Pinay et al. 2009, Quinn et al. 2009, Lisi and Schindler

2011, Koshino et al. 2013, Rinella et al. 2013). In streams above the reach of spawning salmon, we found that more than 60% of the carbon and nitrogen in the bodies of juvenile Coho salmon and Dolly Varden had an allochthonous source (Dekar et al. 2012), further demonstrating the potential importance of connectivity between streams and riparian wetlands. In the same area where our project was conducted, we previously found that the inorganic nitrogen content of streams was related to the amount of Alder (*Alnus* spp.) on the watershed (Shaftel et al. 2012). We also found that inorganic nitrogen and dissolved organic matter content of the headwater streams influenced in-stream processes such as metabolism N-uptake, bacterial production, decomposition, and the abundance of macroinvertebrates in in-stream litter (Shaftel et al. 2011, Robbins et al. In press).

While it is clear that Alder on the watershed influences in-stream processes, it is not clear if the amount of Alder impacts the structure and function of riparian wetlands immediately adjacent to streams. Knowing how the presence of Alder influences both streams and wetlands adjacent to streams would be important from a management perspective (e.g., Soranno et al 1996). We conducted a field study to test the hypothesis that Alder cover at the watershed scale influenced the structure and function of riparian wetlands associated with headwater streams. Specifically, we tested the hypothesis that biomass production, the distribution of biomass in streamside vegetation, the decomposition of biomass, and the chemical characteristics of groundwater would differ between watersheds with and without Alder. The hypothesis was tested by comparing the amount of aboveground and belowground biomass and nitrogen in wetland vegetation, the amount of litter biomass overhanging the creek bank, and the chemical characteristics of interstitial water. We also conducted a nitrogen fertilization experiment to test the hypotheses that aboveground biomass production would be higher and litter turnover rates would be lower in wetlands that did not have any Alder on the watershed.

2. Study sites

This study was conducted on two headwater streams located in the Kenai Lowlands on the southern portion of the Kenai Peninsula in south-central Alaska between Kachemak Bay, Cook Inlet and the Kenai Mountains. The Kenai Lowlands are a broad, low shelf, predominantly less than 120 m above sea level, with four major drainage basins: Ninilchik River, Deep Creek, Stariski Creek and the Anchor River (Figure 1). Climate of the Kenai Lowlands transitions from maritime to continental from south to north and is typically characterized by long cool winters from September to May, and relatively short, warm summers, from June to August. The geology of the Kenai Lowlands consists primarily of complex glacial deposits or glacial till overlying weakly lithified Tertiary bedrock (Karlstrom 1964). Soils are generally poorly drained silt loams or silt clay loams below an organic soil layer or histic epipedon (Hinton 1971, Ford and Bedford 1983). Topography of the Kenai Lowlands is largely the result of five major Pleistocene glaciations and two minor post-Pleistocene glacial advances) which resulted in a complex system of moraines and unconsolidated glacial till throughout the area (Karlstrom 1964, Nelson and Johnson 1981).

Water tables are mostly shallow, approximately 1 to 2 m below the surface, and wetlands and water bodies are common, covering approximately 41% of the land surface (Karlstrom 1964; Gracz 2005, Gracz and Glaser 2016). Peatlands in the study have been found to be important sources of groundwater to headwater streams, especially during dry periods (Gracz et al. 2015). Atmospheric nitrogen deposition in Alaska is low and the primary sources of nitrogen to headwater streams are nitrogen-fixing plants such as *Alnus* spp. (Shaftel et al. 2012). Headwater streams in the study area flow through mixed forests of lutz spruce (*Picea lutzii*), paper birch (*Betula papyrifera*), and stands of willow (*Salix* spp.) and Alder (*Alnus* spp.) (Walker et al. 2012). Three types of Alder have been previously described on the Kenai Peninsula: Green Alder (*Alnus viridis* ssp. *fruticosa*), Sitka Alder (*Alnus viridis* ssp. *sinuata*), and Thin-leaf Alder (*Alnus incana* ssp. *tenuifolia*) (Viereck and Little 2007). These species co-

occur in the study area and are only at the subspecies level, thus we have grouped them for the purposes of this study as Alder (*Alnus* spp.).

Riparian wetland vegetation associated with headwater streams in the study area is dominated by *Calamagrostis* (Shaftel et al. 2011; Whigham et al. 2012, Gracz and Glaser 2016). Riparian wetland vegetation, particularly *Calamagrostis*, provides important allochthonous organic matter inputs (Shaftel et al. 2011) and food web contributions for juvenile salmonid production in headwater streams in this region (Dekar et al. 2012). Streams in the Kenai Lowlands support anadromous salmonid species such as Chinook (*Onchorynchus tshawytscha*), coho (*O. kisutch*), and pink (*O. gorbuscha*) salmon as well as Dolly Varden char (*Salvelinus malma*) and steelhead trout (*O. mykiss*) (Walker et al. 2012). These species are important to local and regional economies through recreational and commercial fishing. Our recent studies have found juvenile salmonids in the Kenai Lowlands headwater streams throughout the year, indicating their importance as rearing habitats (King et al. 2012). Walker et al (2007) estimated that the headwater streams in this area support at least ¼ million juvenile salmonids.

We selected riparian wetlands associated with two streams that were as similar as possible with respect to sinuosity, wetland cover, and geomorphic setting, one with 12.6% Alder cover on the watershed (Alder) and one with no Alder cover (No Alder) (Figure 1). More comprehensive descriptions of the study sites, and region can be found in Shaftel et al. (2011, 2012), King et al. (2012), Walker et al. (2012) Whigham et al. (2012), and Callahan et al. (2017). Characteristics of both streams and their associated watersheds are shown in Appendix 1.

3. Methods

3.1 Stream water levels

At both sites, water levels were continuously measured hourly using Model 3001 Levellogger Gold pressure transducers and dataloggers (Solinst, Inc., Georgetown, Ontario). Each sensor was secured to the streambed using stainless steel wire attached to rebar pounded approximately 1m into the streambed. Figure 2 shows water level fluctuations and precipitation from June to October 2012, a pattern that was similar during all three years of the study (S. Baird, unpublished data). The mean level of the top of the creek bank was determined at both sites relative to the water levels using LIDAR to determine water level during base flow and top of creek bank.

3.2 Riparian vegetation

3.2.1 Species composition

In June 2012, we established three sets of paired plots at each site and each pair was separated by at least 100 meters distance along the stream. Each plot was 2 X 4 m with the longest dimension placed as close as possible to the creek bank. Each plot was divided into 8 subplots, each 1 X 1 m. The downstream plot of each pair received 20 gN/m² (Coastal Blend; Skagit Farmers Supply: 27% NH₄NO₃-N = 27%, P₂O₅ and K₂O = 0%, Ca = 4% and Mg = 1%) in June 2012, 2013, and 2014.

Vegetation was surveyed at the beginning of the study by estimating the cover (%) of each species in each plot. We used the cover and frequency data to calculate importance values (sum of relative cover and relative frequency) for each species. The mean importance values (IV) of plants in the plots at both stream sites is shown in Appendix 1. As described in Whigham et al. (2012), *Calamagrostis canadensis* was clearly the dominant plant species, with a mean IV that was orders of magnitude higher than almost all other species. The only other species that had mean IVs greater than 10 was *Chamerion angustifolium* at the No Alder and *Equisetum fluviatile* at the Alder site (Appendix 1).

3.2.2 Aboveground biomass

We harvested three randomly located 50 X 50 cm subplots in each plot on September 2, 2014. The harvested subplots were located in the center of three randomly chosen 1 X 1 m subplots in each of the larger 2 X 4 m plots. In the laboratory, biomass was separated into *Calamagrostis canadensis* and all other herbaceous species. Wet weights were measured and subsamples were used to determine the moisture content of the samples. Following drying at 60°C for a minimum of 36 hours, moisture content was determined, and the moisture data were used to determine dry weight equivalents of the harvested biomass. The dried subsamples were ground into a powder in a coffee grinder and returned to the Smithsonian for further processing, additional grinding if necessary, and analysis of N using a CE-440 Elemental Analyzer. Percent N data were used to calculate total N standing stocks of *Calamagrostis canadensis* and other herbaceous species.

On September 2, we also sampled the aboveground biomass of plants that were growing at the streamside edge of each control plot and subsequently would have become litter that would overhang the creek bank at the end of the growing season. We sampled three randomly chosen 50 X 50 cm plots within each of the larger 2 X 4 m plots, such that one side of each 50 X 50 cm plot was formed by the creek bank. Aboveground biomass was harvested and processed as described in the previous paragraph.

3.2.3 Litter biomass

In June-July (2014) we measured litter biomass that overhung the creek bank at the control plots by harvesting three 50 cm long segments from each 4 m long plot. In the laboratory, the litter was separated into one year old litter (litter from the 2013 growing season) and litter that was older than one year. It was possible to distinguish one year old litter based on color. Litter samples were dried at

60 C for a minimum of 36 hours, weighed, and ground for nitrogen determination using procedures as described for aboveground biomass.

3.2.4 Litter decomposition

We employed the standard Tea Bag Index technique (Keuskamp et al. 2013) to assess decomposition rates. The technique involved placing two types of tetrahedron-shaped synthetic tea bags into the soil. One of the bags contains green tea (89 %) that has a faster decomposition rate and the other contained roiboos (red) tea (93 %) that has a slower decomposition rate. By using the two types of tea it is possible to concurrently assess litter decomposition rate and long-term carbon stabilization (Keuskamp et al. 2013). In September, 2013 we placed five roiboos tea bags and five green tea bags in each plot. They were placed into the soil by removing a 10 cm deep plug of soil with a sharp knife, placing the tea bags into the holes and replacing the soil plug. The tea bags were retrieved after a year (August 2014). They were returned to the laboratory and gently washed to remove sediment on the outside of the bags. We also removed fine roots that had adhered to the outside of the bags or had grown into them. The bags were dried at 60°C and dry weights of the contents were determined. The tea bags were commercially available (Lipton) and each bag contained about two grams (dry weight) of tea. Initial tea weight was determined by measuring the weight of tea in 10 bags of each type at the beginning of the experiment. The amount of tea in the green and red tea bags at the beginning of the study was 1.72 ± 0.05 g (1 standard deviation) and 1.60 ± 0.04 , respectively.

3.2.5 Root biomass and Interstitial Water Chemistry

During the growing season of 2014 (late June to mid-July) we sampled the substrates beneath each of the plots for determination of root biomass and the chemistry of interstitial water ($\text{NO}_3 + \text{NO}_2$, NH_4 , PO_4 , CDOM). We used a 50 cm long by 10 cm wide fabricated aluminum coring device to collect samples. Cores were collected by standing in the stream and measuring the distance between the top of the creek bank and the water level in the stream. The vertical distance was divided into three equal components and a core was taken in the middle of each segment. We pushed the corer horizontally into the substrate and divided the extracted cores into 10 cm segments. We repeated the coring at three locations within each plot resulting in 9 cores per plot.

One of the 10 cm segments from each core was returned to the laboratory where they were stored in a refrigerator until they were processed for root biomass by washing the core through a series of stacked sieves to remove sediment. Roots, identified by their white color, were hand-picked from the screens, dried at 60°C and weighed. Because of the small amount of biomass in individual cores, the three cores at each depth from each area sampled were combined for N analysis using the same procedures described above for aboveground biomass and litter.

A second 10 cm segment of each larger core was placed into a plastic sandwich bags in the field and returned to the laboratory where interstitial water was extracted by inserting ceramic soil sippers (Rhizon soil moisture samplers: Model 12.01.SA, Eijkelkamp, Giesbeek, The Netherlands) into each core through the plastic bag. Rhizons were connected to 50 ml syringes and suction was placed onto each by pulling the plunger and fixing it into position with a stopper. Interstitial water samples were collected for analysis of $\text{NO}_3 + \text{NO}_2$, NH_4 , and PO_4 , CDOM. Samples were filtered in the field using a 0.45 μm filter and syringe (Monoject Syringe with Luer Lock, Tyco Healthcare Group LP, Mansfield, MA, USA + 0.45 μm Whatman Syringe Filters, GE Healthcare, Pittsburgh, PA, USA). Immediately after collection, water samples were held in a refrigerator until they were shipped to Baylor University (nitrogen and phosphorus) or Smithsonian Environmental Research Center (CDOM) for analysis. $\text{NO}_2 + \text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$,

and $\text{PO}_4\text{-P}$ were analyzed according to Quikchem methods (Dissolved P method 10 – 115 – 01 – 1 – F, $\text{NH}_4\text{-N}$ method 10 – 107 – 106 – 1 – J, Dissolved N method 10 – 107 – 04 – 1 – J) using a flow-injection auto-analyzer (Lachat QuikChem 8500 series 2 FIA and Series 520 XYZ Autosampler, Hach, Loveland, Colorado, USA).

The optically active, or chromophoric, component of dissolved organic matter (CDOM) in interstitial filtrates was measured as an indicator of overall dissolved organic matter content using UV-visible spectrophotometry. Absorption spectra were measured using a CARY-IV dual beam spectrophotometer. Due to the high optical thickness of the samples, absorbance measurements were performed using 1-cm path length, acid-cleaned and DI-rinsed water, quartz cuvettes. Measurements were baseline corrected using deionized (DI)-water. Instrument drift was monitored by measuring a DI-water blank before each sample. Measurements covered the spectral range from 270 to 750 nm (1-nm bandwidth and interval). CDOM absorption coefficients were estimated from measured optical densities (OD) after multiplying by 2.303 and dividing by the path length (0.01 m for a 1-cm cuvette). We also estimated the spectral slopes in the intervals 275-295 nm ($S_{275-295}$) and 350-400 nm ($S_{350-400}$) and estimated the slope ratio S_R as the ratio of $S_{275-295}$ to $S_{350-400}$ following Helms et al. (2008). $S_{275-295}$ and $S_{350-400}$ were calculated using linear regression of the log-transformed absorption spectra.

3.2.6 In-stream *Calamagrostis* pot experiment

In September 2012, we collected plugs of *Calamagrostis* from a streamside wetland at the No Alder site. The plugs were planted into 20 cm diameter plastic pots that first had a layer of gravel placed on the bottom for drainage. Commercial peat was used to complete the planting of each *Calamagrostis* plug in each pot. Two pots were placed into the stream at the downstream end of each 2 X 4 m plot. The pots were located as close as possible to the creek bank. To support the pots, they were placed into frames made of ½" PVC. Foam was sprayed into the PVC frames during fabrication to make them

buoyant. When placed into the streams, the frames were tied to wooden stakes and rebar so that they could float up and down with changes in water depth. The pots were removed at the end of the 2012 and 2013 growing seasons. Biomass was clipped and the pots were stored for the winter. They were placed back into the streams in early June of 2013 and 2014. In September of 2014, the pots were harvested for the last time and we determined the N content of the *Calamagrostis* aboveground biomass using procedures described above for other biomass samples. We did not determine dry weights of the biomass in the pots because of the high degree of variability that resulted from damage and lodging of the biomass during flooding events (i.e., shoots were lodged and partially covered with sediment).

4. Data analysis

Our primary interests were to compare the characteristics of the streamside wetlands that were located in watersheds with and without Alder to test the assumption that wetlands which have similar vegetation would have different structural and functional characteristics based on nutrient inputs from the upstream watershed. As described earlier, headwater stream at the Alder site had a mean oxidized N concentration of 284-618 $\mu\text{g L}^{-1}$ and the watershed had 12.6% alder cover. In comparison, the No Alder watershed had a stream oxidized N concentration that ranged from 10-14 $\mu\text{g L}^{-1}$ (Shaftel et al. 2012).

With the exception of one comparison, described below, analyses were performed on data collected from the control plots. We first tested the data for normality of the residuals using the UNIVARIATE procedure in SAS. Data that were normally distributed and deemed significant by one-way ANOVA were compared using the post-doc Tukey test in the GLM procedure in SAS. Heteroscedasticity was tested using the HOVTESYT in the GLM procedure. For variables that were not normally distributed

we used the Kruskal-Wallis test in the NPAR1WAY procedure in SAS. All percentage data were arcsine and square root transformed prior to determining if they were normally distributed and subsequently analyzed using GLM or NPAR1WAY procedures. Means were considered to be significantly different at $P < 0.05$.

We used the biomass data from control and fertilized plots to test the hypothesis that streamside wetlands at the Alder site, which had 12.6% Alder cover on the watershed, would have a lower response to the addition of N fertilizer compared to the site which had no Alder on the watershed (Figure 1 and Shaftel et al. 2012). This technique for comparing the responses of vegetation to nitrogen additions at sites with different N inputs is also described in Callahan et al. (2017). We tested this hypothesis by calculating and comparing the ratio of biomass of *Calamagrostis* in fertilized plots to biomass in control plots. We only used *Calamagrostis* biomass data for this comparison because other herbs were present in only 14 of the 36 plots that were sampled, and most of the plots that had other herbs (10 of 14) occurred in the Alder plots. For each plot, we first calculated the mean biomass of *Calamagrosits* in the three subplots in the control and fertilized plots and then used the mean values to calculate the ratio for each pair of plots.

Decomposition data were analyzed in R version 3.2.2 (R Core Team 2015). The decomposition rate (k) and stabilization factor (S), a proxy for how much of the material being decomposed is expected to be retained, were calculated according to Keuskamp et al. (2013). The resulting k and S values were fitted to mixed linear models with treatment and site as fixed factors and the experimental plots as random factors, using the nlme 3.1-121 (Pinheiro et al. 2016). Residuals were tested for heteroscedacity and normality using the Bartlett's and Shapiro-Wilk's tests, respectively. Significance of effects was tested with type II sum of squares ANOVA procedure of car 2.1-0 (Fox and Weisberg 2011) and the glht procedure of multcomp 1.4-6 (Hothorn et al. 2008).

5. Results

5.1 Stream water levels

Water levels in the stream at both sites was well below the wetland surface during most of the growing season, except for one flooding event during the time period shown in Figure 2. Similar patterns occurred each year of the study (data not shown).

Aboveground biomass - The mean biomass of *Calamagrostis*, at the scale of the 2 X 4 m plots and at the scale of the streamside plants that would become litter input to the stream, was higher at the Alder watershed site but the differences were not significant (Table 1). The biomass of other herbaceous species did not follow the same pattern as *Calamagrostis*. At the plot scale, the biomass of other herbaceous plants at the No Alder site averaged 139.9 g m² compared to 86.2 g m² the Alder watershed plots but the means were not significantly different. Streamside biomass of other herbaceous species was also higher at the No Alder sites (Table 1).

The mean N content and Total N of *Calamagrostis* also followed the expected pattern being higher at the Alder watershed compared to the No Alder site but the differences were not significant (Table 2). The mean N content of other herbaceous was also higher at the Alder watershed site but Total N of other herbaceous species differed for samples at the whole plot scale compared to plants that were growing at the edge of the plot closest to the stream (Table 2). At the plot scale, Total N was highest at the No Alder site because the biomass was higher compared to the Alder site (Table 2). Biomass of other species at the streamside scale showed the same pattern as *Calamagrostis* (i.e., higher at the Alder sites).

5.2 Response of *Calamagrostis* to fertilization

The response of *Calamagrostis* to fertilization was significantly higher at the No Alder site (Table 1). The relative increase in biomass at the No Alder site was almost double the response at the Alder

site (Figure 3). The in-stream pot experiment also resulted in significantly higher N content of *Calamagrostis* growing in pots that were placed in the streams at the Alder site compared to No Alder site (Table 2).

5.3 Decomposition

The initial decomposition rate (k) did not differ significantly between the No Alder and Alder sites (Table 1) but the litter stabilization factor (S) was significantly lower (28%) at the No Alder site (Table 1). The decomposition rate k did not differ between control and fertilized plots at the Alder and No Alder sites (data not shown). Testing the effect of fertilization at the two study sites showed that the difference in S was significantly higher in fertilized plots at the No Alder site while there was no response of S to fertilization at the Alder site (Figure 4).

5.4 Litter

Differences in *Calamagrostis* aboveground biomass followed the expected pattern of greater biomass with higher N levels (Table 1), however, the pattern for litter was different. The nitrogen content of the litter that was overhanging the streams (1 year and older litter combined) was significantly higher (Table 2) at the Alder site compared to the No Alder site but the biomass and Total N in the litter showed the opposite pattern. Litter at the No Alder site averaged 38.3 g per 50 cm of creek bank which was almost double the amount of litter biomass measured at the Alder site (Table 1). Total N in the litter samples showed the same pattern with significantly more N at the No Alder site (Tables 1 and 2).

5.5 Roots

The pattern for biomass of roots and the Total N in the roots was the opposite of the pattern for

aboveground biomass for *Calamagrostis* but the concentration difference of N in the roots showed a pattern similar to the aboveground biomass and litter samples. The N content of roots was significantly higher at the Alder site (Table 2) but the mean root biomass was almost five times greater at the No Alder site and the difference between the two streams was significant (Table 1).

5.6 Interstitial water chemistry

The concentration of $\text{PO}_4\text{-P}$ in interstitial water was not significantly different between the two sites but the differences in inorganic nitrogen were significant and very large (Table 1). The mean concentration of $\text{NH}_4\text{-N}$ was more than 10 times higher at the Alder watershed site ($91.1 \mu\text{g L}^{-1}$ compared to $8.0 \mu\text{g L}^{-1}$). The mean differences in oxidized N were also significant and even larger (i.e., $605.9 \mu\text{g L}^{-1}$ versus $7.5 \mu\text{g L}^{-1}$). There were 5 measurements out of 36 total of oxidized N at the Alder watershed site that were $> 1000 \mu\text{g L}^{-1}$. Removing those 5 samples still resulted in a mean difference that was more than 10 times higher at the Alder watershed site (91.1 compared to $8.04 \mu\text{g L}^{-1}$).

The quantity of chromophoric dissolved organic matter (CDOM) in the interstitial water was high in both watersheds with absorbance at 300 nm around $80 a_{300} \text{ m}^{-1}$ (Table 1). Similar absorbances have been reported in riparian soil water of other sites in Alaska (Cory et al. 2015). There was considerable variability in the magnitude of absorbance within each watershed, which suggests a patchy distribution of the source material (soil organic matter) within the substrate in the sampled wetland areas. For comparison of watersheds, we therefore focused on the slope ratio (S_R) which is an indicator of the absorbance spectral shape (see Methods). The S_R in both watersheds was < 1 on average (Table 1), similar to measurements of soil associated CDOM in other Alaska (Cory et al. 2015) or alpine (e.g. Fasching et al. 2016) watersheds. However, the mean S_R of the No Alder watershed CDOM was higher (0.92 versus 0.79) but not significantly different (Table 1). The data indicate a trend in which organic matter in the higher N, Alder watershed had higher molecular weight and with greater aromatic

constituents (cf. Helms et al. 2007). In addition, the average S_R in the interstitial water of the No Alder watershed decreased upon N fertilization, from 0.92 ± 0.05 to 0.78 ± 0.03 , which is consistent with the association of N availability and S_R though the difference was not statistically significant (Table 1).

6. Discussion

There have been numerous studies in which watershed characteristics have been related to the structure and function of streams (e.g., Strayer et al. 2003, Allen 2004, King et al. 2005). Clearly watershed characteristics influence stream processes and the spatial arrangements of different cover types on source watersheds is important, as is the total area covered by different land uses. For example, in our study area, the amount of Alder on the watershed was related to the nitrogen dynamics in headwater streams (Shaftel et al. 2012, Hiatt et al. in press). Our study provided evidence that watershed characteristics (presence of absence of nitrogen-fixing Alder) also influences both the structure and function of wetlands that are associated with headwater streams.

Structurally the vegetation was similar at sites with and without Alder (Appendix 1).

Calamagrostis canadensis was the dominant species, similar to what was found earlier studies of vegetation associated with streamside wetlands over a larger area of the Kenai Peninsula (Whigham et al. 2012, Gracz and Glaser 2016). However, the amount of living biomass (above and belowground), differed between the two watersheds and there were also differences in the amount of litter hanging over the creek bank, the nitrogen concentrations in biomass and litter, the decomposition of standard plant material placed into soils at the sites, and the chemistry of interstitial water. We compare and contrast the two systems in Figure 5.

The mean aboveground biomass of *Calamagrostis* in the control plots and the biomass of plants within 50 cm of the creek bank in the control plots were higher at the Alder site (Figure 5A). In contrast, root biomass in 10 cm cores and the biomass of litter overhanging the creek bank at the control plots

showed the opposite pattern with higher means at the No Alder site. The mean values for the litter and root biomass were significantly higher at the No Alder site but the means for the two aboveground biomass variables were not significantly different at the $P < 0.05$ level (Table 1). The results, thus, indicate that at the Alder sites there is a trend toward increased aboveground biomass but lower root biomass. The trend toward higher, but non-significant, aboveground biomass at the Alder site can be explained as follows. First, the number of times that additional nitrogen would be delivered to the surface of the wetland from the watershed is limited to a few flooding events of short duration each year (Figure 2). Over decades, however, even infrequent flooding of the wetland surface would result in additional nitrogen, which could account for higher mean aboveground biomass at the Alder compared to the No Alder site. The response of *Calamagrostis* and the results of the litter bag experiment in response to the addition of nitrogen (Figures 3 and 4) provides further evidence that the Alder sites have higher nitrogen availability compared to the No Alder sites. These results are similar to results of an experiment when we compared biomass production of *Calamagrostis* in streamside wetlands that were at the downslope end of drainage paths with and without alder (Callahan et al. 2017). A second factor could account for variation of aboveground biomass within plots, subsequently resulting in non-significant differences between the Alder and No Alder sites. The wetland surface at both sites was very heterogeneous because *Calamagrostis* forms tussocks that result in a hummock-hollow microtopography. In our study plots, the tops of *Calamagrostis* hummocks were often 20-30 cm above the hollows (D. Whigham, personal observation). Vertical variation would result in differences in water and nutrient availability to plants that could account for spatial differences in biomass production. A third factor to consider is the number of samples that were collected. Limiting the number of samples to three per plot may be, in part, responsible for a higher level of variation, resulting in means that were not significantly different.

There were not any between-site significant differences in the nitrogen content of

Calamagrostis or other species even though there was a consistent pattern of higher values at the Alder site (Figure 5B). These results were not unexpected because we harvested the biomass near the end of the growing season which is a time when nutrient concentrations are lower in aboveground biomass because of translocation to belowground storage (e.g., Bernard and Solsky 1977). As a result of non-significant differences in nitrogen concentrations and aboveground biomass, there was not a significant difference in nitrogen standing stocks (Table 1), but the patterns were consistent: higher at the Alder watershed site.

There were significant differences between the two sites in the amount of litter overhanging the creek bank, the nitrogen concentration of the litter, and the belowground biomass of roots. Litter and root biomass were significantly lower at the Alder site but the %N of the litter and roots was significantly higher. Lower litter biomass with a higher N content indicates that the litter that overhangs the creek bank at the Alder site decomposes faster and a higher percentage of the annual litter production enters the stream foodwebs. This result also supports the findings of Shaftel et al. (2011) who found that *Calamagrostis* litter that is enriched in N decomposes faster in headwater streams. In addition, we had previously demonstrated that allochthonous sources were an important source of nitrogen to the streams in our study area (DeKar et al. 2012). This study thus demonstrates yet another link that functions at the landscape scale and suggests that streamside wetlands in watershed with Alder can play an important role in the nitrogen dynamics of the streams. Nitrogen inputs from watersheds with Alder are incorporated into vegetation in streamside wetlands and passed into the streams at a higher rate than watersheds with no Alder.

Another influence of the wetlands on adjacent streams is the release of dissolved organic matter (CDOM) from wetland soils into interstitial water that can move into the hyporheic zone and eventually into the stream. The quality of the optically active, or chromophoric, component (CDOM) was influenced by the nitrogen availability in the watershed. At higher N availability, the CDOM had higher

molecular weight and aromaticity as indicated by the lower slope ratio (SR) of the absorbance spectrum. The same trend in slope ratio was observed for No Alder vs Alder plots as well as for the Control vs N fertilized plots in the No Alder watershed. The specific chemical differences in CDOM composition are not known, but may relate to the higher stabilization ratio and inferred greater organic matter availability in substrates at the Alder sites. In any case, the results show that N availability is altering the composition of dissolved organic matter that is eventually entering stream ecosystems, an aspect that deserves further study. The decomposition study also demonstrated the importance of nutrient availability on the watershed. The higher stabilization factor (S) of litter in the Alder plots was most likely to due to higher N availability. As a result, more of the organic matter that is produced by vegetation on the watershed would be retained on sites with Alder. The effects of higher N on the decomposition of recalcitrant compounds is supported by previous studies (Berg 2000, Hobbie et al. 2012) but the consequences of increase nutrient availability may not always be the same. Hobbie et al. (2005) found, for example, that the consequences of N addition in an arctic environment had the opposite results in acidic versus non-acidic habitats, even though the study sites shared the same regional pool of plant species.

Our finding that root biomass at the No Alder sites was more than 8 times the mean at the Alder sites (Figure 5A) was consistent with studies of nitrogen allocation to roots in plants with and without nitrogen additions (Dzeletovic and Glamoclija 2015, Meyer-Gruenefeldt et al. 2015, Wurzburger and Wright 2015), especially in wetland where the high moisture levels in combination with nutrient additions result in lower belowground biomass production (Edwards 2015). Lower root biomass would impact soil nutrient pools and the movement of nutrients in interstitial water. We did not measure total N pools in the soil as both sites had highly organic soils and we decided that it would be more informative to sample interstitial water. Highly significant differences in oxidized nitrogen and ammonium in interstitial water in the Alder plots (Table 1) were another indicator of the long-term

effects of higher levels of nitrogen in stream water from the watershed with alder. Lower root biomass at the Alder site indicates that the vegetation incorporates nitrogen from less of the soil profile and more of the nitrogen that is mineralized in the soil can move through the soil with interstitial water and eventually reach the stream. The consequences of increased levels of nitrogen in stream water were demonstrated in the experiment where *Calamagrostis* grown in pots that were placed in the stream had higher nitrogen concentrations in the aboveground biomass (Table 2).

Collectively the results from this study demonstrate that the characteristics of vegetation on the watershed influence the structure and function of streamside wetlands and that the consequences of the presence or absence of Alder on watersheds play an especially important role in upland-wetland-stream interactions. It further supports our conclusion from a separate study (Callahan et al. 2017) that the transport of nitrogen from stands of Alder via lateral flow paths represents potential nutrient hotspots in headwater streams. There may be additional consequences of the differences in the structure of the streamside vegetation that go beyond nutrient and carbon linkages. We observed, for example, that there was more slumping of the creek banks at the Alder sites which may be a consequence of lower root biomass in the sediments. Slumping of the creek bank would result in dynamic changes along the stream that would increase habitat heterogeneity as well as increase sediment loading to the stream.

The results of this research may also have implications for future conditions in boreal and arctic habitats where *Alnus* is projected to become a more important component of the vegetation in response to increasing temperatures (Mibau et al. 2009) and increased levels of carbon dioxide (Tobita et al. 2016). Increased *Alnus* will result in increased N availability in lakes and streams and higher rates of litter turnover in streams (Boyero et al. 2016, Poreen et al. 2017). Higher rates of litter turnover and lower belowground biomass production in response to increased N availability potentially will also result in lower rates of substrate carbon storage (Mack et al. 2004) and potentially increase rates of carbon

dioxide and methane emissions to the atmosphere. Increased temperatures and increased nutrient availability may, (Sistla et al. 2013) or may not (Jing et al. 2016) result in changes in soil carbon storage suggesting that the expansion of Alder at higher latitude may have both positive and negative consequences. Results of this study demonstrate that it is important to conduct additional research to further elaborate the consequences of linkages between watersheds, streamside wetlands and the ecology of headwater streams that are critically important to populations of juvenile salmonids.

7. Conclusions

We found that wetlands associated with headwater streams on the Kenai Peninsula differ in structure and function depending on whether or not the upstream watershed has or does not have Alder (*Alnus* spp) cover. Alder, a nitrogen-fixing plant, is a source of nitrogen and some of the nitrogen eventually reaches headwater streams (Shaftel et al. 2012) and wetlands that are adjacent to the streams (Callahan et al. 2017). We found that wetland that received N from the watershed had higher aboveground biomass, lower root biomass, and lower amounts of litter that overhangs the creek bank. Interstitial water also differed with significantly higher inorganic nitrogen and a component of dissolved organic matter at the sites that received N from the watershed. These results provide further evidence that there are strong linkages between watersheds, streamside wetlands and headwater streams. These linkages are particularly important in landscapes similar those in our study areas where the headwater streams are overwintering and rearing habitats for millions of juvenile salmonids. The results also have broader implications for boreal and arctic habitats as *Alnus* is projected to migrate northward in response to warming climatic conditions as well as increased levels of carbon dioxide in the atmosphere. The additional fixed nitrogen in those ecosystems will result in ecosystem changes that will influence patterns of ecosystem production and aquatic food webs. The additional N subsidies that result from the northward expansion of *Alnus* are likely to have a positive impact on secondary

production in streams and lakes but potentially negative impacts on soil carbon storage due to increased decomposition rates and lower net belowground biomass production of N enriched vegetation.

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Table 1. Aboveground biomass, root biomass, the ratio of *Calamagrostis* biomass in control and fertilized plots, nutrient and absorbance characteristics of interstitial water from cores, and decomposition data for the No Alder and Alder sites. Interstitial nutrient and decomposition data from control plots and comparison of biomass in fertilized versus control plots at plots along the No Alder and Alder sites. All values are means \pm 1 standard error. Means that are significantly different at $P < 0.05$ are shown in bold. Results of the statistical tests are shown the two right columns. Data that were normally distributed were analyzed GLM in SAS and data that were not normally distributed were analyzed using the NPAR1WAY procedure in SAS.

Variable	Alder	No Alder	Statistical analysis	SAS test
<i>Calamagrostis</i> - biomass in plots (g m ²)	486.2 \pm 104.5	365.8 \pm 82.9	F = 0.82; DF = 1; P > 0.3799	PROC GLM
Other plant biomass in plots (g m ²)	86.2 \pm 22.7	139.9 \pm 67.5	Chi-square = 0.2503; DF = 1; P < 0.6168	PROC NPAR1WAY
<i>Calamagrostis</i> - streamside biomass (g m ²)	365.3 \pm 107.9	200.7 \pm 31.4	Chi-square = 0.4386; DF = 1; P < 0.5078	PROC NPAR1WAY
Other plant biomass in streamside biomass (g m ²)	37.2 \pm 20.8	53.2 \pm 13.0	Chi-square = 01.5559; DF = 1; P < 0.2123	PROC NPAR1WAY
Ratio of <i>Calamagrostis</i> biomass biomass in fertilized versus control plots	2.66 \pm 0.37	1.40 \pm 0.20	F = 9.90; DF = 1; P > 0.0056	PROC GLM
Streamside litter (g per 50 cm creekbank)	19.51 \pm 4.64	38.30 \pm 5.09	F = 7.19; DF = 1; P > 0.0120	PROC GLM
Root biomass (g per 10 cm core)	2.14 \pm 0.29	10.61 \pm 1.41	Chi-square = 28.8545; DF = 1; P < .0001	PROC NPAR1WAY
Interstitial NH ₄ (μg L ⁻¹)	91.1 \pm 13.8	8.0 \pm 1.3	Chi-square = 26.5886; DF = 1; P < .0001	PROC NPAR1WAY
Interstitial NO ₃ + NO ₂ (μg L ⁻¹)	605.9 \pm 221.6	7.5 \pm 3.7	Chi-square = 29.0906; DF = 1; P < .0001	PROC NPAR1WAY
Interstitial PO ₄ (μg L ⁻¹)	17.1 \pm 2.9	10.8 \pm 1.9	Chi-square = 3.3631; DF = 1; P < .0667	PROC NPAR1WAY
CDOM absorbance (<i>a</i> ₃₀₀ m ⁻¹)	78.2 \pm 14.2	86.7 \pm 12.2	Chi-square = 1.3119; DF = 1; P < .2520	PROC NPAR1WAY
CDOM Slope Ratio (S _R)	0.79 \pm 0.03	0.92 \pm 0.05	Chi-square = 2.9675; DF = 1; P < .0848	PROC NPAR1WAY
Litter decomposition constant (k)	0.0113 <u>+0.0005</u>	0.01011 <u>+0.0018</u>	Chi-square = 2.4301; DF = 1; P = 0.119	R:lme
Litter stabilization factor (S)	0.20 \pm 0.01	0.15 \pm 0.01	Chi-square = 10.039; DF = 1; P < . 0.01	R:lme

Table 2. Nitrogen concentration (%) and Total N in biomass for aboveground biomass, litter and roots in control plots at the No Alder and Alder study sites. All values are means \pm 1 standard error. Means that are significantly different at $P < 0.05$ are shown in bold. Results of the statistical tests are shown the two right columns. Data that were normally distributed were analyzed GLM in SAS and data that were not normally distributed were analyzed using the NPAR1WAY procedure in SAS.

Variable	Alder	No Alder	Statistical analysis	SAS test
N in <i>Calamagrostis</i> biomass in plots (%)	1.47 \pm 0.10	1.30 \pm 0.07	F = 1.92; DF = 1; P > 0.18520	PROC GLM
Total N in <i>Calamagrostis</i> biomass in plots (g m ⁻²)	6.76 \pm 1.35	4.71 \pm 1.17	F = 1.321; DF = 1; P > 0.2676	PROC GLM
N in other plant biomass in plots (%)	1.93 \pm 0.21	1.60 \pm 0.11	Chi-square = 0.5767; DF = 1; P = 0.4476	PROC NPAR1WAY
Total N in other plant biomass in plots (g m ⁻²)	1.64 \pm 0.42	2.14 \pm 1.01	Chi-square = 0.2503; DF = 1; P = 0.6168	PROC NPAR1WAY
N in streamside <i>Calamagrostis</i> biomass (%)	1.27 \pm 0.12	1.18 \pm 0.11	Chi-square = 0.7838; DF = 1; P = 0.3765	PROC NPAR1WAY
Total N in streamside <i>Calamagrostis</i> biomass (g m ⁻²)	4.20 \pm 1.14	2.25 \pm 0.28	Chi-square = 0.3294; DF = 1; P = 0.5660	PROC NPAR1WAY
N in other streamside plant biomass (%)	1.61 \pm 0.15	1.44 \pm 0.07	F = 1.32; df = 1; P > 0.2836	PROC GLM
Total N in other plant streamside biomass (g m ⁻²)	0.61 \pm 0.34	0.77 \pm 0.20	Chi-square = 1.3340; DF = 1; P = 0.2481	PROC NPAR1WAY
N in streamside litter (%)	0.83 \pm 0.03	0.71 \pm 0.03	F = 7.19; DF = 1; P > 0.0120	PROC GLM
Total N in streamside litter (g m ⁻²)	0.15 \pm 0.03	0.28 \pm 0.04	F = 6.25; DF = 1; P > 0.0184	PROC GLM
N in root biomass (%)	1.14 \pm 0.06	0.90 \pm 0.04	Chi-square = 10.2011; DF = 1; P < .0014	PROC NPAR1WAY
Total N in root biomass (g 10 cm core)	0.03 \pm 0.004	0.09 \pm 0.002	Chi-square = 24.2245; DF = 1; P < .0001	PROC NPAR1WAY
N in <i>Calamagrostis</i> in pots (%)	1.65 \pm 0.14	0.89 \pm 0.06	F = 31.46; DF = 1; P > 0.0001	PROC GLM

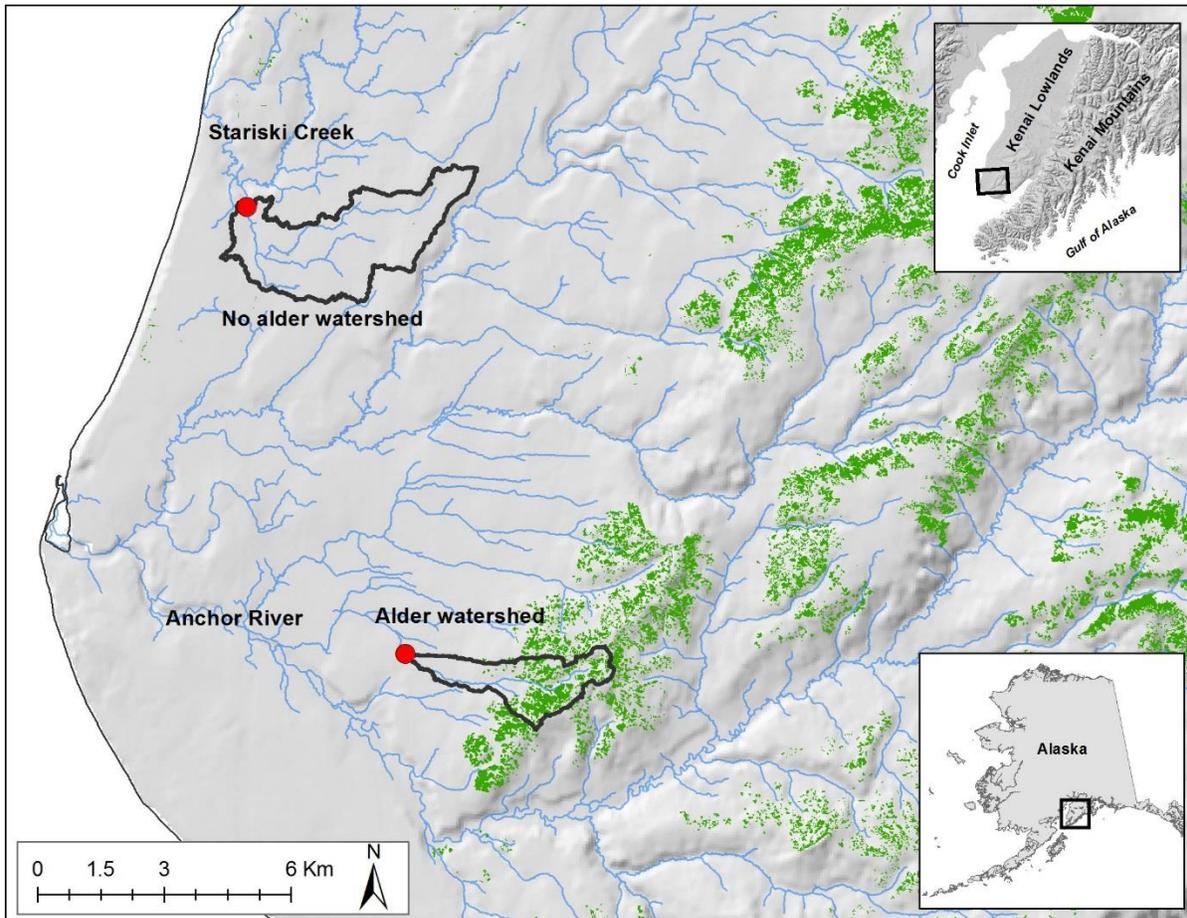


Figure 1. Location of the Alder and No Alder study sites on the Lower Kenai Peninsula of Alaska. The location of the water level recorder and the site of the study described here are represented by the red dots. In addition to the boundaries of each watershed, the distribution of Alder (*Alnus* spp) is shown in green. Information on the watershed, the dominant types of ecosystems on each watershed, and the percent of the watershed that they occupy are given in Appendix 2.

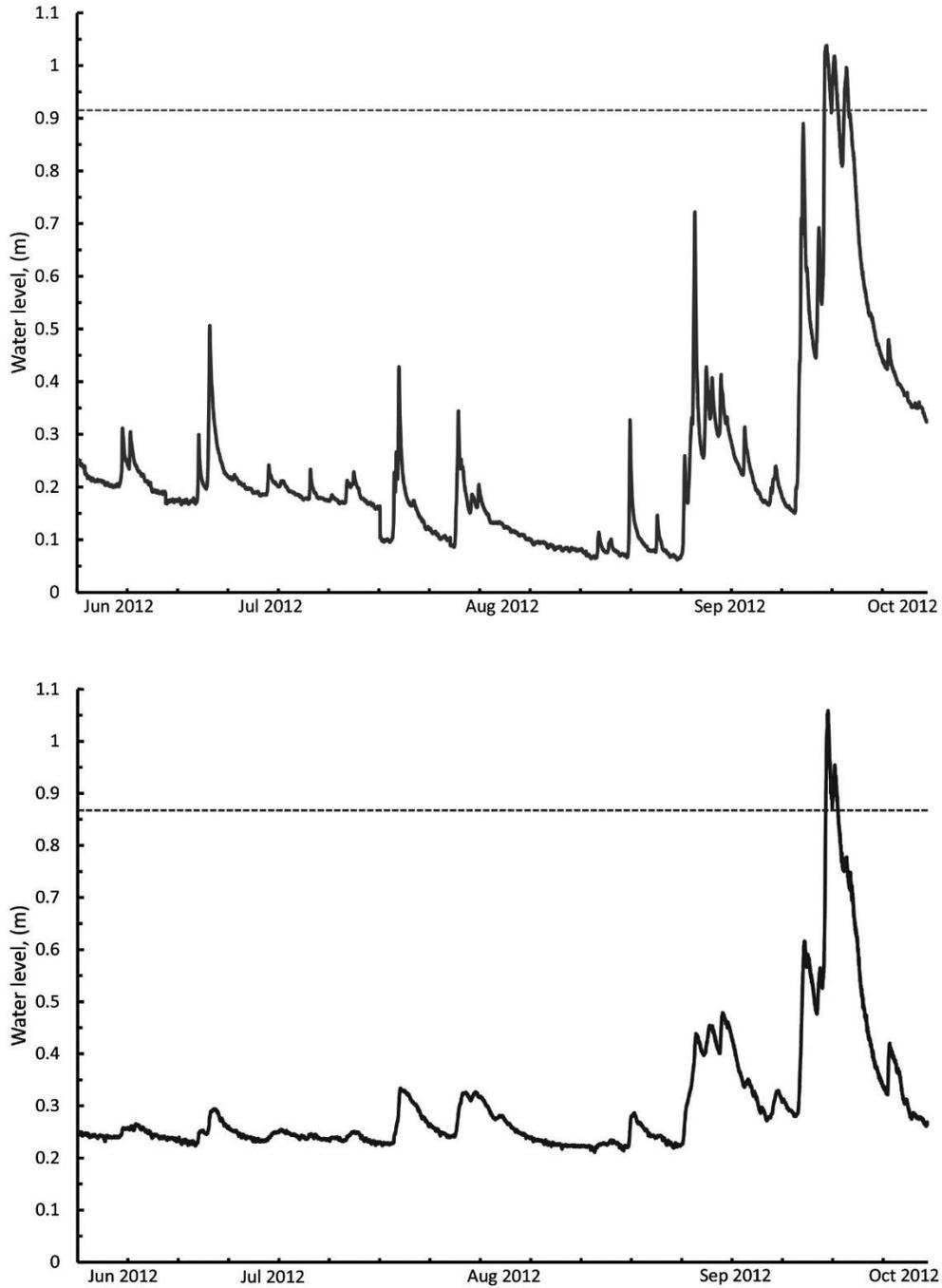


Figure 2. Water levels in the No Alder (bottom) and Alder (upper) streams between June and October 2012. The elevations of the wetland surface relative to water levels in the stream are shown as horizontal lines.

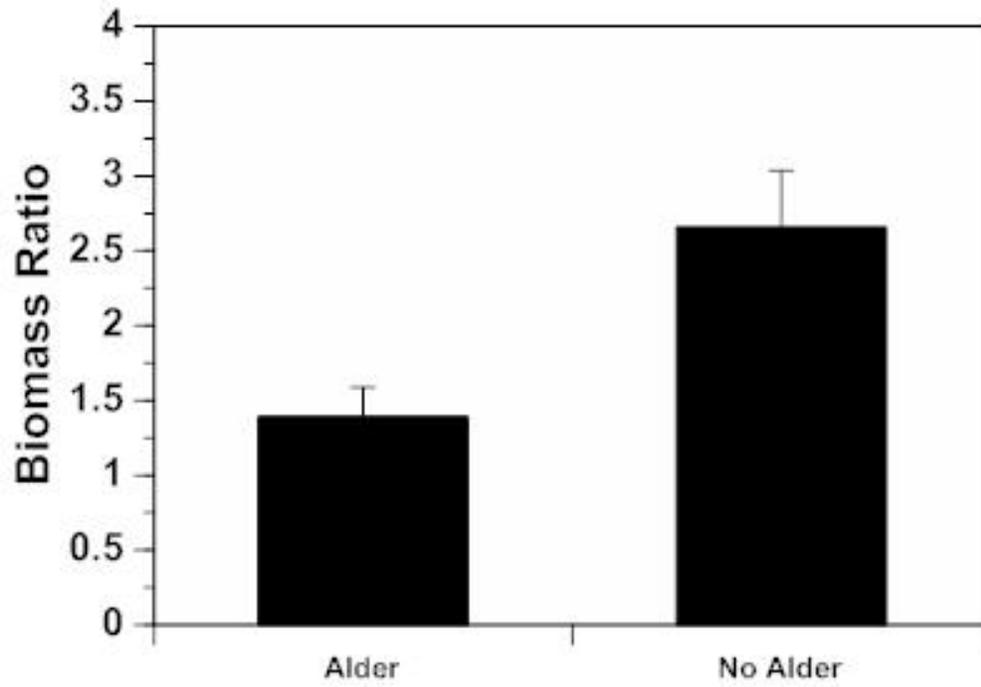


Figure 3. Comparison of the relative increase in biomass (mean \pm 1 standard error) of *Calamagrostis canadensis* between Control and Fertilized plots. The means are significantly different (Table 1).

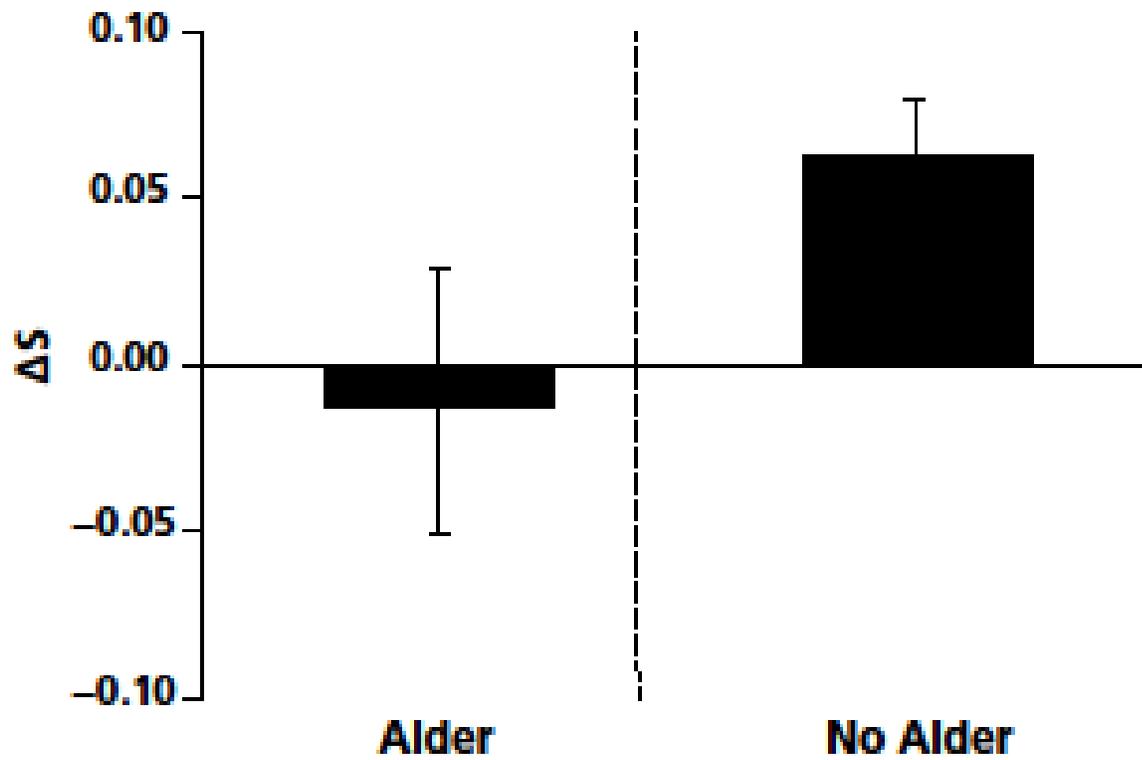


Figure 4. Comparison of the change in litter stabilization (S) between Control and Fertilized plots.

Values are mean \pm 1 standard error. The response was significantly higher at the No Alder site ($p < .001$).

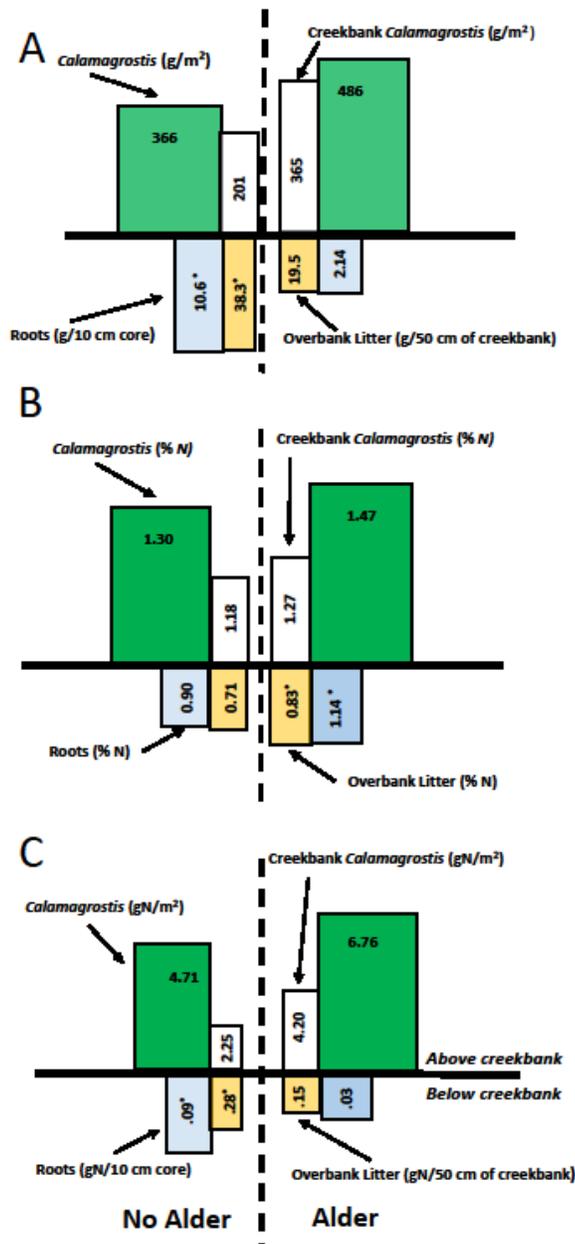


Figure 5. Summary comparisons of the No Alder and Alder sites for biomass (A), %N (B) and Total N (C). The sizes of the boxes are a visual comparison between the No Alder (left of vertical dashed line) and Alder (right of vertical dashed line). Means for each category are provided and means that are different for the No Alder and Alder sites are indicated with an *.

Appendix 1. Importance values of plants in the study plots and water quality data for streams at the Alder and No Alder sites. Water quality data are from Shaftel et al. (2012). Importance values are means (± 1 standard error) for all plots at each stream at the beginning of the project in 2012. Means were based the presence of plants in 96 1 X 1 m plots at each stream (see Methods for explanation of how the plots were set up). Importance values are a combination of relative frequency (how often a species appeared in plots) and relative cover.

	No Alder	Alder Watershed
<i>Angelica genuflexa</i>	9.86 \pm 6.12	
<i>Calamagrostis canadensis</i>	56.46 \pm 14.96	60.38 \pm 15.44
<i>Cardamine praetensis</i>	0.32 \pm 0.29	
<i>Carex sp.</i>	0.92 \pm 0.63	
<i>Chamerion angustifolium</i>	27.12 \pm 11.27	4.17 \pm 2.90
<i>Comarum palustre</i>	4.80 \pm 2.94	
<i>Dryopteris expansa</i>	1.35 \pm 1.25	
<i>Epilobium palustre</i>	1.95 \pm 1.92	
<i>Equisetum arvense</i>		0.68 \pm 0.48
<i>Equisetum fluviatile</i>	1.36 \pm 1.11	25.29 \pm 10.25
<i>Equisetum palustre</i>	6.02 \pm 4.40	7.59 \pm 5.37
<i>Galium trifidum</i>	3.27 \pm 2.54	4.42 \pm 5.95
<i>Galium triflorum</i>	0.73 \pm 0.58	
<i>Galium sp.</i>		8.28 \pm 8.77
<i>Geum marophyllum</i>	0.73 \pm 0.50	0.75 \pm 0.51
<i>Gymnocarpium dryopteris</i>	1.00 \pm 0.00	1.31 \pm 0.92
<i>Heracleum maximum</i>		1.88 \pm 1.24
<i>Juncus sp.</i>	0.54 \pm 0.40	
<i>Luzula sp.</i>	0.47 \pm 0.41	0.53 \pm 0.47
<i>Polygonum acutiflorum</i>	0.55 \pm 0.51	7.86 \pm 4.28
<i>Rumex articus</i>		6.49 \pm 4.93
<i>Taraxacum officinale</i>	0.71 \pm 0.48	
<i>Thalictrum sparsiflorum</i>		9.86 \pm 6.12
<i>Tientalis europaea</i>	3.08 \pm 1.95	2.38 \pm 1.81
<i>Urtica dioica</i>		8.57 \pm 5.64
Stream data (from Shaftel et al. 2012)		
Discharge (m ³ S ⁻¹)	0.017-0.0220	.015-0.023
Flow (m ³ S ⁻¹)	0.05-0.17	0.09-0.17
NO _x -N (µg L ⁻¹)	10-14	268-618
NH ₄ -N (µg L ⁻¹)	4-16	3-19

Total N ($\mu\text{g L}^{-1}$)	204-273	351-617
NO _x -N yield ($\text{g ha}^{-1} \text{ day}^{-1}$)	0.04-0.06	1.13-3.76

Appendix 2. Characteristics of the Alder (Anchor River) and No Alder (Starski) watersheds above the hydrology monitoring station. Data are compiled from Gracz et al. 2008.

Ecosystem	Area (Ha)	% of watershed
Alder – watershed area	393	
Discharge Slope	45	43.5
Kettle	1	.6
Lakebed	17	16.9
Riparian	38	36.7
Wetland/Upland Complex	2	2.3
Watershed	393	
Wetlands in watershed	102	26/1
No Alder - watershed area	844	
Depression	<1	<.1
Discharge Slope	80	9.5
Drainageway	28	3.4
Kettle	14	1.7
Lakebed	496	58.8
Riparian	33	3.9
Wetland/Upland Complex	15	1.8
Wetlands in watershed	666	78.9