NITROGEN SUBSIDIES FROM HILLSLOPE ALDER STANDS TO STREAMSIDE WETLANDS AND HEADWATER STREAMS, KENAI PENINSULA, ALASKA[1]

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ABSTRACT: We examined nitrogen transport and wetland primary production along hydrologic flow paths that link nitrogen-fixing alder (*Alnus* spp.) stands to downslope wetlands and streams in the Kenai Lowlands, Alaska. We expected that nitrate concentrations in surface water and groundwater would be higher on flow paths below alder. We further expected that nitrate concentrations would be higher in surface water and groundwater at the base of short flow paths with alder and that streamside wetlands at the base of alder-near flow paths would be less nitrogen limited than wetlands at the base of long flow paths with alder. Our results showed that groundwater nitrate-N concentrations were significantly higher at alder-near sites than at no-alder sites, but did not differ significantly between alder-far sites and no-alder sites or between alder-far sites and alder-near sites. A survey of ^{15}N stable isotope signatures in soils and foliage in alder-near and no-alder flow paths indicated the alder-derived nitrogen evident in soils below alder is quickly integrated downslope. Additionally, there was a significant difference in the relative increase in plant biomass after nitrogen fertilization, with the greatest increase occurring in the no-alder sites. This study demonstrates that streamside wetlands and streams are connected to the surrounding landscapes through hydrologic flow paths, and flow paths with alder stands are potential "hot spots" for nitrogen subsidies at the hillslope scale.

(KEY TERMS: surface water/groundwater interactions; surface water hydrology; groundwater hydrology; watershed management; *Alnus*; *Calamagrostis*; connectivity; nitrogen; ^{15}N.)

INTRODUCTION

Headwater streams in undisturbed locations commonly rely on energy and nutrient subsidies from the surrounding landscape, including the direct input of allochthonous litter from adjacent streamside vegetation (Fisher and Likens, 1973; Richardson, 1999; Dekar *et al.*, 2012). As stream order increases, there is a shift from terrestrial dependence to more in-stream or autochthonous production (Vannote *et al.*, 1980; Battin *et al.*, 2008). Through the tight

connection between terrestrial habitats and headwater streams, energy is transferred from the upper reaches of watersheds down to the higher order and main stem rivers (Vannote *et al.*, 1980; Wipfli *et al.*, 2007). Therefore, headwater streams, streamside wetlands, and adjacent hillslopes should be considered as important elements in whole watershed management approaches, even when the focus is on downgradient fish-bearing and/or navigable waters (Nadeau and Rains, 2007; Janisch *et al.*, 2011; Choi *et al.*, 2012).

Allochthonous inputs to headwater streams include leaf litter and terrestrial invertebrates (Vannote *et al.*, 1980; Wallace *et al.*, 1997; Kawaguchi and Nakano, 2001; Shaftel *et al.*, 2011). However, surface water and groundwater inflow can also be important sources of additional organic and inorganic subsidies to streams and streamside wetlands (Tipping *et al.*, 1999; Judd and Kling, 2002; Asano *et al.*, 2006; Greathouse *et al.*, 2014). The flow of surface water and groundwater from uplands to streams is a function of hydrologic connectivity, defined as the transfer of matter, energy, or organisms by surface or subsurface water flow (Pringle, 2001), that is the result of climatic, geologic, and topographic controls combining to form hydrologic flow paths that connect hillslopes to streams and streamside wetlands. As nutrients flow along these flow paths, they can be taken up or transformed, with the degree to which they are taken up or transformed controlled by the flux and residence time of nutrients on the flow path and rate of uptake and/or transformation of nutrients by vegetation and microbes located along the flow path (Stieglitz *et al.*, 2003; Jencso *et al.*, 2009; Weller *et al.*, 2011; Liu *et al.*, 2014). Therefore, flow path characteristics can act as fundamental controls on the movement of nutrients from upland sources to streams.

Surface water and groundwater flows may provide important subsidies to headwater streams from surrounding terrestrial landscapes in relatively undisturbed locations. For example, nitrogen fixed by symbiotic actinomycete bacteria (*Frankia* spp.) living in alder (*Alnus* spp.) root nodules have been shown to be a source of nitrogen to the surrounding soil in both Northwest Alaska (Rhoades *et al.*, 2001) and the Pacific Northwest (Bormann *et al.*, 1994; Hart *et al.*, 1997), resulting in increased nitrate concentrations in associated streams (Compton *et al.*, 2003). In the area where our study was done, a positive relationship was demonstrated between nitrate concentrations in headwater streams and the percent cover of alder in the watersheds (Shaftel *et al.*, 2012). In their study, percent cover of alder explained two-thirds of the variation in stream nitrate concentration. The remaining one-third remained unexplained, even after analysis of watershed physiographic characteristics (*e.g.*, slope). Notably absent from their analyses was an analysis of the spatial arrangement of the alder, especially the distance from the alder patches to the streams, that is, the flow path length. In closing, Shaftel *et al.* (2012) hypothesized that the unexplained variation might be related to water residence time and related contact time between nitrate, roots, and microbes, which would be strongly related to flow path length.

Once mineralized, biological-fixed nitrogen can have many fates: for example, uptake by microbes or vegetation, volatilization or denitrification, or transport downgradient by flowing water (Van Breemen *et al.*, 2002). The concentration of nitrogen at any location between an alder stand and a headwater stream is a function of the relative rates of these processes and the amount of alder-fixed nitrogen in groundwater should diminish with distance from an alder stand, implying that alder stands do not contribute nitrogen equally to streams and streamside wetlands. Alder-fixed nitrogen contributions to riparian ecosystems should be, for example, greater from alder stands close to the streams and streamside wetlands. For this study, we focused on alder stands that were connected to headwater streams by flow paths, defined as any surface water or groundwater pathway that water could take from the alder stand or upper hillslope to the downgradient stream and streamside wetlands. We hypothesized that flow paths that connect upslope alder stands to headwater streams and adjacent wetlands represent potential nitrogen hotspots along stream corridors. We tested the hypothesis that nitrogen transport to streams and streamside wetlands was greatest on hillslopes with alder close to the streams and streamside wetlands (alder-near), moderate on hillslopes with alder far from the streams and streamside wetlands (alder-far), and least on hillslopes with no alder at all (no-alder). If this were to be the case, then we expected that both nitrogen concentrations in surface water and groundwater and nitrogen limitation in streamside wetlands would reflect these trends.

To test our hypothesis, we (1) measured nitrate concentrations in shallow groundwater along short and long flow paths with alder at the upslope end compared to flow paths with no alder; (2) measured nitrate concentrations in stream water where shallow groundwater from flow paths with and without alder at the upslope end entered headwater streams; (3) conducted a fertilization study of wetland vegetation at the downslope end of flow paths with and without alder to test the hypothesis that the length of flow paths with alder at the upslope end impacted biomass production and flow paths that included alder at the upslope end were nitrogen hot spots along headwater stream corridors; and (4) analyzed natural abundance

of ^{15}N in shallow soils and plant tissues in flow paths with and without alder.

METHODS

Study Location

The Kenai Lowlands comprise ~9,400 km^2 on the Kenai Peninsula in south-central Alaska, and are bounded by Kachemak Bay to the south, Cook Inlet to the west, and the Kenai Mountains to the east (Figure 1). The Kenai Lowlands are a broad, low shelf predominantly less than 120 m above sea level. The four major drainage basins in the southern Kenai Lowlands are the Ninilchik River, Deep Creek, Stariski Creek, and the Anchor River, the latter being the largest of the four drainage basins. The climate of the Kenai Lowlands transitions from maritime to continental influences from south to north, and is typically characterized by long cool winters from November to May and relatively short warm summers from June to August. Mean annual precipitation is 612 mm (Homer Airport, AK US, GHCND:USW00025507, 1933-2011) and the majority of precipitation occurs during the fall (September-October).

The geology of the Kenai Lowlands consists primarily of complex glacial deposits or glacial till overlying weakly lithified Tertiary bedrock (Karlstrom, 1964). Bedrock consists of poorly to moderately consolidated sandstone, siltstone, claystone, and coal of the Kenai Group (Nelson and Johnson, 1981). 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
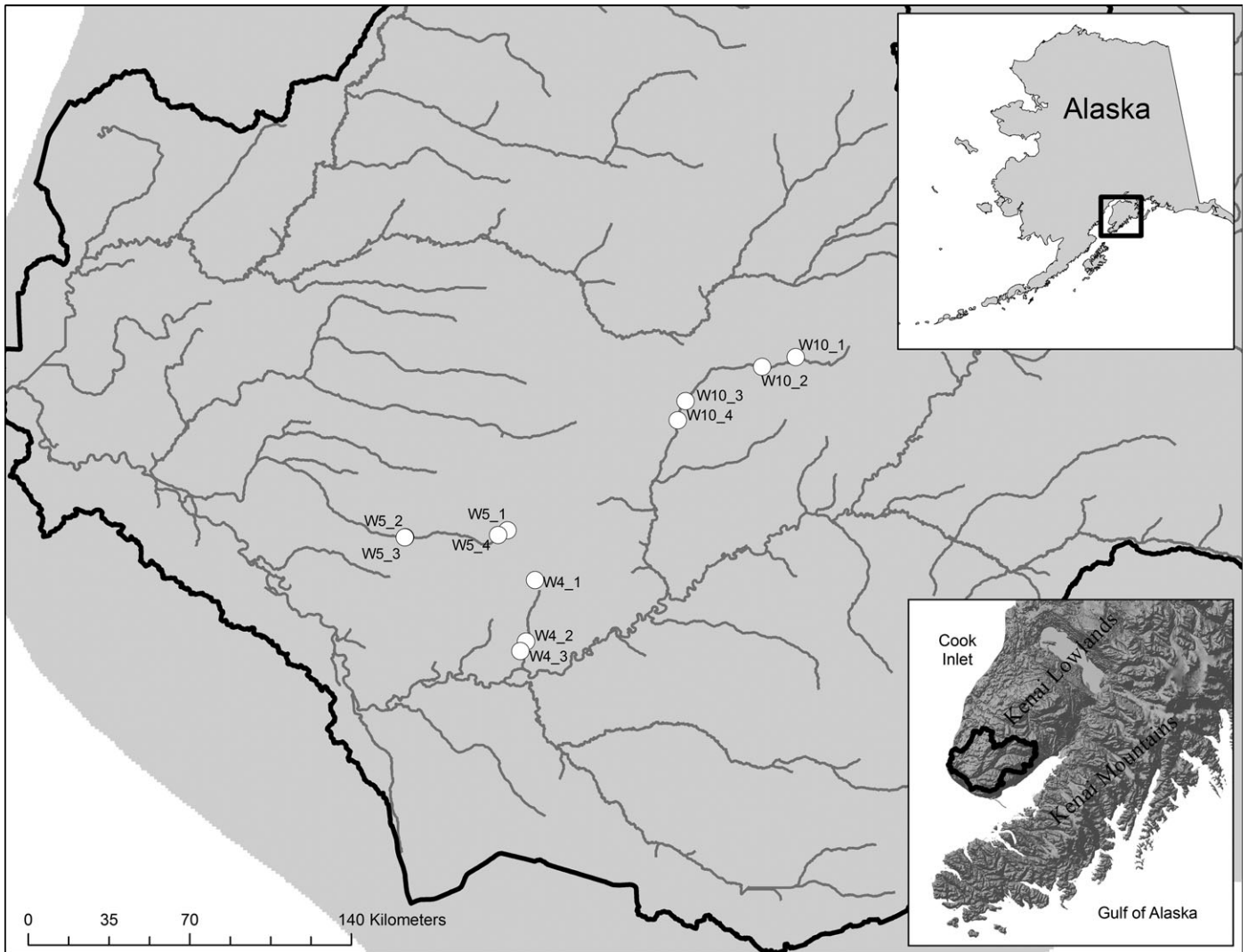

FIGURE 1. Location of the Study Area in the Kenai Peninsula, Alaska.

till throughout the area (Karlstrom, 1964; Nelson and Johnson, 1981). The Kenai Lowlands are generally permafrost free and soils in the study area are generally poorly drained silt loams or silt clay loams below an organic soil layer or histic epipedon (Hinton, 1971; Ford and Bedford, 1983), mostly mapped as Beluga silt loams (Van Patten, 2005). Research was conducted on both private and state-owned lands.

Water tables are mostly shallow, approximately 1-2 m below the surface, and wetlands and water bodies are common, covering approximately 41% of the land surface (Karlstrom, 1964; Gracz et al., 2004). Atmospheric nitrogen deposition in Alaska is generally low, with mean nitrogen deposition between 2009 and 2014 for Katmai National Park being 0.82 kg/ha/year (National Atmospheric Deposition Program; nadp.sws.uius.edu), a value slightly lower than those measured elsewhere in the western United States (U.S.) and much lower than those measured in the eastern U.S., especially in the industrialized northeastern U.S. (Holland et al., 2005). Local terrestrial nitrogen sources exist, however, including several nitrogen-fixing plant genera, with the dominant contributor being Alnus spp. (Shaftel et al., 2011). Headwater streams 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 closely related, therefore, we have grouped them for the purposes of this study as alders (Alnus spp.). Estimates of alder nitrogen-fixation rates can vary substantially, with Alaska estimates ranging from 2.5 to 6.6 kg/ha/year (Alnus viridis; Mitchell and Ruess, 2009), 59 kg/ha/year (Alnus incana; Uliassi and Ruess, 2002), and 164 kg ha/year (Alnus sp.; Klingensmith and Van Cleve, 1993). Riparian wetland vegetation associated with headwater streams is dominated by bluejoint grass, Calamagrostis canadensis (Shaftel et al., 2011; Whigham et al., 2012). Riparian wetland vegetation, particularly C. canadensis, provides important litter inputs and other allochthonous organic matter inputs for juvenile salmonid production in headwater streams in this region (Shaftel et al., 2011; Dekar et al., 2012).

Flow Path Delineation

This study was conducted in three watersheds that were part of previous and ongoing headwater stream studies in the Kenai Lowlands (e.g., King et al., 2012;

Walker et al., 2012; Whigham et al., 2012; Callahan et al., 2015). In each watershed, ArcGIS™ 10.0 (ESRI®, Redlands, California) was used to identify potential flow paths that connected upland habitats to wetlands adjacent to streams. Flow paths were created from 10 m resolution digital elevation models (DEMs) using the Spatial Analyst Tools in ArcGIS 10.0. Alder canopy cover was determined by visually identifying alder stands and hand-digitizing polygons in ArcGIS using 2003 IKONOS and Quickbird color satellite imagery. The distance between alder stands and the headwater stream along potential flow paths were measured in ArcGIS.

We hypothesized that concentrations of inorganic nitrogen in groundwater would decrease as it moved along flow paths between alder stands and headwater streams. If this hypothesis was true, the absolute length of a flow path would be irrelevant beyond some threshold distance. Therefore, we created a priori categories of alder-near (i.e., flow path length <80 m) and alder-far (i.e., flow path length >80 m), thereby separating the delineated flow paths into two roughly equal halves. The selected alder-near and alder-far flow paths served as treatments, and other selected no-alder flow paths served as controls. The locations of alder stands and the general routes of mapped flow paths were field verified.

To ensure that anthropogenic sources of nitrogen, including atmospheric deposition, were minimized, only the most remote sites were selected for the field analysis, which limited the total number of sites that could be selected and accessed. A total of 11 flow paths were selected (Figure 1) and the area of upland habitat that was the source of water for each flow path was calculated from 1 m resolution DEMs in ArcGIS. Watershed area for the alder-near sites ranged from 751 to 18,132 m^2 (Table 1). Percent alder canopy cover on the alder-near source areas ranged from 27 to 41%. One alder-near site (W5_2) and one alder-far site (W10-3) contained a mosaic of spruce and alder preventing an accurate estimation of percent alder canopy cover. At the alder-far sites, drainage area ranged from 6,432 to 83,918 m^2 (Table 1) and percent alder canopy cover ranged from 16 to 24%. At the no-alder control sites, drainage area ranged from 2,887 to 21,320 m^2.

Physical and Chemical Hydrologic Measurement and Analysis

Monitoring wells were installed approximately 1.0-1.5 m below the ground surface in ten stream reaches: four at alder-near sites, two at alder-far sites, and four at no-alder sites (Table 2). Monitoring wells were constructed of 5 cm inside-diameter

TABLE 1. Drainage Area Characteristics for the Flow Paths at the Alder-Near, Alder-Far, and No-Alder Sites.

Site Name	Alder Category	Alder Flow Path Length (m)	Drainage Area (m²)	Alder Area (m²)	Percent Alder Cover
W4_1	Alder-near	47	2,814	752	27%
W5_1	Alder-near	22	751	243	32%
W5_2	Alder-near	48	18,132	nc	nc
W10_2[1]	Alder-near	50	6,503	2,639	41%
W4_2	Alder-far	468	83,918	13,840	16%
W5_4	Alder-far	85	42,629	10,303	24%
W10_3	Alder-far	197	6,432	nc	nc
W4_3	No-alder	nc	4,404	0	0%
W5_3	No-alder	nc	14,438	0	0%
W10_4	No-alder	nc	2,887	0	0%
W10_1[2]	No-alder	nc	21,320	0	0%

Notes: Percent alder could not be calculated at two sites (*i.e.*, nc = not calculated). Alder flow path length could not be calculated at the no-alder sites.
[1]Denotes the detailed alder-near site.
[2]Denotes the detailed no-alder site.

TABLE 2. Number of Water Samples and Vegetation Plots at the Alder-Near, Alder-Far, and No-Alder Sites.

Site Name	Alder Category	No. of GW Sample Pts	No. of SSW Sample Pts	No. of HSW Sample Pts	Total No. of Water Samples Collected	No. of Vegetation Plots
W4_1	Alder-near	1	1	0	6	6
W5_1	Alder-near	1	1	1	8	0
W5_2	Alder-near	1	1	1	8	6
W10_2[1]	Alder-near	5	1	3	26	6
W4_2	Alder-far	1	1	1	7	6
W5_4	Alder-far	0	0	0	0	6
W10_3	Alder-far	1	1	1	7	6
W4_3	No-alder	1	1	0	5	6
W5_3	No-alder	1	1	1	8	6
W10_4	No-alder	1	1	0	6	6
W10_1[2]	No-alder	3	1	1	11	0

Notes: GW, groundwater; SSW, stream surface water; HSW, hillslope surface water.
[1]Denotes the detailed alder-near site.
[2]Denotes the detailed no-alder site.

polyvinyl chloride (PVC) and screened over 30 cm intervals approximately 1.0-1.5 m below the ground surface. The monitoring wells were placed near the lower end of each flow path, on the terrace well above the streams and approximately 1-5 m above the point where the flow paths entered the streamside wetlands (Figure 2). Two out of the ten flow paths with wells were chosen for detailed study of nitrate-N; one flow path in the alder-near category (hereafter called the detailed alder-near site) and the other in the no-alder category (hereafter called the detailed no-alder site) (Figure 3). No detailed alder-far site was established because the focus on the detailed study sites was simply nitrate-N dynamics downgradient of an alder path in general (*e.g.*, over what length scale does nitrate-N return to background values), so the spatial relationship of the alder stands to the stream was not relevant for that part of the study.

Monitoring wells were installed along the topographic gradient at the two detailed sites from the top of the topographic divide (detailed no-alder sites) or the alder stand closest to the stream (detailed alder-near sites) along the flow path to locations immediately upslope of the streamside wetlands. At the detailed alder-near site, five monitoring wells were installed along a ~65 m long flow path; at the detailed no-alder hillslope site, three monitoring wells were installed along a ~30 m long flow path.

Groundwater, hillslope surface water, and stream surface water were collected at all sites during three sampling events; June 21-26, July 12-16, and July 25-29, 2011. Hillslope surface water originated from seeps or springs along the flow path and then flowed toward the streamside wetlands in small, poorly defined channels. This water sometimes flowed directly into the headwater stream after passing
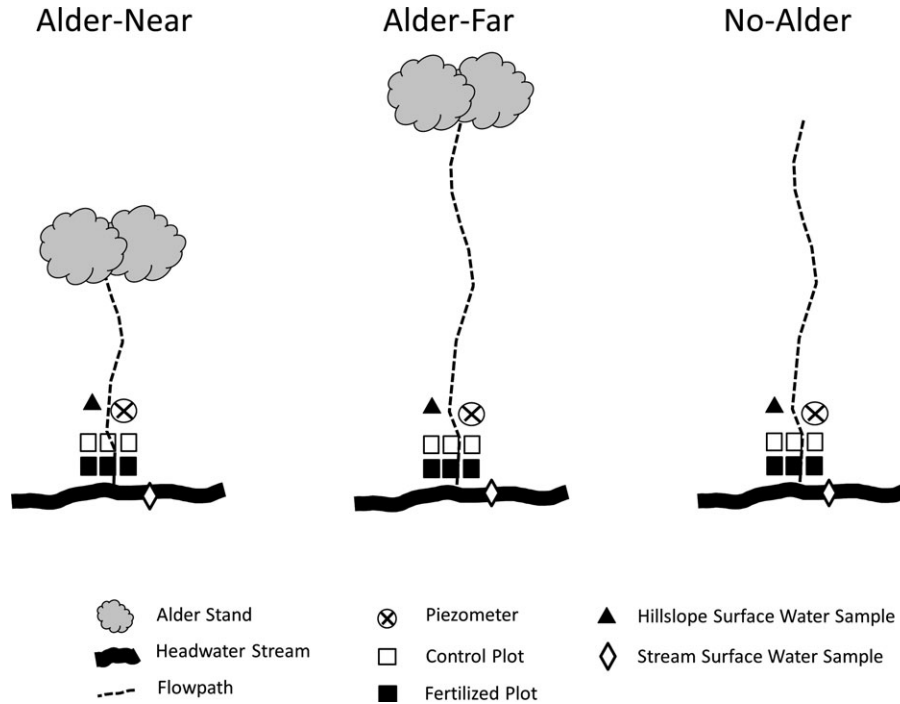
FIGURE 2. Schematic Diagram of the Three Site Categories, Alder-Near (<80 m), Alder-Far (>80 m), and No-Alder Sites Showing the Location of Monitoring Wells and Vegetation Plots (control and fertilized plots) in the Streamside Wetland Adjacent to the Headwater Stream. Figure is not to scale.

through the streamside wetland but, more commonly, inundated and saturated the substrates in streamside wetlands before reaching the stream. When present, hillslope surface water samples were collected at the foot of the hillslope and upslope of the vegetation plots (Figure 2). We assumed that stream surface water would reflect both watershed and adjacent hillslope conditions, with adjacent hillslope conditions particularly important because nitrogen is nonconservative and is likely taken up, or otherwise transformed close to the source. Stream surface water samples were collected from the headwater stream just downstream of the point where the flow paths entered the streamside wetlands (Figure 2). Hillslope surface water and stream surface water samples were collected by hand and filtered in the field through 0.45 μm PTFE membrane plunging filters (FilterMate™, Environmental Express, Mount Pleasant, South Carolina). Groundwater samples from the monitoring wells were collected using a peristaltic pump and inline 0.45 μm capsule filter (Whatman, Newton, Massachusetts). A total of 92 samples were collected. Water samples were collected and stored in 50 mL bottles at or below 4°C until analyses could be completed. Water samples were analyzed shortly after collection (generally within 72 h) for nitrate-N (NO_3^--N) concentrations using the cadmium reduction method (Hach Method 8039; 0.3-30.0 mg/L NO_3^--N) in the laboratory with a Hach DR 2700™ spectrophotometer (Hach, Loveland, Colorado).

Water levels were continuously measured for approximately two months and slug tests were performed at the detailed alder-near and no-alder sites. Water levels were measured with Model 3001 Levelogger Gold pressure transducers and dataloggers (Solinst, Inc., Georgetown, Ontario). Slug-test data were analyzed using the Hvorslev slug-test method (1951). The Hvorslev slug-test method estimates hydraulic conductivity using the equation:

$$K = r^2 \ln\left(\frac{l_e}{R}\right) / 2L_e T_{37} \qquad (1)$$

where K is the hydraulic conductivity of the aquifer, r is the radius of the well casing, R is the effective radius of the well screen, L_e is the effective length of the well screen, and T_{37} is the time it takes for the water level to rise or fall to 37% of the initial change. Hydraulic gradients (dh/dl) were calculated using the difference between hydraulic heads at the uppermost and lowermost wells. Specific discharge was calculated by multiplying the hydraulic conductivity (K) by the hydraulic gradient (dh/dl), or $q = K$(dh/dl). The specific discharge was divided by the effective porosity for silt loam (0.50 Freeze and Cherry, 1979) to
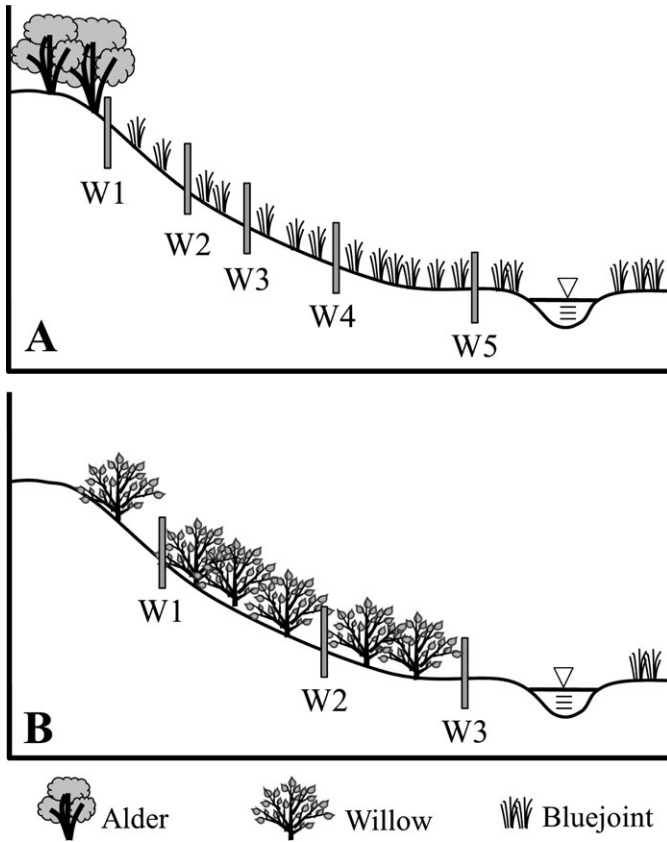
FIGURE 3. Schematic Diagram of the (a) Detailed Alder-Near Site and the (b) Detailed No-Alder Site. Figure is not to scale.

calculate mean groundwater velocity and related travel times along the flow path.

Soil and Foliage Sampling and Analysis

At the detailed alder-near and no-alder sites, an isotopic analysis of foliage and soil samples was conducted based upon the [15]N "natural abundance" approach (Black and Waring, 1977; Binkley et al., 1985). Naturally occurring variations in abundance of the stable nitrogen isotope, ^{15}N, have been utilized for decades to study the nitrogen cycle in managed and natural ecosystems (Peterson and Fry, 1987; Högberg, 1997; Matsushima et al., 2014). In particular, the distinctly low $\delta^{15}N$ value characteristic of nitrogen-fixing species, such as legumes and alder, has been used as a tracer to detect transfer of nitrogen originating from nitrogen-fixing species to neighboring species and soils (Peoples et al., 2015). While attempts to *quantify* nitrogen transfer using the stable isotope method have been questioned due to the current lack of knowledge of the potential for fractionation during nitrogen transfer, the distinct signature associated with the foliage of nitrogen-fixing species continues to be a useful tool for semi-quantitative studies of nitrogen cycling (Bedard-Haughn et al., 2003; Peoples et al., 2015).

Three foliage samples were collected from each of the three dominant types of vegetation: alder (*Alnus* spp.), willow (*Salix* spp.), and aerial shoots of *C. canadensis*. Willow was not present at the detailed alder-near site, while alder and *C. canadensis* were not present at the detailed no-alder site. Consequently, alder leaves and *C. canadensis* shoots were collected from the detailed alder-near site and willow leaves were collected from the detailed no-alder site. At the detailed alder-near site, alder leaves were collected from shoots located within the alder stand that was located at the top of the flow path, while *C. canadensis* shoots were collected from the streamside wetland that was contiguous with the stream at the base of the flow path. At the detailed no-alder site, willow leaves were collected at three random locations along the flow path. Replicates of each foliage sampled were placed into plastic bags. In the laboratory, the samples were air dried for 24 h and stored at 4°C until they were ground to a fine powder using a stainless steel coffee grinder. The ground samples were stored in airtight glass vials until subsamples were weighed for analysis.

Soil samples were collected from the organic-rich surface horizons using a hand auger to a depth of 15 to 20 cm below the ground surface. At the detailed alder-near site, three soil samples were collected within the alder stand (0 m) and four soil samples were collected along the flow path at 4, 20, 45, and 65 m from the alder stand. At the detailed no-alder hillslope site, three soil samples were collected at 0, 12, and 21 m from the top of the flow path. Each soil sample consisted of two cores that were oven dried (70°C, 24 h), homogenized, and subsampled and ground into a fine powder prior to analysis.

Soil and vegetation samples were combusted using a Costech ECS 4010 elemental analyzer and the resulting gas was analyzed using a Thermo Scientific Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS) (University of Florida Stable Isotope Lab). The stable nitrogen isotopic composition is reported in standard (δ) notation:

$$\delta = \left[\left(\frac{R_{sample}}{R_{standard}} \right) - 1 \right] \times 1000 \qquad (2)$$

where R is the ratio of the heavy isotope to the light isotope, that is, ^{15}N/^{14}N, in the sample or the standard. Samples were normalized to the V-Air scale using B2151 (Elemental Microanalysis) and an internal carbon/nitrogen standard. $\delta^{15}N$ values are reported with 0.1‰ precision.

Wetland Vegetation Sampling and Analysis

Six pairs of 1 m × 1 m plots were established in each of the streamside wetlands at nine sites (three alder-near, three alder-far, and three no-alder sites) (Figure 2). The wetlands were each located on/near the toeslope, commonly downgradient of where groundwater discharge would occur and thereafter would flow overland to the headwater streams. The wetlands were small enough that there were no discernable differences in soil wetness and the pairs of sites were oriented within each wetland so that the upslope member of each pair received water discharged from the flow path and the downstream member received water from the flow path as well as nitrogen that was added in fertilizer. Each pair thus represented a unit of comparison for testing the hypotheses described in the Introduction. The upslope plot of each pair was the control and the downstream member received 20 g/m^2 of nitrogen in the form of ammonium nitrate (NH_4NO_3). The experimental design consisted of two factors with two levels of one factor (± fertilizer added) and three levels of the other factor (alder stand close to the streamside wetland, "alder-near", alder stand far from the streamside wetland, "alder-far", and no alder stand upslope of the wetland, "no-alder"). The plots were established and fertilized in May 2011 and a 50 cm × 50 cm subplot from the center of each plot was harvested in late August 2011. Vegetation was cut at the soil surface and divided into *C. canadensis* and, when present, all other herbaceous species. Samples were weighed in the field with a portable scale. A composited subsample of each field-weighed sample was dried (60°C, 72 h), ground, and flown to the Smithsonian Environmental Research Center for nitrogen content analysis (Perkin-Elmer 2400 CHN analyzer, Waltham, Massachusetts).

Statistical Analysis

Nitrate-N concentrations in groundwater were analyzed using an analysis of variance (ANOVA) to test for a statistically significant difference among three alder site categories (alder-near, alder-far, and no-alder). Subsequent pairwise comparisons were analyzed using the Tukey honest significant difference (HSD) test, thereby reducing the chance of a statistical type I error. Both the ANOVA and Tukey HSD test were conducted using R version 3.1.1 (R Project for Statistical Computing, http://www.r-project.org/). We report results of the fertilization study for the only species present in all 54 plots, that is, *C. canadensis*. We used the Kruskal-Wallis test in NPARW1WAY procedures in SAS to determine if

there were differences in the response of *C. canadensis* to fertilization between the alder-near, alder-far, and no-alder sites. We compared the difference in *C. canadensis* biomass in the paired fertilized (BiomassF) and control (BiomassC) plots as follows: ((BiomassF−BiomassC)/BiomassC). We also used the Kruskal-Wallis test to compare the nitrogen content of *C. canadensis* in the control plots to determine if there were differences among the three types of sites.

RESULTS

There was a significant difference (ANOVA; $p = 0.03$; Table 3) in groundwater nitrate-N concentrations measured at the downstream end of flow paths. The highest values were measured at the alder-near (0.49 ± 0.07 mg/L) and alder-far (0.54 ± 0.14 mg/L) sites compared with the no-alder sites (0.25±0.06 mg/L) (Figure 4). Groundwater nitrate-N concentrations were significantly higher at the alder-near sites compared to the no-alder sites (Tukey HSD Test; $p = 0.05$) but the difference between the alder-far sites and the no-alder sites were not different at the $p = 0.05$ level (Tukey HSD Test; $p = 0.07$). Hillslope surface water nitrate-N concentrations did not differ significantly (ANOVA; $p = 0.43$) among the three types of flow paths even though the means were in the expected order with highest concentrations at the alder-near (0.88 ± 0.35 mg/L) sites compared to the alder-far (0.43 ± 0.19 mg/L), and no-alder

TABLE 3. Summary Table of Statistical Analyses Performed for Groundwater, Hillslope Surface Water, and Stream Surface Water Nitrate-N Concentrations and the Fertilization Plots among the Alder-Near, Alder-Far, and No-Alder Sites.

Statistical Analysis Summary

|	Statistical Analysis	d.f.	*F* Value	*p* Value
Nitrate concentrations				
Groundwater	ANOVA	2	4.093	0.03
Alder-near *vs.* no-alder	Tukey HSD			0.05
Alder-near *vs.* alder-far	Tukey HSD			0.92
Alder-far *vs.* no-alder	Tukey HSD			0.07
Hillslope surface water	ANOVA	2	0.908	0.43
Alder-near *vs.* no-alder	Tukey HSD			0.47
Alder-near *vs.* alder-far	Tukey HSD			0.61
Alder-far *vs.* no-alder	Tukey HSD			0.99
Stream surface water	ANOVA	2	3.63	0.04
Alder-near *vs.* no-alder	Tukey HSD			0.05
Alder-near *vs.* alder-far	Tukey HSD			0.11
Alder-far *vs.* no-alder	Tukey HSD			0.99
Fertilization study				
Biomass	Chi-square	2	2.95	0.04
N content	Chi-square	2	0.96	0.62
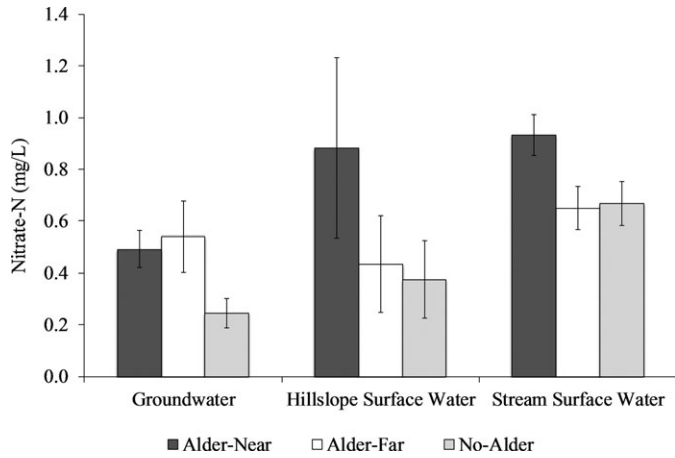
FIGURE 4. Mean Nitrate-N (NO_3^--N) Concentrations ($\pm$ SE) of the Groundwater, Hillslope Surface Water, and Stream Surface Water Samples for the Three Site Types, Alder-Near (<80 m), Alder-Far (>80 m), and No-Alder Sites. Groundwater sample sizes are alder-near $n = 12$, alder-far $n = 5$, and no-alder $n = 11$. Hillslope surface water sample sizes are alder-near $n = 6$, alder-far $n = 3$, and no-alder $n = 4$. Stream surface water sample sizes are alder-near $n = 12$, alder-far $n = 6$, and no-alder $n = 12$.

sites (0.38 ± 0.15 mg/L) (Figure 4). Stream surface water nitrate-N concentrations differed significantly (ANOVA; $p = 0.04$) (Figure 4) and, similar to groundwater concentrations, the alder-near sites (0.93 ± 0.08 mg/L) had significantly higher concentrations (Tukey HSD Test; $p = 0.05$) than the no-alder sites (0.67 ± 0.08 mg/L). The alder-far (0.65 ± 0.08 mg/L) sites did not differ significantly from the no-alder sites (Tukey HSD Test; $p = 0.99$) or from the alder-near site (Tukey HSD Test; $p = 0.11$).

At the detailed alder-near and no-alder sites, nitrate-N concentrations decreased with increasing distance from the top to bottom of the flow paths (Figure 5). Although small sample sizes prevent a rigorous statistical analysis, some overall trends are distinguishable. At the detailed alder-near site, the mean nitrate-N concentration was 1.43 ± 0.15 mg/L immediately adjacent to the alder stand and decreased to 0.37 ± 0.18 mg/L at 59 m. Hillslope surface water nitrate concentrations also decreased along the flow path from 0.93 ± 0.09 mg/L immediately adjacent to alder stand to 0.60 ± 0.10 mg/L adjacent to the streamside wetlands at 59 m (Figure 5). At the detailed no-alder site, groundwater nitrate-N concentrations were lower compared to the detailed alder-near site but concentrations along the flow path also decreased from a high of 0.60 ± 0.06 mg/L at the upper end to 0.23 ± 0.19 mg/L at 21 m downslope. Hillslope surface water was only observed at one location along the detailed no-alder flow path and the mean value of 0.50 ± 0.20 mg/L was only slightly less than the mean value of groundwater nitrate concentrations measured nearby (Figure 5).
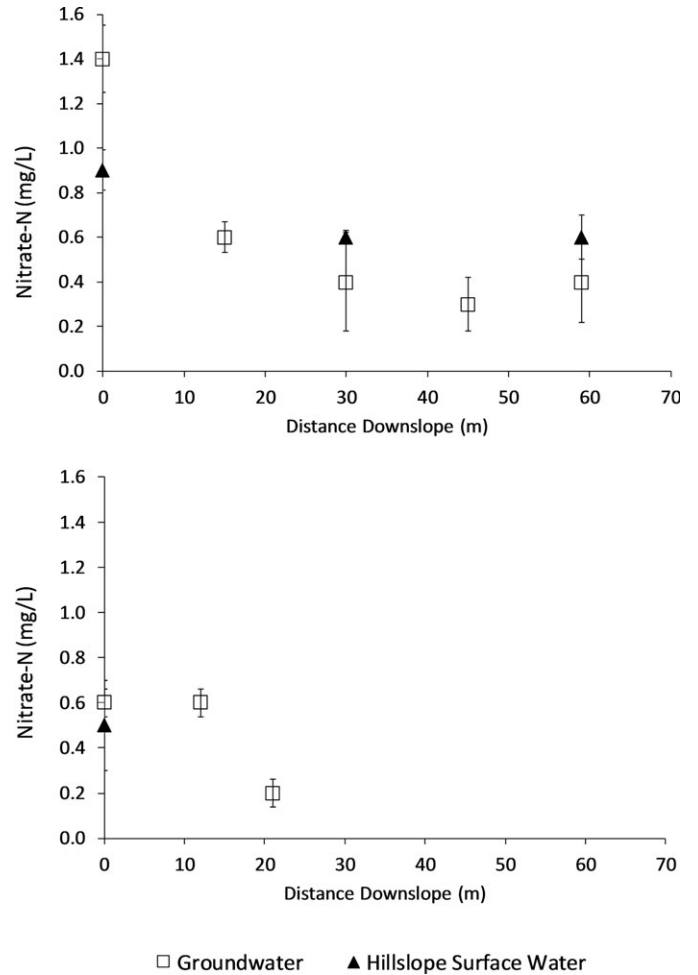

FIGURE 5. Mean Nitrate-N (NO_3^--N) Concentrations $\pm$ SE vs. Distance Downslope from the Edge of the Alder Stand for the Groundwater and Hillslope Surface Water for the (a) Detailed Alder-Near Site and (b) the Detailed No-Alder Site. At the detailed alder-near site, sample sizes are $n = 3$ for all water samples except for $n = 2$ at the hillslope surface water sample at 59 m. At the detailed no-alder site, sample sizes are $n = 3$ for all water samples except for $n = 2$ at the hillslope surface water samples at 0 m.

At the detailed alder-near and no-alder sites, mean hydraulic conductivities were similar ($7.1 \times 10^{-6} \pm 4.1 \times 10^{-6}$ m/s and $6.2 \times 10^{-6} \pm 1.1 \times 10^{-6}$ m/s, respectively). Hydraulic gradients, however, differed between the two sites with a mean of 0.18 ± 0.00 at the detailed alder-near site compared to 0.36 ± 0.01 at the detailed no-alder site, neither varying throughout the course of the study (hydraulic gradients are length divided by length, and are therefore unitless). Assuming the mean hydraulic conductivity and an effective porosity $n_e = 0.50$ for silt loam (Freeze and Cherry, 1979), particle travel times on a 20 m length of flow path would be ~90 day and ~50 day for the detailed alder-near and no-alder sites, respectively.

$\delta^{15}N$ values differed among the three tissue types (alder leaves, willow leaves, and *C. canadensis* shoots),

with mean of $-0.71 \pm 0.08\permil$, $-0.55 \pm 0.04\permil$, and $5.52 \pm 0.56\permil$, respectively. Although small sample sizes prevent a rigorous statistical analysis, some overall trends are distinguishable. At the detailed alder-near site, mean soil $\delta^{15}N$ values immediately adjacent to the alder stand were $3.20 \pm 0.39\permil$, increased to $5.43 \pm 0.36\permil$ at a distance of 4 m from the alder stand, then decreased and remained relatively constant along the remainder of the flow path, being $4.79 \pm 0.20\permil$ at 20 m, $4.51 \pm 0.30\permil$ at 45 m, and $4.58 \pm 0.20\permil$ at 65 m. At the detailed no-alder hillslope site, mean soil $\delta^{15}N$ values decreased downgradient, being $3.61 \pm 0.21\permil$ at 0 m, $3.19 \pm 0.01\permil$ at 12 m, and $2.83 \pm 0.09\permil$ at 21 m.

Calamagrostis canadensis was present in all the fertilization study plots and accounted for between 84 and 95% of the aboveground biomass (Table 4). Other herbaceous species (primarily *Polemonium acutiflorum*, *Chamerion angustifolium*, *Equisetum arvense*, *Sanguisorba canadensis*, *Comarum palustre*, *Thalictrum sparsiflorum*, and *Trientalis europaea*) were present but measurable amounts of biomass were only present in 25 of the 54 plots. The mean biomass of *C. canadensis* in the control plots at the alder-far and alder-near sites was higher than the mean value in the control plots at the no-alder sites (Table 4), while the mean values were not different at the control sites, the higher biomass at the two alder sites indicates that the downslope movement of nitrogen from upslope sources, especially as groundwater (Figure 4), supports production in streamside wetlands. The importance of the nitrogen from upslope sources was also demonstrated by the comparison of biomass in N-fertilized plots compared to control plots. The mean increase in *C. canadensis* biomass in the fertilized plots at the no-alder sites was larger than the response to fertilization at the alder-far and alder-near sites (Figure 6) and there was a significant difference between sites (chi-square = 6.3175, d.f. = 2; ChiF = 2.95; p = 0.0425; Table 3). There was no significant difference in nitrogen content of *C. canadensis* in the control plots (chi-square = 0.9565, d.f. = 2, p = 0.6199), a result that was not unanticipated because the biomass was harvested late in the growing season when nutrients had been translocated to belowground storage (Hogg and Lieffers, 1991).

DISCUSSION

It has been previously demonstrated that elevated concentrations of nitrate occur in shallow groundwater under alder stands (Bormann *et al.*, 1994; Hart *et al.*, 1997; Rhoades *et al.*, 2001) and that alder are a significant source of nitrogen to headwater streams (*e.g.*, Shaftel *et al.*, 2012). In this study, we focused on the hypothesis that flow paths that connect upslope alder stands to headwater streams and adjacent wetlands represent potential nitrogen hotspots along stream corridors. We further hypothesized that nitrogen input to streams and streamside wetlands was greatest on hillslopes with alder close to the streams and streamside wetlands (alder-near), moderate on hillslopes with alder far from the streams and streamside wetlands (alder-far), and least on hillslopes with no alder at all (no-alder). Collectively, our results support the hypothesis that flow paths that include stands of alder represent potential hotspots along headwater streams but results to test the effects of flow path length on nitrate input to streamside wetlands and headwater streams were ambiguous. While trends in measured variables generally supported the hypotheses, differences were seldom consistently statistically significant. A lack of statistical power may have resulted in part due to too few replicates, *a priori* selection of an alder-far flow path that was too long to capture the transitional differences, and/or confounding factors, such as differences in hydrologic gradients and alder cover. Here, we interpret the results of each component of the study in light of the hypotheses addressed.

First, results from sampling groundwater at different distances along flow paths at the detailed alder-near and no-alder sites demonstrated that there would be a downslope reduction in nitrate-N

TABLE 4. Means ($\pm$SE) for the Nitrogen Content (%N), Biomass (g/m^2) of *Calamagrostis canadensis*, Biomass (g/m^2) of Other Species, and the Percentage of Total Biomass that Was *C. canadensis* in Control and Fertilized Streamside Wetlands at the Alder-Near, Alder-Far, and No-Alder Sites.

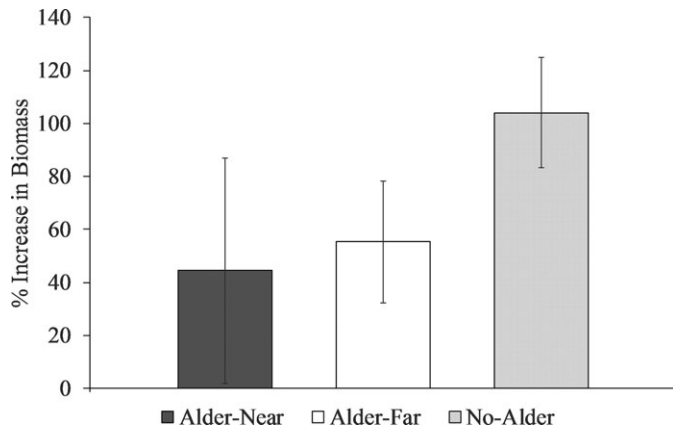|	Alder-Near		Alder-Far		No-Alder	
	Control	Fertilized	Control	Fertilized	Control	Fertilized
%N	0.99 (0.13)	1.36 (0.15)	1.09 (0.10)	1.66 (0.18)	0.98 (0.12)	1.37 (0.12)
C. canadensis biomass (g/m^2)	388 (75)	408 (44)	396 (62)	562 (71)	236 (41)	493 (102)
Biomass (g/m^2) — other species	60 (17)	75 (22)	39 (23)	77 (44)	17 (7)	30 (16)
% Biomass = *C. canadensis*	84 (0.05)	84 (0.04)	90 (0.06)	90 (0.06)	95 (0.02)	94 (0.03)

FIGURE 6. Percent Increases in *C. canadensis* Biomass in Fertilized Compared to Control Paired Plots. Values are means ± SE.

concentrations (Figure 5). The decrease in nitrate-N occurred within 10-30 m downslope. Soil $\delta^{15}N$ values provide further confirmation that nitrogen was being removed or altered chemically within short distance downslope of alder. Soil $\delta^{15}N$ increased from 3.20 to 5.43‰ within 4 m and only changed slightly (4.58-4.51‰ between 20 and 65 m) along the remainder of the flow path at the detailed alder-near site. Combined, these two results indicate that nitrate-N is taken up within a relatively short distance and the distance between alder stands and streamside wetlands and headwater streams may not be important unless flow paths are within a critical distance or there are mechanisms for rapid transport of nitrate-N over longer distances.

Groundwater moves slowly in our study area; water level measurements and slug-test results indicate that the mean travel time of shallow groundwater over distances of 10-30 m are 45-135 day, thus, providing sufficient time for nitrogen uptake or transformation. At the time of this study (*i.e.*, June-July), biological demand for nitrogen would have been high, especially early in the growing season when vegetation was actively accumulating nitrogen in biomass (*e.g.*, Hogg and Lieffers, 1991; Gloser, 2002). In addition to nitrogen uptake by vegetation and microbes, denitrification can become a dominant microbial process in saturated soils, transforming nitrate (NO_3^-) and nitrite (NO_2^-) to nitrogen gas (N_2) and further reducing nitrate concentrations in groundwater (Firestone and Davidson, 1989; Davidson and Schimel, 1995). The *a priori* cutoff between alder-near and alder-far sites was 80 m, much greater than the 10-30 m over which nitrate-N concentrations diminished to background levels at the detailed alder-near site (Figure 5). After 10-30 m, nitrate-N concentrations may settle to background concentrations of ~0.5 mg/L

prior to discharging at the toeslopes to the streamside wetlands or stream. Therefore, this *a priori* cutoff may have been too large to see significant differences between the alder-near and alder-far sites, especially with the small sample size (*i.e.*, low statistical power) and large variances.

We observed hillslope surface water as groundwater discharging to the surface at seeps or springs, then flowing rapidly overland downslope to streamside wetlands and headwater streams. While we did not measure flow rates associated with hillslope surface water, the presence of flowing surface water during the course of our study demonstrates that it is a potential pathway for the rapid movement of water and solutes between alder stands and streamside wetlands and headwater streams (Dennis F. Whigham, Mark C. Rains, and Michael K. Callahan, personal observations, 2011). Nitrate-N concentrations in hillslope surface water were not significantly different between the sites, though concentrations followed hypothesized gradients and mean concentrations at the alder-near sites were more than double the mean concentrations at the alder-far and no-alder sites (Figure 4). Though not conclusive, these results lend support to the hypothesis that the shorter the distance between an alder stand and a headwater stream, the greater the potential for nitrogen to reach the wetland vegetation and headwater stream. If true, the lower concentrations at the alder-far sites may have been due to the longer flow path associated with the alder-far sites resulting in an increased potential for surface water to interact physically and chemically with vegetation and microbes as it moved downslope.

In any case, nitrate-N concentrations in stream water were significantly higher at the alder-near sites than at the alder-far and no-alder sites (Figure 4). The magnitudes of the concentrations and the general pattern of the concentrations at the different sites were similar between the hillslope surface water and stream water (Figure 4). This lends support to the hypothesis that hillslope surface water may provide an important nitrate-N subsidy immediately downstream from point discharge locations.

Though a pattern emerges, ambiguity remains due to small sample sizes and confounding variables. To minimize anthropogenic sources of nitrogen, including atmospheric deposition, only the most remote sites were selected for this study. That made access difficult, especially for the purposes of instrumentation installation (*e.g.*, wells). Furthermore, we endeavored to avoid pseudoreplication, which might have occurred had we established multiple sites in the same subwatersheds. With small sample sizes, statistical power was low, with some nitrate-N concentration trends significant (*e.g.*, stream water) and

others not (*e.g.*, hillslope surface water). This was exacerbated by potentially confounding variables, such as alder percent cover. Shaftel *et al.* (2012) showed that stream nitrate-N concentrations are positively correlated with percent cover of alder. However, higher percent cover of alder in general is likely correlated with higher percent cover of alder within 10-30 m of streamside wetlands and headwater streams and higher percent cover of alder along flow paths with seeps and springs and related hillslope surface water flows. We believe that neither Shaftel *et al.* (2012) nor this article tell the story in its entirety unto themselves, and instead tell a more complete story when considered together about how alder contributes to nitrogen subsidies in streamside wetlands and headwater streams.

The response of streamside wetlands to fertilization supported our hypothesis that nitrogen was the limiting nutrient and that nitrogen was more limiting when there was no alder along the flow path. There was a significant difference between sites in the relative increase in biomass in fertilized *vs.* control paired plots (chi-square = 6.3175; d.f. = 2; p = 0.0425) with the greatest response occurring at the no-alder sites, an intermediate response at the alder-far sites, and the lowest response at the alder-near sites (Figure 6). The response to fertilization at one pair of plots at the alder-far sites, however, accounted for a mean site response that was not very different from the mean at the alder-near sites. The fertilized plot at one of the nine paired plots at the alder-far sites had lower biomass than the paired control plot and if the data for that pair were removed from the analysis, the mean site response at the alder-far sites increased from 55 to 67%. In comparison to the no-alder and alder-far sites, five of the nine fertilized plots at the alder-near sites had less biomass than the paired control plot and, as a result, the standard error was almost the same as the mean (Figure 6). We interpret the large differences among the paired plots at the alder-near sites to be the consequence of spatial variation in nitrogen availability in response to variations in pattern of movement into and through the wetland from upslope nitrogen sources.

Although our study focus was on nitrate-N, other forms of nitrogen, such as dissolved organic nitrogen (DON) and ammonium may also be transported along flow paths downslope of alder stands and into streamside wetlands. Some wetland plant species, including *C. canadensis*, have demonstrated the ability to rapidly take up ammonium (Hangs *et al.*, 2003) and to readily assimilate glycine, a simple form of organic nitrogen (Miller and Bowman, 2002; Rains and Bledsoe, 2007), while other common species may additionally benefit from associations with ecto- or ericoid mycorrhizal fungi to acquire nitrogen from more complex organic sources (Michelsen *et al.*, 1998; Lin *et al.*, 2011). Since transport of additional forms of nitrogen downslope of alder is likely to be occurring and to be ecologically relevant, the impact of alder stands on streamside communities may be even greater than suggested by the presence of elevated levels of nitrate in surface water and groundwater in alder-near transects.

Rapid utilization of alder-derived nitrogen downslope of alder stands was supported by the isotopic analysis of foliage and soil samples. Within the alder stands, both soils and foliage have relatively low $\delta^{15}N$ values, suggesting the local soil nitrogen pool is influenced by the nitrogen-fixing activities of alder. The $\delta^{15}N$ values of shallow soil layers (sampling depth, 0-20 cm) increased within four meters downslope of the alder stand indicating alder-derived nitrogen transported downslope was quickly integrated into local nitrogen pools. Similarly, others have observed ^{15}N enrichment of soil nitrogen pools following application of fertilizer depleted in ^{15}N or upon decomposition of plant tissues of nitrogen-fixing species (Matsushima *et al.*, 2012; Peoples *et al.*, 2015). When the supply of nitrogen is sufficient that reactions do not go to completion, nitrogen cycling processes, such as assimilation, nitrification, denitrification, ammonia volatilization, and leaching, have been shown to discriminate against the heavier isotope, resulting in ^{15}N enrichment of the residual soil nitrogen pool (Delwiche and Steyn, 1970; Handley and Raven, 1992; Peoples *et al.*, 2015). The higher $\delta^{15}N$ values detected in soils below the alder stands relative to soils within the alder stands or along the no-alder flow paths suggest the alder-derived nitrogen is incorporated into nitrogen cycles downslope of alder stands.

Calamagrostis canadensis foliage sampled in the streamside wetlands was enriched in ^{15}N relative to soil samples or to the foliage of other species sampled along the flow paths. Similarly, Michelsen *et al.* (1998) noted $\delta^{15}N$ values were higher in *Calamagrostis lapponica* foliage than in topsoil or in the foliage of *Salix* spp. or *Alnus incana*. Interspecific differences in foliar $\delta^{15}N$ values have been attributed to differential access to soil nitrogen pools through differences in rooting depth, nitrogen uptake kinetics, nitrogen-fixation ability, and/or mycorrhizal status (Nadelhoffer *et al.*, 1996; Högberg, 1997; Miller and Bowman, 2002; Matsushima *et al.*, 2014). *C. canadensis,* which has been observed rooting at depths of 50 cm (Chapin *et al.*, 1996), may be assimilating nitrogen from deeper, more highly enriched locations in the soil than those sampled in our study (0-20 cm) or by Michelsen *et al.* (1998) (0-5 cm). The $\delta^{15}N$ values we observed in *C. canadensis* foliage ($5.52 \pm 0.56\permil$) are higher than those cited in the

literature [*e.g.*, approximately $-1.0‰$ (Michelsen *et al.*, 1996), $3.0‰$ (Michelsen *et al.*, 1998), $0.77 \pm 0.38‰$ (Miller and Bowman, 2002), -0.7 to $2.3‰$ (Matsushima *et al.*, 2014)], although they approach the high end of the range for *C. canadensis* foliage reported by Schulze *et al.* (1994) in northern Alaska (approximately -3.0 to $+5.0‰$). Schulze *et al.* (1994) additionally observed an interesting, though nonsignificant, correlation between $\delta^{15}N$ in *C. canadensis* foliage and concentrations of soil ammonium or of soil nitrate. Similarly, Matsushima *et al.* (2014) noted the $\delta^{15}N$ of *C. canadensis* foliage increased $3‰$ two years after fertilization despite the relatively low $\delta^{15}N$ of the applied urea ($0.87 \pm 0.03‰$). They interpret this paradoxical enrichment of foliar nitrogen levels in the presence of ^{15}N-depleted fertilizer as evidence of increased isotopic fractionation when the soil is amended with nitrogen. We lack the sampling replication necessary to fully investigate this trend as it applies to our study, but it is worth noting that our sampling site for the ^{15}N-enriched *C. canadensis* foliage was a streamside wetland in the alder-near flow path, where the results of our fertilization study indicate nitrogen may be more abundant than in no-alder flow paths.

Hillslopes, streamside wetlands, and headwater streams are all parts of an integrated and connected hydrologic system that allows for exchanges between all elements of the continuum (Fisher *et al.*, 2004; Nadeau and Rains, 2007). In the Kenai Lowlands, the productivity of the streamside wetlands, including the ubiquitous dominant species *C. canadensis* (Whigham *et al.*, 2012), is most likely dependent on nutrients, especially nitrogen, from adjacent uplands. The study by Shaftel *et al.* (2012), which show that stream nitrate concentrations are correlated with alder percent cover at the watershed scale, together with the results of this study, which show the importance of flow path length on the fate of alder-fixed nitrogen, provide a more complete picture of the dynamic nature of the upland-wetland-stream continuum in the Kenai Lowlands. Local hydrologic flow paths (either as groundwater or hillslope surface water) can connect upslope alder stands with streamside wetlands creating potential nitrogen "hot spots" resulting in increased nutrient availability, a factor that is related to increased nutrient uptake by wetland vegetation (Iversen *et al.*, 2010). Increased nutrient availability clearly results in increased local wetland productivity and greater potential for the streamside wetland to directly or indirectly influence the dynamics of the adjacent headwater streams. Therefore, it is necessary to apply an integrated systems approach that incorporates hillslope vegetation patterns and nutrient transport processes, streamside wetlands, and headwater streams to management issues related to streams that support economically important juvenile salmon on the Lower Kenai Peninsula.

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