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ECOSYSTEMS

A Non-Native Riparian Tree (*Elaeagnus angustifolia*) Changes Nutrient Dynamics in Streams

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ABSTRACT

Russian olive (*Elaeagnus angustifolia*) is a non-native riparian tree that has become common and continues to rapidly spread throughout the western United States. Due to its dinitrogen (N_2)-fixing ability and proximity to streams, Russian olive has the potential to subsidize stream ecosystems with nitrogen (N), which may in turn alter nutrient processing in these systems. We tested these potential effects by comparing background N concentrations; nutrient limitation of biofilms; and uptake of ammonium (NH_4-N), nitrate (NO_3-N), and phosphate (PO_4-P) in paired upstream-reference and downstream-invaded reaches in streams in southeastern Idaho and central Wyoming. We found that stream reaches invaded by Russian olive had higher organic N concentrations and exhibited reduced N limitation of biofilms compared to reference reaches. However, at low inorganic N background concentrations, reaches invaded by Russian olive exhibited higher demand for both NH_4-N and NO_3-N compared to their paired reference reaches, suggesting these streams have the potential to retain the N subsidy from Russian olive N_2 fixation and diminish its downstream export and effects. Our findings demonstrate the potential for a non-native riparian plant to significantly alter biogeochemical cycling in streams. Finally, we used our results to develop a conceptual model that describes predicted effects of Russian olive and other non-native riparian N_2 fixers on in-stream N dynamics.

Key words: *Elaeagnus angustifolia*; Russian olive; invasive species; nitrogen fixation; nutrient limitation; nutrient spiraling; subsidy; DON.

INTRODUCTION

Streams and their adjacent riparian zones are closely linked. Riparian plants strongly affect the ecological character of streams, especially through subsidies (for example, leaves, wood, nutrients, invertebrates) that affect stream food webs and aquatic ecosystem processes (Wallace and others 1997; Baxter and others 2005). Riparian zones also modify the amount, form, and timing of nutrient export from watersheds to streams (Gregory and others 1991; Mulholland 1992; Naiman and Décamps 1997; Groffman and others 2002). Direct nutrient uptake by riparian vegetation can significantly reduce nutrient loads entering waterways from the terrestrial portion of the watershed (Peterjohn and Correll 1984; Zhang and others 2010). Groundwater and hyporheic exchange with

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the stream channel can modify the forms and fluxes of nutrients delivered to the stream (Triska and others 1993; Dahm and others 1998; Dent and others 2000); moreover, some of these nutrient processes are mediated by riparian plants (Schade and others 2001). However, if riparian vegetation is dominated by plants associated with dinitrogen (N_2) fixation such as alder (*Alnus* sp.), the riparian zone can become a source of additional nitrogen (N) to streams, which may lead to elevated surface water N concentrations (Goldman 1961) and nitrate (NO_3-N) and dissolved organic nitrogen (DON) export (Compton and others 2003).

Nitrogen is often the nutrient limiting primary production in terrestrial and aquatic systems (Elser and others 2007), and alteration of N by anthropogenic activity, including changing the abundance of native N_2-fixing plants or introducing N_2-fixing crops or invasive species, can have strong ecosystem effects. For instance, *Myrica faya*, a N_2-fixing plant invading young volcanic soils in Hawaii, contributes four times more available N than any other source in the native system, and consequently alters N cycling and terrestrial primary production (Vitousek and Walker 1989). Altered resource availability may occur when invasive species create additional trophic or nutrient subsidies, or disrupt previously existing subsidies to a system (Baxter and others 2004; Maron and others 2006). Globally, creation of reactive N by biological N_2 fixation associated with cultivated crops such as alfalfa and soybeans is approximately 32–50 Tg N per year; the N_2-fixation rate by these crops is variable and ranges from 4 to 30 g N m^{-2} y^{-1} (Galloway and others 2004). Nutrient subsidies created by crops and abundant N_2-fixing plants have the potential to propagate from land to nearby water bodies, especially if they occur in riparian areas. Thus, increased abundance of riparian plants that fix N_2 may strongly affect the structure and function of stream ecosystems by creating subsidies of nutrients or by altering their availability and retention in the aquatic system. This effect may be particularly strong in the American West, where stream primary producers are commonly N limited (Fisher 2006).

Russian olive (*Elaeagnus angustifolia*) is a non-native tree that has spread along riparian corridors in the western USA since its introduction from Eurasia in the late 1800s (Olson and Knopf 1986; Katz and Shafroth 2003). Friedman and others (2005) estimated that, for the period from 1997 to 2002, Russian olive was the fourth-most frequently occurring woody riparian plant species in this region. Establishment and spread of Russian olive appears to be facilitated by altered stream flow regimes, such as damming or irrigation water withdrawals (Howe and Knopf 1991; Lesica and Miles 1999; Katz and Shafroth 2003), which are common in the West (Poff and others 1997). Other factors promoting the establishment and spread of Russian olive are horticultural cultivation, its large seed size and long seed longevity (Katz and Shafroth 2003), and tolerance to mean annual minimum temperature (Friedman and others 2005). A major difference between Russian olive and the native vegetation it replaces is its high capacity to fix N_2 (>18 g m^{-2} y^{-1}; USDA 2010) through an association with *Actinomycetes* (Miller and Baker 1985). This capacity to fix N_2 is higher than most native plants (<9.5 to >18 g m^{-2} y^{-1}; USDA 2010) and soil cyanobacteria (0.1–0.5 g m^{-2} y^{-1}; Chapin and others 2002), and exceeds rates for all other common woody riparian vegetation in the region except for red alder (Follstad Shah and others 2010).

N_2 fixation by Russian olive and other closely related species have been associated with elevated soil and soil water N in riparian zones. Autumn olive (*Elaeagnus umbellata*), a tree closely related to Russian olive that is invading riparian areas in the midwestern and eastern USA, has also been linked to elevated soil water NO_3-N compared to plots dominated by grasses (Baer and others 2006). DeCant (2008) found that in a riparian zone along the Rio Grande soils in areas under mixed Russian olive and cottonwood (*Populus* sp.) had three times the available N compared to those under cottonwood alone, and though the mechanism was not clear the authors attribute the pattern to Russian olive. Where high N content of soils is associated with Russian olive, it could be caused by root exudation (Roggy and others 2004), or leaching and decomposition of Russian olive leaves (Simons and Seastedt 1999; Harner and others 2009). Follstad Shah and others (2010) found that Russian olive leaf fall explained 59% of variation in soil inorganic N concentrations over multiple years in riparian areas along the Rio Grande in New Mexico. Due to its riparian habit and potential for N fertilization, Russian olive may subsidize stream ecosystems with N, and thus, alter nutrient availability, demand, and retention in these systems. Here we present results of one of the first studies to investigate the potential in-stream effects of Russian olive invasion.

We investigated the effects of Russian olive on in-stream nutrient availability, demand, and retention to better understand the aquatic consequences of the presence of a non-native N_2-fixing riparian plant. We hypothesized that stream N concentrations would be higher in the presence of Russian olive, and we predicted that nutrient limitation of streambed biofilms would be shifted from N limitation typical in this region towards phosphorus (P) limitation or co-limitation by N and P. We also hypothesized that nutrient spiraling would be altered, and predicted lower in-stream demand (V_f) for N where Russian olive was abundant. To test these hypotheses, we conducted a field study whereby we compared background nutrient concentration, nutrient limitation of biofilms and nutrient uptake in stream reaches where riparian habitat was dominated by Russian olive (invaded) and reference reaches where Russian olive was absent. We conducted this study in the Intermountain West region of the USA where Russian olive invasion is widespread and may potentially have important impacts on stream ecosystems. Based on our findings, we also developed a conceptual model predicting effects of a generalized, non-native riparian N_2 fixer on stream ecosystem N dynamics.

METHODS

Study Design

Our study streams are located in the Intermountain West region of the USA, in southeastern Idaho near Pocatello (42.88°N 112.44°W, elevation 4549 ft) and in central Wyoming near Lander (42.82°N 108.74°W, elevation 5396 ft). This region has a semi-arid climate with annual mean precipitation of approximately 25 cm (Barton 2004; Swanson and others 2002). Mean air temperature in July is 22°C and −5°C in January. As is typical of watersheds where Russian olive invasion is most pervasive, land use in our study areas was dominated by diffuse agriculture, mainly as pasture land, and some sub-urban development. Streams in this region typically have nutrient concentrations with low N:P and primary N limitation of biofilms (Fisher 2006; Marcarelli and others 2009; Sanderson and others 2009). Russian olive may have large impacts on in-stream nutrient processing in this typically N-limited region because it is increasingly abundant (Friedman and others 2005) and can attain high rates of N_2 fixation (USDA 2010).

We compared background nutrient concentrations, nutrient limitation of biofilms, and nutrient uptake in paired reference (upstream) and invaded (downstream) reaches in the same streams. Reference sites were located in the nearest accessible reach upstream from the invaded site that had no Russian olive present in or upstream of the reach. The riparian vegetation at the reference sites was dominated by grasses and forbs but sometimes included patches of native woody vegetation such as sagebrush and small willows. The invaded reaches all had dense corridors of Russian olive along the stream which often formed a contiguous canopy on each bank. Selected streams had accessible reaches with invaded and reference conditions ranging from 3 to 8 km apart. Paired reaches were of the same geomorphic reach class and included similar channel unit forms (Frissell and others 1986). They also had similar discharge, channel morphometry (Table 1), and land use.

All measurements were made in reach pairs in 3 ID and 3 WY streams (6 streams and 12 reaches total, Table 1). We used two additional invaded-reference pairs in ID where, due to access and methodological limitations, we only evaluated nutrient limitation. These two streams had physical characteristics and Russian olive density within the range of conditions encompassed by the other streams included in the study. At the 12 reaches where all measurements were made, we measured density and total basal area (TBA) of Russian olive. For a representative section (50–100 m of stream length) of each of these reaches, we counted and measured the basal circumference of all Russian olive trees larger than 20 cm in circumference and within 10 m of the wetted edge of the stream. These size and location criteria excluded very few trees from being counted at the invaded reaches. All measurements were scaled to TBA of Russian olive per 100 m of stream length (Table 1).

Nutrient Limitation of Biofilms

We evaluated nutrient limitation of biofilms in eight paired upstream-reference and downstream-invaded reaches. Nutrient limitation status of streambed biofilm was evaluated during summer low flow (July–August) at all sites in 2009 using nutrient diffusing substrate (NDS) bioassays (Gibeau and Miller 1989). We positioned the NDS bioassays at the downstream end of all reaches that were also used in nutrient uptake measurement to minimize any possible interaction between the two. At one stream, Deep Creek, we placed NDS racks at four locations (200, 400, 900, and 1150 m from upstream edge of Russian olive presence) in the invaded reach, to test for a possible gradient of accumulating impact of Russian olive on biofilm nutrient limitation along the reach. These spatially distributed measurements were conducted during the summers of 2007 and 2008 and were not included in the analysis with other paired sites.

Each NDS bioassay included four nutrient treatments (control, NO_3-N-enriched at 0.5 mol/l,

Table 1. Site Characteristics of Streams in Which We Measured Nutrient Uptake in Summer 2009

Stream	Reach	Distance (km)	RO area (m^2/100 m)	Q (l/s)	W (m)	Z (m)	DON (mg/l)	NH_4-N (mg/l)	SE	NO_3-N (mg/l)	SE	PO_4-P (mg/l)	SE
Baldwin	Reference	4	0	131	3.21	0.27	0.124	0.006	0.0004	0.004	0.0001	0.010	0.0005
	Invaded		1.38	56	3.36	0.26	0.197	0.007	0.0003	0.008	0.002	0.006	0.0003
Squaw	Reference	4	0	192	2.51	0.29	0.186	0.020	0.0003	0.290	0.001	0.011	0.0008
	Invaded		3.69	264	3.43	0.29	0.288	0.015	0.0001	0.246	0.001	0.009	0.0004
Willow	Reference	3	0	115	1.97	0.22	0.130	0.021	0.0005	0.110	0.0008	0.012	0.0005
	Invaded		7.56	188	3.26	0.19	0.177	0.014	0.0005	0.130	0.0005	0.028	0.001
City	Reference	3	0	24	1.52	0.09	0.109	0.007	0.0002	0.066	0.0006	0.041	0.0004
	Invaded		1.28	24	1.56	0.08	0.143	0.005	0.0004	0.022	0.0005	0.055	0.0006
Deep	Reference	8	0	32	1.29	0.15	0.127	0.005	0.0004	0.020	0.0005	0.016	0.0004
	Invaded		3.02	12	5.60	0.18	0.121	0.005	0.0002	0.001	0.0002	0.002	0.0001
Battle	Reference	6	0	39	1.65	0.24	0.547	0.045	0.0003	0.845	0.005	0.047	0.003
	Invaded		0.64	90	2.39	0.20	NA	0.062	0.001	NA		NA	
Mean	Reference		0	89	2.03	0.21	0.135	0.017	0.006	0.098	0.05	0.018	0.006
	Invaded		2.93	106	3.27	0.20	0.185	0.018	0.009	0.081	0.05	0.020	0.01
t-test	(df) *t*		(5) 2.82	(5) 0.70	(5) 1.93	(5) 1.00	(4) 2.73	(5) 0.19		(4) 1.30		(4) 0.36	
	P value		**0.02**	0.52*	0.11*	0.36*	**0.03**	0.43		0.13		0.37	

*RO area is total basal area of Russian olive within 10 m of wetted edge in 100 m section of stream. Q is discharge, W is reach average wetted width, and Z is reach average water depth. Nutrient concentrations are background levels. NH_4-N, NO_3-N, and PO_4-P are average of all background samples and DON represents a single sample. SE is standard error. * Two-tailed P value used due to lack of hypothesized difference; all other P values are one-tailed test. Some background measurements for the invaded reach of Battle Creek were not made due to sampling failure (NA signifies not available). Both Battle Creek reaches were removed from the analysis if data for either reach are missing. Bold values designate statistically significant differences* phosphate (PO_4-P)-enriched at 0.2 mol/l and NO_3-N + PO_4-P -enriched). Six replicate vials, each containing a 2% agar solution amended with one of the nutrient treatments, were capped with porous porcelain disks and distributed haphazardly on an aluminum rack which was secured to the stream bottom for a 14 day incubation period. After incubation, vials were removed from the rack, placed in plastic bags, and returned to the laboratory on ice where they were frozen until analysis. The porous porcelain disks were separated from the vials and analyzed for chlorophyll-*a* (chl-*a*) and ash-free dry mass (AFDM) using standard methods (American Public Health Association 2005). Nutrient limitation effect was determined using the criteria of Tank and Dodds (2003). To compare the magnitude of response among treatments, we calculated the coefficient of response to each treatment, expressed as the log of (treatment/control) such that the value for the control is zero, a positive coefficient represents a stimulation effect of a treatment, and a negative coefficient represents a suppression effect (Tank and Dodds 2003).

Nutrient Spiraling

We measured nutrient uptake of NO_3-N, ammonium-N (NH_4-N) and PO_4-P using short-term nutrient releases in 6 paired reaches. Due to unforeseen difficulties in the field, we were unable to measure NO_3-N and PO_4-P uptake at both Battle Creek reaches as well as NO_3-N, PO_4-P and DON background concentrations at the Battle Creek invaded reach. Battle Creek was therefore eliminated from this analysis. To evaluate the effect of Russian olive invasion on stream nutrient demand, uptake velocities (V_f) of NO_3-N, NH_4-N, and PO_4-P were measured using short-term plateau additions (Tank and others 2006). We made these measurements at low flow conditions during July - August 2009. One day before uptake measurements, discharge was measured in a stream cross-section using either a Flo-mate (Hach/Marsh-McBirney, Frederick, MD, USA) or a Flow-Tracker Handheld (SonTek/YSI, San Diego, CA, USA) flow meter. The length of each experimental reach was set to achieve a 1 h water travel time, estimated using average velocity from the discharge estimate. Uptake measurements were made in paired reaches on subsequent days. In each reach, the NH_4-N addition was conducted first, then the reach was allowed to clear for at least 1 h before a combined NO_3-N and PO_4-P addition was conducted. A concentrated solution of NH_4Cl or $NaNO_3$ and KH_2PO_4 mixed with a conservative tracer, rhodamine WT, was pumped at a continuous rate into a well mixed section of stream until the tracer reached steady-state concentration throughout the reach (≥ 90 min). Target enrichment was 50% above background concentrations for all nutrients or 5 μg/l if background was less than 10 μg/l (Appendix 1 in Supplemental Materials). For rhodamine, target enrichment was 10 μg/l for all sites. Each experimental reach was divided into five sampling transects, where triplicate water samples were taken before and after enrichment. Water samples were immediately filtered (0.45 μm Millipore membrane) and placed on ice until analyzed for ammonium or frozen for later analysis. NH_4-N samples were analyzed using the fluorometric method (Holmes and others 1999; Taylor and others 2007) the same day that samples were collected. Both rhodamine and NH_4-N were measured using an Aquafluor handheld fluorometer (Turner Designs Company, Sunnyvale, CA, USA). NO_3-N and PO_4-P samples were analyzed at Utah State University using an Astoria-Pacific auto analyzer (Astoria-Pacific, Clackamas, Oregon, USA). NO_3-N was measured using the cadmium reduction technique (Nydahl 1976) and PO_4-P was measured using the ascorbic acid reduction colorimetric method (APHA 2005). At each reach, total dissolved nitrogen (TDN) was also analyzed for a single background sample, as NO_3-N following a potassium persulfate digestion (Valderama 1981). We inferred DON concentration by subtracting NO_3-N and NH_4-N concentrations from TDN concentrations. After nutrient additions, reach length, transect locations, water depth, and wetted width were measured for use in uptake calculations. We made a minimum of ten wetted width measurements at haphazard locations along each reach and at each of these, ten water depth measurements were made across the channel.

We used data collected during the nutrient uptake measurements to calculate mean background concentration and load of NO_3-N, NH_4-N, and PO_4-P. We used the mean of all background samples ($n = 15$) taken prior to uptake measurements at each reach to determine the reach concentration of NO_3-N, NH_4-N, and PO_4-P. We also calculated the daily loads of these nutrients at each reach for the day we measured nutrient uptake by multiplying the reach background concentration by the discharge and scaling to a 24 h period.

Data Analysis

First, we tested all of our response variables for a geographic area (ID vs. WY) effect using a two-way ANOVA (factors = treatment and region). We found no significant treatment by region interaction (all

$P \geq 0.1$) and therefore did not consider region as a factor in our subsequent analyses. To determine nutrient limitation status in each individual reach, we used a two-factor ANOVA (factors N and P) to test for a significant effect of N enrichment or P enrichment on chl-*a* and AFDM (Tank and Dodds 2003) with $P \leq 0.05$ as criteria to determine significance. Both the chl-*a* and AFDM values were log transformed prior to analysis. To determine if there was a Russian olive effect on nutrient limitation, we first used a full factorial three-factor ANOVA (factors N, P, and Russian olive) to determine if there were interactions among N, P, and Russian olive presence on chl-*a* and AFDM responses across all reaches. Because this three-way ANOVA did not show any significant Russian olive effects or interactions, we subsequently used a two-factor ANOVA (factors N and P) run separately for reference versus Russian olive reaches to determine if Russian olive presence or absence caused different nutrient limitation responses of chl-*a* and AFDM. In the case of the invaded reach at Deep Creek, the effect of distance downstream on the strength of biofilm response to NDS treatments was tested using a two-way ANOVA (factors = nutrient treatment and distance downstream) using chl-*a* as the dependent variable. We evaluated the possible influence of background NO_3-N and NH_4-N on differences observed in V_f between paired invaded and reference reaches (invaded V_f − reference V_f) using linear regression. For this regression analysis, we used the N concentration at the reference site because we took it to represent the ambient (pre-invasion) condition for each stream. We used paired *t*-tests to assess differences in background nutrient concentrations, spiraling measures and NDS coefficient of response between reference and invaded reaches. In these cases, because of small sample size and the potential for small differences in these measures to be biologically important, we used a significance criteria of $P = 0.1$. All analyses were conducted using SAS (SAS Institute Inc., Cary NC, version 9.1).

Results

Background Nutrient Concentrations

We observed a trend of higher TDN concentrations in reaches invaded by Russian olive (0.275 mg l^{-1}) compared to their paired reference reaches (0.245 mg l^{-1}). Though this difference was not statistically significant (paired *t*-test $t_4 = 1.48$, $P = 0.11$), it was driven by a significant difference in DON between invaded and reference reaches. Reaches invaded by Russian olive had, on average, 0.05 mg l^{-1} more DON than their paired reference reach (Table 1). Some reaches invaded by Russian olive also had higher dissolved inorganic N (DIN = NH_4-N + NO_3-N) than their paired reference reach; however, this pattern was not consistent (Table 1). In contrast to DON, there were no significant differences in average background concentrations of NO_3-N, NH_4-N, or PO_4-P between the reference and Russian olive invaded reaches (Table 1). Though differences in concentrations were small, the difference in mean load indicates that Russian olive reaches export on average 334 g day^{-1} more NO_3-N and 51 g day^{-1} more NH_4-N than their paired reference reaches.

Nutrient Limitation of Biofilms

Significant limitation of either chl-*a* or AFDM was rare in our bioassay experiments when examined at each reach individually (Appendix 1 in Supplemental Material). However, based on the average coefficient of response, chl-*a* response to N addition was negligible at sites invaded by Russian olive (Figure 1). Chl-*a* at the reference sites exhibited a strong N stimulation effect (mean coefficient = 0.11) whereas it was weakly suppressed by N addition at sites invaded by Russian olive (mean coefficient = −0.003; Figure 1). In concurrence with these differences in chl-*a* coefficients of response, N enrichment had a significant stimulation effect on chl-*a* at reference reaches ($F_{3,183} = 4.92$, $P = 0.03$) but not at Russian olive invaded reaches ($F_{3,165} = 0.16$, $P = 0.57$). However, we found no significant interaction between N and Russian olive

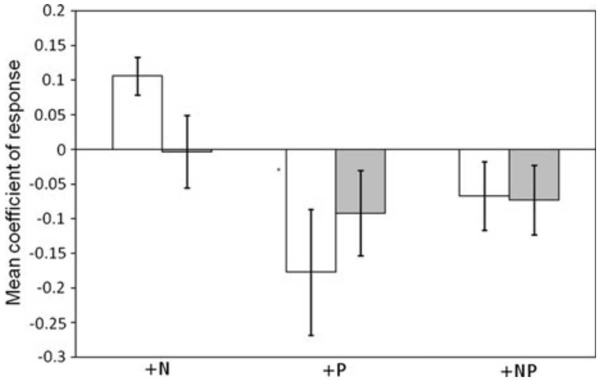

Figure 1. Average chlorophyll-*a* coefficients of response (log [treatment/control]) for three nutrient diffusing substrate bioassay treatments (+N, +P, and +NP) in reference reaches ($n = 8$; *white bars*) and those invaded by Russian olive ($n = 8$; *gray bars*). *Error bars* represent ±1SE.

when tested together for all reaches ($F_{7,359} = 0.48$, $P = 0.49$). In contrast to chl-*a*, AFDM response to N enrichment was similar in reference and invaded reaches ($F_{3,185} = 34.44$, $P < 0.001$ and $F_{3,167} = 37.44$, $P < 0.001$). AFDM response coefficients for the N, P, and NP treatments were not significantly different in reference and invaded reaches.

When we evaluated biofilm nutrient limitation at multiple locations along the invaded reach of Deep Creek, the response coefficient of chl-*a* for the P treatments alone and N + P in combination increased 13- and 4-fold, respectively, with distance downstream (two-way ANOVA had significant nutrient treatment × distance interaction $F_{15,75} = 2.93$, $P = 0.005$; Figure 2), and the greatest response coefficients for P and N + P treatments were observed 900 and 1100 m from the upstream edge of Russian olive occurrence (Figure 2).

Nutrient Spiraling

Contrary to our hypothesis, uptake velocities of NH_4-N and NO_3-N were significantly higher in invaded reaches than in associated reference reaches (Table 2). Mean NH_4-N V_f was 0.68 mm min^{-1} faster in Russian olive invaded compared to reference reaches. Mean NO_3-N V_f was 1.33 mm min^{-1} faster in Russian olive invaded reaches, and was almost double the velocity for reference reaches. We observed the opposite pattern in only one set of paired reaches (Battle Creek), which had by far the highest background concentrations of DIN among all streams sampled (Table 1). Though there were significant differences in V_f, mean per area uptake (U) of NH_4-N was almost identical at Russian olive invaded reaches and reference reaches (0.057 and 0.058 mg m^{-2} min^{-1}; Appendix 1 in Supplemental Material). Mean U for NO_3-N was higher in Russian olive invaded reaches than in paired reference reaches, though not significantly so (0.172 and 0.116 mg m^{-2} min^{-1}, respectively; Appendix 1 in Supplemental Material). Uptake length (S_w) for both NH_4-N and NO_3-N were not significantly different but tended to be shorter in Russian olive reaches than the reference reaches, indicating that the invaded reaches may be more retentive of these nutrients (Appendix 1). We observed a negative relationship between the difference in V_f between reaches (invaded V_f − reference V_f) and the background concentration of N at the reference sites (Figure 3). This linear decline in V_f difference was significant for NO_3-N ($r^2 = 0.86$, $F_{1,4} = 18.57$, $P = 0.02$) but not for NH_4-N ($r^2 = 0.38$, $F_{1,5} = 2.44$, $P = 0.19$). PO_4-P uptake velocities did not differ in any consistent manner between invaded and reference reaches (Table 2).

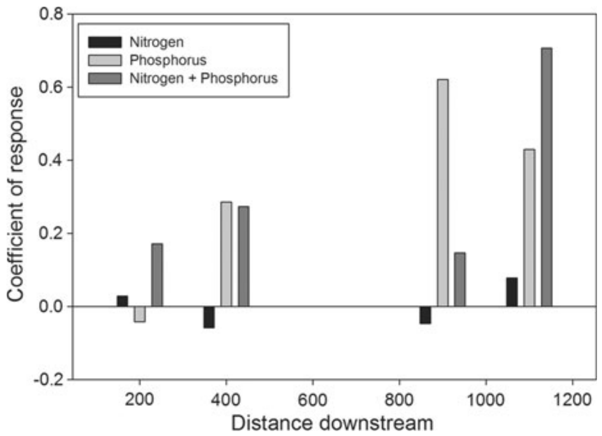

Figure 2. Coefficient of response (log [treatment/control]) in relation to distance downstream from spring (upstream end of the invasion) at the Deep Creek invaded site. Control values are represented by the zero line. Data are from 2008 nutrient diffusing substrate experiment except at 900 m which are from 2007.

DISCUSSION

Our results support the hypothesis that the presence of Russian olive is associated with changes in stream water N concentrations, nutrient limitation of biofilms and nutrient uptake. Though nutrient uptake was different in the presence of abundant Russian olive, we observed a pattern opposite of that which we had hypothesized. Nonetheless, these findings support the broader hypothesis that N_2 fixation by Russian olive in riparian zones alters in-stream nutrient processing. If the effect we observed with Russian olive is common for other non-native N_2 fixers, the impact of biological N_2 fixation by these species, particularly when added to other anthropogenic N sources, may have a significant impact on water quality and nutrient processing where these invasions are occurring.

Russian olive decreased the degree of N limitation in invaded streams, and in some cases even changed the primary limiting nutrient from N to P. In the absence of Russian olive, undisturbed streams in our study region are typically N limited (Tank and Dodds 2003; Fisher 2006; Marcarelli and others 2009). In most of our reference reaches, neither chl-*a* nor AFDM were significantly N limited, but when averaged across sites, mean chl-*a* and AFDM coefficients of response showed a strong stimulation effect to the N addition treatment, suggesting some degree of N limitation. For reaches invaded by Russian olive, the average response of chl-*a* did not exhibit any N stimulation effects, which suggests that the autotrophic component of

Table 2. Uptake Velocities of NH_4-N, NO_3-N, and PO_4-P

Stream	Reach	NH_4-N V_f	NO_3-N V_f	PO_4-P V_f
Baldwin	Reference	5.81	3.40	5.38
	Invaded	6.04	5.75	4.05
Squaw	Reference	5.07	1.70	NSU
	Invaded	6.54	1.74	NSU
Willow	Reference	3.04	0.13	1.69
	Invaded	4.06	1.62	9.32
City	Reference	1.02	0.65	0.24
	Invaded	2.56	NSU	0.37
Deep 09	Reference	3.35	0.81	0.69
	Invaded	4.01	3.69	2.75
Deep 08	Reference	NM	0.14	NM
	Invaded	NM	0.05	NM
Battle	Reference	2.74	NM	NM
	Invaded	1.91	NM	NM
Mean	Reference	3.51	1.24	2.00
	Invaded	4.19	2.57	4.12
t-test	(df)T	(5)1.88	(4)2.23	(3)1.08
	P value	**0.06**	**0.04**	0.18

V_f is in mm/min. NSU is no significant uptake (hence, V_f calculation not possible), NM is not measured. NO_3-N means exclude City Creek due to NSU at invaded reach. Some background measurements for the invaded reach of Battle Creek were not made due to sampling failure. Both Battle Creek reaches were removed from the analysis if data for either reach were missing.

Bold values designate statistically significant differences

the biofilm was released from N limitation in these stream reaches. These results further support the hypothesis that in reaches invaded by Russian olive nutrient limitation of biofilms may be shifted from N limitation towards co-limitation or P limitation. At Deep Creek in 2007 and 2008, we observed significant P limitation in the Russian olive invaded reach (Figure 2; Appendix 1). Furthermore, the significant increase in chl-*a* response coefficient to P and N + P treatments along the invaded reach of Deep Creek suggests that concentrations of N from Russian olive may increase as one moves downstream from the upstream extent of Russian olive distribution.

As we expected, we observed a trend of elevated TDN in reaches with Russian compared to their reference reaches; however, this increase was driven by increased DON, not DIN. The mechanism causing the increase in DON is uncertain. Though we did not explicitly measure in-stream N_2 fixation as a potential N source confounding our results, it was likely a small input compared to Russian olive N_2 fixation. For example, annual inputs of N via in-stream N_2 fixation in a desert stream with very large populations of cyanobacteria were 8–12.5 g m^{-2} y^{-1} (Grimm and Petrone 1997), which is 44–69% of Russian olive N_2 fixation (18 g m^{-2} y^{-1}; USDA 2010). Although the literature reporting N_2-fixation rates in streams is very limited, is it probable that annual N_2-fixation rates in most streams are 1–2 orders of magnitude lower than this, as in-stream N_2 fixation is often limited by environmental conditions and/or suppressed by high availability of DIN (Marcarelli and others 2008). It is unknown what proportion or in what form N_2 fixed by Russian olive or in-stream N_2 fixers may ultimately be added to stream water. There is evidence that Russian olive has a poor ability to retain N and that it may contribute large amounts of the N it fixes to soils and neighboring plants via root exudates which are likely dominated by organic N (Roggy and others 2004). Furthermore, 69% of N contained in Russian olive leaf litter is water soluble N (Roggy and others 2004). Combined, root exudates and litter leaching from Russian olive could be direct sources of organic N to streams assuming transport is conservative.

DON is typically the dominant form of N present in stream water in undisturbed watersheds (Perakis and Hedin 2002), and in streams included in this study, though most of these watersheds were at least moderately impacted by anthropogenic land use. Most streams in this study had low background DIN concentrations (three pairs mean NH_4-N $<$ 10 µg/l and four pairs mean NO_3-N $\leq$ 20 µg/l), and DON was the dominant form of N in these streams. It may be that the N subsidy from Russian olive is delivered to streams as DON. Leaf litter and

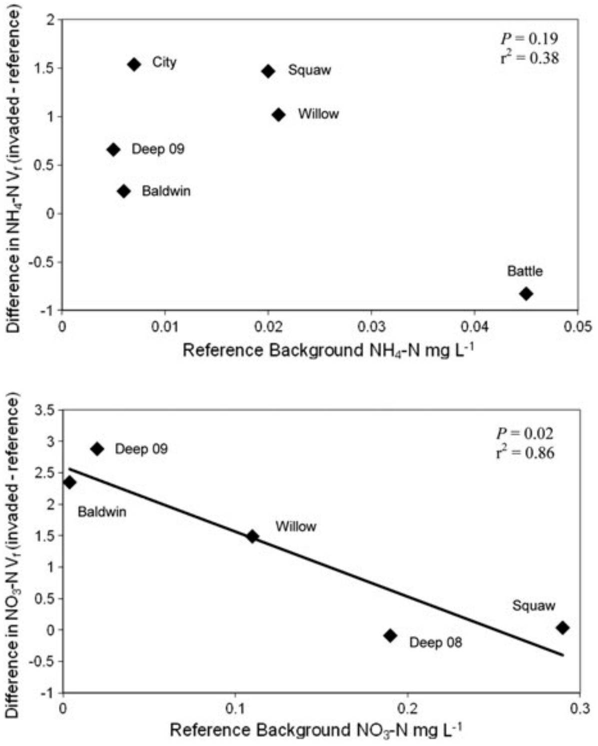

Figure 3. Uptake velocity (V_f) difference (Invaded V_f − Reference V_f) as a function of background concentration at the reference site for NH_4-N (*top*) and NO_3-N (*bottom*). In *bottom*, uptake measurements at Deep Creek from summer 2008 as well as 2009 are included and City Creek was omitted because significant uptake was not detected at the invaded reach, which precluded calculation of V_f.

root leaching from Russian olive may add carbon to riparian soils and contribute to DON loss from soils to streams (Brookshire and others 2007; Harner and others 2009). In addition, Russian olive leaf litter has a low carbon (C) to N ratio (Royer and others 1999; Harner and others 2009; Follstad Shah and others 2010); thus, N-rich litter inputs may alter soil stoichiometry, which can also lead to loss of DON from riparian soils and increased input to streams (Brookshire and others 2007). Both of these mechanisms may be acting so that invaded riparian zones deliver more DON to streams than reference sites with native vegetation that has higher C:N ratio. Neff and others (2003) suggest that DON leaching from terrestrial systems represents a significant leak of N because plants and microbes cannot prevent these losses even if N demand is high. Some DON may also be produced in-stream due to biological processing of DIN by stream biota (Brookshire and others 2005). Hall and others (2009) suggest that export as DON is a probable ultimate fate for assimilated NO_3-N in streams. We suspect that the elevated DON we observed at sites invaded by Russian olive is most likely due to a combination of input from the terrestrial system via Russian olive root exudates and litter leaching and increased in-stream processing and assimilation of DIN as indicated by our spiraling measures.

The increase in biological demand measured as V_f for DIN in reaches with Russian olive may be due to coupled C and N inputs from this riparian invader. Denitrification in riparian soils and at the soil-stream boundary is often limited by the availability of oxidizable C and is significantly increased when C is added either by vegetation (Schade and others 2001) or experimentally (Hedin and others 1998). Russian olive may increase C availability for soil and stream heterotrophs by the same pathways by which it is provides the N subsidy, via leaf litter and root exudates. Allochthonous litter input is likely much greater at reaches invaded by Russian olive compared to the reference reaches. For example, at Deep Creek, the annual allochthonous litter input was 300.5 g AFDM m^{-2} y^{-1} (SE 41.2) at the invaded reach compared to only 21.6 g AFDM m^{-2} y^{-1} (SE 8.8) at the reference site (Mineau 2010). On or in riparian soils, Russian olive litter reportedly decomposes faster than that of native cottonwood (Simons and Seastedt 1999; Harner and others 2009). If this were generally the case, it might be a mechanism for increases in total input or input rate of DOC and DON to riparian soils and adjacent streams. However, the fate of Russian olive litter delivered into streams is uncertain. Results of additional studies at Deep Creek (Mineau 2010) suggest this material may decompose more slowly than litter from native trees, but Royer and others (1999) showed this may depend on species and environmental context. Because stream water DON and DOC concentrations are typically coupled (Goodale and others 2000; Perakis and Hedin 2002) it is reasonable to hypothesize that the increased DON concentrations we observed in stream water were accompanied by proportional increases in DOC. Bernhardt and Likens (2002) found that DOC addition in a New Hampshire stream resulted in increased uptake of NH_4-N and NO_3-N; however, this increase was due to assimilative bacterial uptake and not denitrification. Johnson and others (2009) found that NH_4-N uptake was significantly higher with experimental release of labile DOC, indicating that NH_4-N demand is limited by labile DOC availability. Increased uptake of DIN in reaches invaded by Russian olive with low background DIN is likely caused by a combination of denitrification, assimilatory uptake by N-limited autotrophs, and assimilatory uptake by N- and C-limited heterotrophs. Both denitrification and heterotrophic uptake could be stimulated by alleviation of C limitation, whereas autotrophic uptake would not be expected to increase due to increased C supply. Autotrophic uptake may have been stimulated due to increased algal growth caused by the reduction of N limitation. However, without knowledge of which pathway is dominant, it is impossible to determine if DIN is temporarily retained and transformed (assimilation) or permanently removed (denitrification).

Streams with low background DIN may have the capacity for increased biological demand that might reduce the effects of any N subsidy derived from Russian olive through increased assimilation, and subsequently N export may not be affected. We observed a significant increase in biological demand for N in all reaches invaded by Russian olive except for Battle Creek. Correspondingly, and in contrast to the other streams, Battle Creek had exceptionally high background DIN. We also observed a negative relationship between the V_f difference between reaches (invaded V_f − reference V_f) and background NO_3-N concentration. As suggested by the differences we observed for Deep Creek across two years, the status of a stream may shift along this line (for example, with changes in background NO_3-N); however, the relationship deserves investigation across a broader spatio-temporal context to evaluate its generality. Under low background DIN conditions, it may be that an N subsidy from Russian olive may cause increases in biofilm accrual and subsequent N demand and assimilation. However, such increased demand may not be possible under conditions of elevated background DIN such as we observed in Battle Creek. Like many agricultural streams, Battle Creek is also affected by high suspended sediment loads, which may constrain the capacity of autotrophic stream biota to assimilate additional N. Also, if streams receiving additional N from Russian olive N_2 fixation are P limited, increased assimilation of N to moderate N export may not be possible (see Costello and Lamberti 2008).

Because it was introduced for use as shelterbelt and ornamental planting, Russian olive is common in agricultural and urban–suburban areas, where it may be one among many sources of anthropogenic N. The N subsidy from Russian olive to riparian zones, in addition to existing anthropogenic N loading, may result in conditions approaching N saturation. N saturation can occur at the watershed scale (Stoddard 1994) or at smaller scales such as a stream reach due to localized N inputs. In systems already stressed, additional N loading may contribute to nutrient enrichment and lead to increased export from reaches invaded by Russian olive. For instance, decreased demand and processing of NH_4 in the Battle Creek reach invaded by Russian olive may be due to conditions that exceed biotic nutrient processing capacity, or nutrient saturation (Bernot and Dodds 2005; Earl and others 2006). As a result, additional DON contributed from Russian olive may be exported from this and other highly impacted watersheds to downstream rivers, lakes, and reservoirs, which might exacerbate problems of eutrophication and oxygen deficiencies in those systems. However, actual measurements of DIN and DON uptake across multiple seasons and a larger range of N background are required to actually verify that Russian olive is contributing to saturation conditions.

To generalize our results, we developed a conceptual model regarding the effects of N_2 fixation, by Russian olive and other riparian invasive species, on stream N pools and DIN retention. Contrary to most anthropogenic impacts to N loading in rivers, Russian olive appears to increase DON and not DIN, which alters the proportional importance of DON in the invaded system. Because of the increased stream water DON concentrations we observed in the presence of Russian olive, we hypothesized that invasion by a similar riparian N_2 fixer would increase the proportion of the TDN pool in streams that is DON (Figure 4A). This would cause DON to remain the dominant form of N (DON:NO_3-N > 1) at higher than expected stream water DIN concentrations (Figure 4A). DON:NO_3-N would also be higher overall compared to streams without a high abundance of riparian N_2 fixers (Figure 4A). It is possible that Russian olive and other N_2 fixers would reduce their N_2 fixation if soil N becomes more abundant because of their high rates of N_2 fixation over time, which could diminish the N subsidy to streams at high riparian soil DIN concentrations (Allos and Bartholomew 1959). However, riparian vegetation may remain N limited and be associated with active N_2 fixation even if N concentrations in stream water are high, if the N in stream water is due to inputs from elsewhere in the watershed. We further hypothesize that DIN demand and retention as V_f at low background DIN would be increased by C inputs from the invasive tree, which could increase denitrification, assimilation, or both (Figure 4B). However, at higher background DIN levels, the total N load, including DON from Russian olive, may cause N saturation and decrease efficiency of DIN uptake (Bernot and

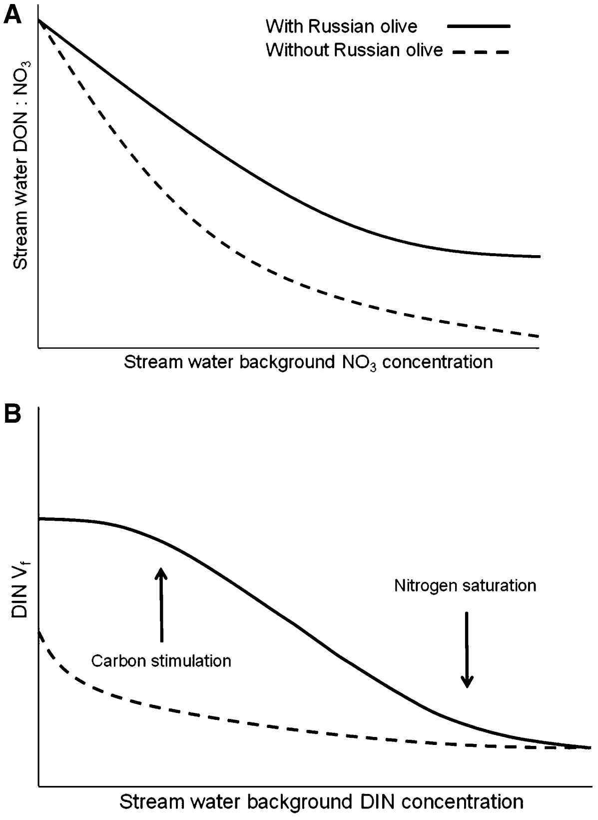

Figure 4. Hypothesized effects of Russian olive or other non-native, riparian N_2 fixer on stream N pools and retention. Stream water DON:NO_3-N is higher with Russian olive and DON remains the dominant form of N even at high DIN background concentration (**A**). **B** shows that in the presence of Russian olive, DIN demand and retention as V_f increases at low background DIN due to carbon stimulation (C inputs from the invasive tree, which could increase denitrification, assimilation, or both) and decreases at higher background DIN due to N saturation.

Dodds 2005; Earl and others 2006; Figure 4B). This decreased uptake efficiency could, in turn, increase N export from invaded watersheds. We observed sustained elevated DIN V_f across a range of low background DIN, which leads us to conclude that the relationship between DIN V_f and background concentration, in the presence of riparian N_2 fixers, is sigmoidal instead of negative exponential (Figure 4B). Further research is needed to test these hypotheses.

N_2 fixation from agricultural crops and invasive plants represents a very large input of reactive N to ecosystems and may be altering stream nutrient processing on a large scale. N_2 fixation in crop land has been recognized as a major source of reactive N in global (Galloway and others 2004) and regional (Howarth and others 1996) N budgets. Boyer and others (2002) found that N_2 fixation by crops represented 24% of N sources to the combined area of 16 catchments in the Northeastern USA. In addition to N_2 fixation from crops, anthropogenic introduction of N_2-fixing invasive species to new environments could also be a large source of N. Invasive species with a medium to high capacity to fix N_2 are common and widespread, and include Russian olive in the western USA (USDA 2010), Autumn olive in the mid-western and eastern USA (USDA 2010), kudzu in the southeastern USA (Forseth and Innis 2004), *Myrica faya* in Hawaii (Vitousek and Walker 1989), acacia in the Mediterranean (Marchante and others 2003) and Africa (Stock and others 1995), and *Mimosa pigra* in Australia (Lonsdale 1993). Many of these invasions are occurring in areas where stream biofilms are typically P limited, and additional riparian N inputs may be predominantly exported from these systems with little effect on in-stream processing. Considering the large number and wide range of distribution of N_2-fixing invasive plants, as well as our findings regarding the apparent effect of Russian olive invasion on stream N processing in N-limited streams, these invasions may have an important effect on either in-stream nutrient processing and/or N export at the reach scale. Alteration of these processes at the reach scale in streams and rivers has important implications for the management of water quality in rivers.

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