



Reduced Impacts or A Longer Lag Phase? *Tamarix* in the Northwestern U.S.A.

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Abstract *Tamarix* spp. (tamarisk) have caused ecological impacts in the southwestern United States; however, such impacts have not been extensively studied in the Northwest where tamarisk is a relatively new invader. Here we present the results of soil, arbuscular mycorrhizal fungi, and vegetation studies from tamarisk-occupied and unoccupied areas on the dammed Bighorn River, Fort Peck Reservoir, and the free flowing Yellowstone River, in Montana. Soil sample results indicated that at Fort Peck Reservoir soil salinity was twice as high at occupied sites compared to unoccupied ones, and at the Bighorn River occupied sites nitrate, phosphorus and potassium were 2.2, 4, and 1.9 times higher, respectively, than at unoccupied sites. No soil differences were observed on the Yellowstone River. Mycorrhizal infectivity potential was high in both occupied and unoccupied soils, with a slight reduction (from 73% to 65% colonization) in tamarisk occupied soils. These impacts were statistically but not ecologically significant and did not extend to other metrics of impact such as richness, Simpson's diversity or composition of plant communities. Our results indicate that either tamarisk has minimal impacts in the northwest, or it is still in a lag phase.

Keywords Community · Diversity · Invasive plant · Monitoring · Mycorrhizae · Saltcedar

Introduction

Many newly introduced non-native plant species require a lag phase before they become invasive (Hobbs and Humphries

1995) and begin to impact local ecosystems. It has been hypothesized that this lag phase may represent the time required for species to evolve to flourish in their new habitat (Ellstrand and Schierenbeck 2000, Hellmann et al. 2008). However, the existence or duration of the lag phase could also be related to the degree of climate and environmental overlap between the original and the new habitat. Longer lag times would be expected for populations at the extremes of a species range or climate envelope. A changing climate, if it provides favorable growth conditions for an invasive species, may serve to reduce the time of the lag phase, accelerate invasions and increase the ecological impact (Hellmann et al. 2008). This research focused on the invasive plant *Tamarix* spp. (*Tamarix* or saltcedar, hereafter *Tamarix*) and investigated its impacts at the edge of its range in North America where it is a relatively new invader, potentially still in a lag phase and limited by climate.

Tamarix, introduced from Europe and Asia in the early 1800 s, has been implicated in considerable geomorphological and ecological change throughout much of the western and southwestern United States (U.S.) (Howe and Knopf 1991, Everitt 1998, Friedman et al. 2005). In particular, *T. chinensis*, *T. ramosissima*, and their hybrids (Gaskin and Schaal 2002) have been able to readily invade and establish along rivers where natural flow regimes have been altered (Stromberg et al. 2007). Direct impacts of *Tamarix* include decreased erosion rates and channel narrowing (Blackburn et al. 1982), altered plant communities through the salinization of soil (Busch and Smith 1995, Bagstad et al. 2006), and increased water use (Sala et al. 1996, Devitt et al. 1998). However, *Tamarix* water use has been shown to be less than previously reported and similar to other riparian woody species (Allen et al. 2009). Indirect effects of *Tamarix* invasion include limiting recruitment of native *Populus* and *Salix* species through increased salinity (Shafroth et al. 1995) and suppression of arbuscular mycorrhizal fungal (AMF) communities (Beauchamp et al. 2005). Finally,

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Tamarix has been reported to have negative (Brand et al. 2008), neutral (Brand and Noon 2011), and positive (van Riper et al. 2008) effects on avian diversity and richness.

Tamarix has been present in the northern region of the U.S. since at least 1960 (Swenson et al. 1982), but little is known about its impacts as most research has been conducted in the southwestern U.S. A study conducted in Montana by Lesica and Miles (2001) indicated that while *Tamarix* commonly formed thickets on open terraces along the Bighorn, Powder, and Yellowstone rivers, it was less dense below *Populus deltoides* canopies. *Tamarix* has been found to be abundant at Fort Peck Reservoir in northeast Montana (Pearce and Smith 2003, Lesica and Miles 2004), where its density and survival is closely related to reservoir level, with full pool levels causing *Tamarix* mortality and drawdown periods being times of recruitment (Lesica and Miles 2004, Lehnhoff et al. 2011).

The purpose of our research was to assess the ecological impacts of *Tamarix* in Montana, an area in which there has been relatively little research compared to the southwestern U.S. Specifically, our goals were to evaluate the impacts of *Tamarix* on (1) soil properties, (2) arbuscular mycorrhizal fungi (AMF), and (3) riparian plant communities at three sites in Montana, including a regulated river, a reservoir, and an unregulated river.

Methods

Site Descriptions

Research was conducted at three water bodies (*sites*) in Montana with a history of *Tamarix* invasion—Fort Peck Reservoir (hereafter Fort Peck) in the Charles M. Russell National Wildlife Refuge and the Bighorn and Yellowstone Rivers (Fig. 1). The climate of the region is continental and semi-arid (Table 1). Fort Peck, located in northeast Montana, is a 215 km (134 mile) long impoundment of the Missouri River, created in 1940 with the construction of the Fort Peck Dam. The Bighorn River flows from its headwaters in the Bighorn and Absaroka mountains of Wyoming through the Bighorn Canyon northeast into Montana. This river is regulated by the Yellowtail Dam, which was constructed at the north end of Bighorn Canyon in 1965, and flows below the dam for approximately 135 km (84 miles) to the confluence of the Yellowstone River. The Yellowstone River, unregulated for its entire distance, flows north out of Yellowstone National Park into Montana and then east-northeast through eastern Montana. Five study locations (hereafter *sub-sites*) were selected at Fort Peck (Bone Trail, Dam, Dry Arm, Sand Arroyo, and West End), three on the Bighorn River (Arapoosh, General Custer, and Grant Marsh), and three on the Yellowstone River (Bundy Bridge, Duck Creek Bridge,

and Isaac Homestead). Sub-sites were selected based on *Tamarix* abundance as well as availability and ease of access. At four of the sub-sites, *Tamarix* had been treated by herbicide and in some cases removed by the responsible land management agencies (Table 2). At each sub-site, sampling locations (hereafter *microsites*) were selected from *Tamarix*-occupied and adjacent unoccupied areas (i.e., areas where *Tamarix* was either present, formerly present but treated via herbicide (a subset of the *Tamarix* present sites), or absent (i.e., never present). The intent of the study was to pair each site where *Tamarix* was present with an adjacent site treated with herbicide and with sites where *Tamarix* was not present; however, site conditions (high water) and lack of access to private lands precluded our being able to access all of the paired herbicide treated sites.

Soil Samples

Soil samples were collected between June and July 2009 at each microsite for laboratory analysis of physical and chemical properties. Three evenly spaced locations were sampled along each transect, with soil samples collected from 0–2 cm and 2–5 cm depth at each location. A sample consisted of 7 aliquots, collected from a 0.5 by 0.5 m area, which were homogenized and composited to comprise the sample. Soil samples were dried, sieved (No. 10 sieve), and submitted to the Analytical Sciences Laboratory at the University of Idaho where they were analyzed for pH, electrical conductivity (EC), and concentrations of calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}) and sodium (Na^+). Sodium adsorption ratio (SAR) was calculated as the Na^+ concentration divided by the square root of one half of the sum of the Ca^{2+} and Mg^{2+} concentrations.

Soil was also collected from all sub-sites, except the Bone Trail and West End sites at Fort Peck during May 2010 for use in AMF experiments. Three intact plugs of soil were collected at random locations in each *Tamarix*-occupied and unoccupied microsite. The plugs were then placed in 10 cm square by 13 cm deep pots and transported to the Montana State University Plant Growth Center (PGC). A final set of soil samples also collected May 2010 was analyzed for concentrations of nitrate-nitrogen (N), Olsen phosphorus (P), potassium (K^+) and percent organic matter (OM) by Agvise Laboratories. These samples were composites from three different randomly placed aliquots of 0 to 5 cm deep collected at each microsite

Arbuscular Mycorrhizal Fungi (AMF) Infectivity Potential

The relative density of AMF propagules is estimated by the mycorrhizal infectivity potential (MIP) of a soil (Giovannetti and Mosse 1980). The potted soil collected from the microsites was placed in the PGC with conditions of ambient light

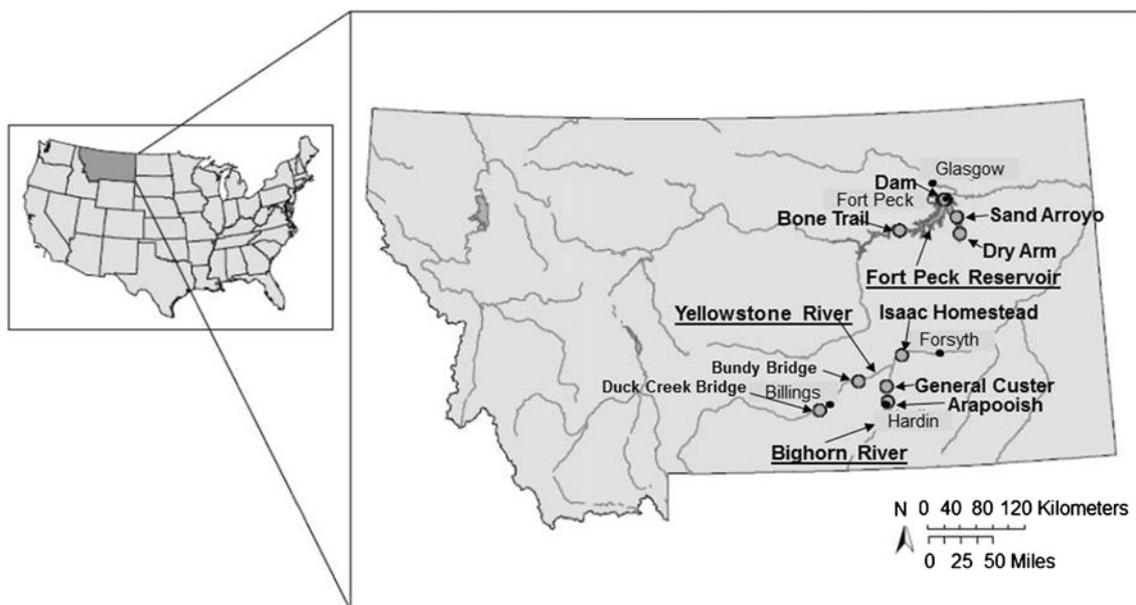


Fig. 1 Soil and plant community sampling locations on the Fort Peck Reservoir, Bighorn River (regulated), and Yellowstone River (unregulated) sites

and temperatures of 21°C (16 h) and 16.5°C (8 h). Each pot was seeded with approximately 20 seeds of Sudan grass (*Sorghum sudanese*), a species known to readily form mycorrhizal partnerships. After approximately 7 weeks of growth, plants were harvested, and the roots were cleared and stained for microscopic quantification of AM colonization levels (McGonigle et al. 1990).

Vegetation Community Analysis

Transects were sampled in June and July 2009 to characterize vegetation at each sub-site (Table 2), except Fort Peck Dry Arm and Bighorn River Grant Marsh. Plant occurrence was recorded at 0.1 m intervals as point and line intercept data along 50 m transects. At Fort Peck transects were sampled at four of the five sub-sites, totaling three transects in areas treated by herbicide (2007), two in untreated *Tamarix*, and four in unoccupied microsites. At the Bighorn River, transects were sampled at two occupied but untreated and two unoccupied sites. At the Yellowstone River, one, two and three transects

were sampled at herbicide-treated (2009), untreated, and unoccupied sites, respectively. From the transect data, the point intercept method was used to calculate percent cover, or abundance, for herbaceous species, while the line intercept method was used for trees and shrubs (Elzinga et al. 1998).

Data Analysis

Soil Samples

Data were analyzed at the overall site level (i.e., Fort Peck, Bighorn and Yellowstone) with sub-sites treated as replicates. All soil data except pH were log transformed for normality and analyzed by two factor analysis of variance (ANOVA) using site and *Tamarix* presence (binary variable) as independent factors. Differences in soil parameters between occupied and unoccupied microsites were also compared to the time since *Tamarix* establishment at the sites as determined by Lehnhoff et al. (2011) (Table 2). All data

Table 1 Temperature and precipitation of eastern Montana

Location	January mean daily temperature C ^a	July mean daily temperature C	Annual precipitation cm	April – October precipitation (% of Annual)
Glasgow, MT ^b	-11.8	21.2	28.5	84
Billings, MT ^b	-4.4	22.2	37.5	73

^a All data are 30-year averages from the Western Regional Climate Center (<http://www.wrcc.dri.edu/summary/Climsmem.html>)

^b Glasgow, MT is just north of Fort Peck Reservoir. Billings, MT is near the Yellowstone and Bighorn Rivers

Table 2 Sub-site description and sampling summary

Site	Sub-site (number of microsites (n) in parentheses)	<i>Tamarix</i> Stand Age (years) (Lehnhoff et al. 2011)	Microsite Invasion Status	Vegetation Analysis Transects	Soil Samples for Laboratory Analysis (collected 2009)	Soil samples for N, P, K & OM Analysis (collected 2010)
Fort Peck Reservoir	Bone Trail (2)	33	<i>Tamarix</i> treated via cut stump	Yes	Yes	No
			Untreated <i>Tamarix</i>	Yes	Yes	No
			Not occupied	Yes	Yes	No
	Dam (2)	9	<i>Tamarix</i> treated via foliar herb.	Yes	Yes	Yes
			Not occupied	Yes	Yes	Yes
	Dry Arm (2)	25	Untreated <i>Tamarix</i>	No	No	Yes
			Not occupied	No	No	Yes
	Sand Arroyo (2)	9	Untreated <i>Tamarix</i>	Yes	Yes	Yes
			Not occupied	Yes	Yes	Yes
	West End (2)	NA	<i>Tamarix</i> treated via foliar herb.	Yes	Yes	No
			Not occupied	Yes	Yes	No
	Bighorn River (regulated)	Arapooish (2)	37	Untreated <i>Tamarix</i>	Yes	Yes
Not occupied				Yes	Yes	Yes
General Custer (2)		27	Untreated <i>Tamarix</i>	Yes	Yes	Yes
			Not occupied	Yes	Yes	Yes
Yellowstone River (unregulated)	Grant Marsh (1)	NA	Not occupied	No	No	Yes
	Bundy Bridge (2)	12	Untreated <i>Tamarix</i>	Yes	Yes	Yes
Not occupied			Yes	Yes	Yes	
Isaac Homestead (2)	23	<i>Tamarix</i> treated via basal bark	Yes	Yes	Yes	
		Not occupied	Yes	Yes	Yes	
		Untreated <i>Tamarix</i>	Yes	Yes	Yes	
			Not occupied	Yes	Yes	Yes

analyses were performed in R, version 2.12.1 (R Development Core Team 2010).

Mycorrhizal Infectivity Potential

Percent colonization by mycorrhizal fungi of the *S. sudanese* grown in the greenhouse was compared across sites and invasion status as a measure of relative infectivity potential of mycorrhizal propagules. A two-way ANOVA was used to test the effects of site and *Tamarix* presence on mycorrhizal propagules, and data were analyzed using R.

Vegetation Community Analysis

Species richness, diversity, and rank abundance were used to evaluate plant community differences across sites and invasion status. Richness and diversity (Simpson's diversity, 1-day) at each sub-site were calculated from species presence and abundance, respectively, using the

“vegan 1.17–6” package in R. Site and microsite differences (including effects of herbicide treatment) in richness, species abundance and diversity were evaluated by ANOVA, and Welch's two sample t-tests were used to evaluate pairwise differences. Rank abundance was calculated with “BiodiversityR” package in R using abundance data.

Differences in plant community composition between sites were analyzed by Principal Coordinates Analysis (PCoA) using Euclidean distances in R with the package “vegan 1.17–6”. Factors resulting in the separation of points in the PCoA analyses were investigated with linear models with the Euclidean distances between points as the response variables and soil and plant community data as the predictor variables. The best models were determined by Akaike's Information Criterion coefficient (AICc) values using the package “pgirmess” in R. Plant community composition variation between sub-sites was also evaluated via hierarchical clustering and the Ward's minimum variance method using the “stats” package in R.

Results

Soil Analysis

For all variables, there were no differences ($P>0.05$) between surface and subsurface soil samples; thus data were pooled. There were generally no, or only minimal, differences between the soil properties measured on *Tamarix*-occupied and *Tamarix*-free microsites. However, some of the cations associated with soil salinity were elevated at some occupied microsites (Table 3). For example, Calcium ($F_{1,58}=15.90$, $P<0.001$), Mg^{2+} ($F_{1,58}=16.42$, $P<0.001$) and K^+ (2009 sample) ($F_{1,58}=11.40$, $P=0.001$) concentrations were 2.7, 2.8 and 1.8 times higher, respectively, on occupied microsites at Fort Peck (reservoir) compared to unoccupied Fort Peck microsites. Electrical conductivity was 2.0 times higher on occupied Fort Peck sites ($F_{1,58}=14.90$, $P<0.001$) than unoccupied microsites. However, there were no differences for these soil properties between microsites at Bighorn River (regulated) and Yellowstone River (unregulated) sites ($P>0.05$).

Soil fertility was higher at occupied Bighorn River microsites compared to unoccupied microsites, as measured by N ($F_{1,4}=44.83$, $P=0.003$, 2.2 times higher), P ($F_{1,4}=192.8$, $P<0.01$, 4.0 times higher) and K^+ (2010 sample) ($F_{1,4}=7.18$, $P=0.055$, 1.9 times higher) (Table 3). There were no differences in these soil properties or OM between other sites ($P>0.05$). *Tamarix* stand age (Lehnhoff et al. 2011) (Table 2) at occupied sites was a significant predictor of K^+ , P and pH, but not for other soil properties, with K^+ (slope=0.040, $P=0.036$) and P (slope=0.053, $P=0.020$) increasing, and pH (slope=-0.019, $P=0.005$) decreasing with time since invasion.

Mycorrhizal Community

Mycorrhizal colonization levels were consistently high in the Sudan grass grown in the greenhouse, with an average colonization level of 69% of the root intersections. Soils from *Tamarix* sites had a lower MIP than non-occupied sites (65% colonization versus 73% colonization, respectively) ($F_{1,48}=6.53$, $P=0.014$), although the level of colonization at both sites suggests that mycorrhizal propagules will not

Table 3 Soil chemistry at sites with and without *Tamarix*. Means are presented with standard deviations in parentheses. Bold indicates significant differences ($P=0.05$) of soil property between *Tamarix*-occupied and unoccupied sites

Soil Parameter	Invasion			
	Status	Site		
		Fort Peck Reservoir	Bighorn River	Yellowstone River
2009 soil samples				
EC (dS m ⁻¹)	NI	0.48 (0.21)	0.85 (0.42)	1.16 (0.72)
	I	0.97 (0.78)	1.01 (0.30)	1.50 (1.22)
pH (standard units)	NI	7.84 (0.31)	7.54 (0.18)	7.78 (0.19)
	I	7.77 (0.32)	7.41 (0.21)	7.64 (0.16)
Ca ²⁺ (mmol/l)	NI	1.96 (1.37)	4.62 (0.68)	7.92 (5.88)
	I	5.32 (6.60)	5.58 (1.62)	9.44 (8.97)
K ⁺ (mmol/l)	NI	0.56 (0.36)	2.34 (0.80)	0.45 (0.36)
	I	1.02 (0.75)	2.56 (0.69)	0.56 (0.34)
Na ⁺ (mmol/l)	NI	1.17 (1.25)	0.29 (0.15)	1.43 (1.04)
	I	0.95 (0.75)	0.76 (0.46)	2.63 (3.47)
Mg ²⁺ (mmol/l)	NI	1.05 (0.61)	1.63 (0.30)	2.92 (2.27)
	I	2.89 (3.43)	2.20 (0.67)	3.30 (3.04)
SAR	NI	1.29 (1.79)	0.17 (0.08)	0.63 (0.23)
	I	0.52 (0.38)	0.39 (0.25)	0.89 (0.92)
2010 soil samples				
NO ₃ ⁻ (mg/kg)	NI	3.50 (1.80)	11.17 (1.89)	2.83 (1.53)
	I	18.67 (27.15)	24.67 (2.52)	14.83 (15.46)
K ⁺ (mg/kg)	NI	229.67 (111.38)	281.33 (100.07)	150.33 (51.03)
	I	224.67 (57.47)	530.00 (83.86)	220.67 (85.34)
P (mg/kg)	NI	4.00 (2.00)	6.67 (0.58)	6.67 (3.06)
	I	6.33 (4.93)	27.00 (4.00)	9.00 (2.65)
OM (%)	NI	1.20 (0.36)	2.50 (0.79)	0.77 (0.21)
	I	1.37 (0.21)	3.37 (1.66)	1.07 (0.64)

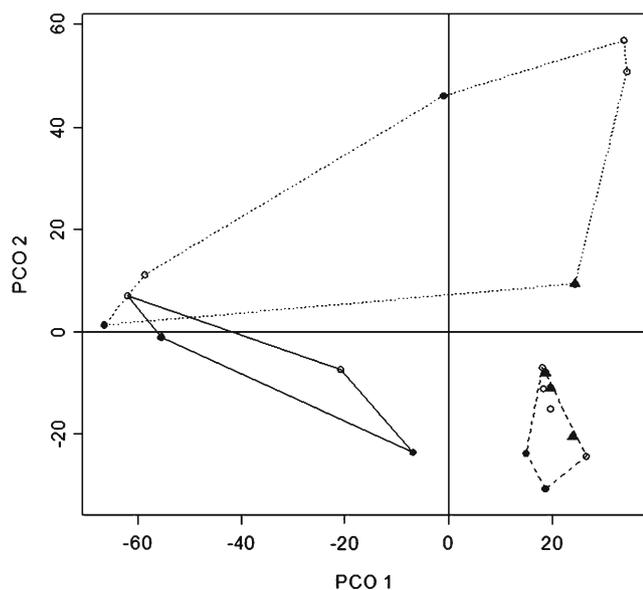


Fig. 2 PCO results for vegetation data at Fort Peck Reservoir, Bighorn River (regulated) and Yellowstone River (unregulated) sub-sites. ●=*Tamarix*-occupied sites. ○=unoccupied sites. ▲=herbicide treated sites. Fort Peck Reservoir is represented by *dashed lines*, Bighorn River is represented by *solid lines* and Yellowstone River is represented by *dotted lines*

be limiting. MIP also varied between sites ($F_{2,48}=11.2$, $P<0.001$), with MIP colonization levels averaging 57% at Bighorn River (regulated) sites, 76% at Fort Peck (reservoir), and 74% at Yellowstone River (unregulated) microsites. There was a significant *Tamarix* × site interaction effect ($F_{2,48}=3.52$, $P=0.037$) on MIP colonization levels, with a decrease in colonization between sites without and with *Tamarix* at Bighorn and Yellowstone Rivers (BR: 67 versus 49% colonization and YR: 79 versus 68% colonization for non-occupied and *Tamarix* present sites, respectively), and an insignificant increase in colonization levels in Fort Peck soils when *Tamarix* was present (74 versus 77% colonization for non-occupied and

Tamarix present sites, respectively). *Tamarix* stand age was a marginally-significant predictor of mycorrhizal colonization rates with less colonization at older sub-sites (slope= -0.011 , $P=0.070$).

Vegetation Community Analysis

PCoA indicated that plant communities differed by site (Fig. 2) with the first two axes explaining 37 and 20% of the variability in plant community, respectively. The first axis separated the Bighorn River (regulated) and Fort Peck (reservoir) sub-sites and the second axis generally separated Yellowstone (unregulated) sub-sites from sub-sites on the Bighorn River and Fort Peck. The presence or absence of *Tamarix* did not appear to have any effect on the community structure (Fig. 2). The four microsites where *Tamarix* was treated via herbicide were grouped to the right of axis one, indicating that the treatment may have played a role in structuring the plant community. The models best explaining the distribution of points on axis 1 and 2, respectively, were the three parameter model including native species abundance, K^+ and P concentrations and the four parameter model including native species richness, site, K^+ and P (Table 4).

There were 62 species recorded overall with 30, 34 and 35 at Bighorn River, Fort Peck and Yellowstone River sub-sites, respectively (Table 5). Of these species, 33 were native and 29 were non-native. The ratio of the proportion (p) of native to the p non-native species was nearly different ($P=0.07$) at *Tamarix* occupied (ratio p native: p non-native=0.44) versus unoccupied sites (ratio p native: p non-native=2.75). Species richness ($F_{1,17}=0.89$, $P=0.33$), vegetative cover or abundance ($F_{1,17}=0.03$, $P=0.87$) and diversity ($F_{1,17}=0.31$, $P=0.59$) did not differ between *Tamarix*-occupied and unoccupied microsites (Table 6). Likewise, there were no differences in either richness ($F_{2,16}=0.93$, $P=0.42$)

Table 4 Top models used to examine the relationship between PCO axes values (response) and environmental variables at Fort Peck Reservoir, Bighorn River (regulated), and Yellowstone River (unregulated) sub-sites. Δ AICc=difference in Akaike's Information Criterion coefficient for each model from the most parsimonious model; k=number of parameters; wAICc=weight of AICc; and %VE=percent variance explained in the response variable by the model

Models	Δ AICc	k	wAICc	%VE
Axis 1				
Native species abundance+P+ K^+	0	4	0.31	53.77
Native species abundance	0.43	2	0.25	39.65
Native species richness	2.12	2	0.11	34.02
Total species abundance	2.31	2	0.10	33.36
Native species richness+site (factor)	3.64	5	0.05	44.01
Axis 2				
Native species richness+site (factor)+ K^+ + P	0	7	0.49	82.94
Native species abundance+site (factor)+ K^+ + P	0.10	7	0.46	82.85
Site (factor)	6.11	4	0.02	61.45
Native species abundance+site (factor)	7.36	5	0.01	60.60
Native species abundance+ K^+ + P	7.81	4	0.01	63.11

Table 5 Top ten species and their proportions at each site (occupied and unoccupied)

Rank	Site ^a	FPNI		FPSC		FPTR		BRNI		BRSC		YRNI		YRSC		YRTR	
		Species	<i>p</i> ^b	Species	<i>p</i>	Species	<i>p</i>	Species	<i>p</i>	Species	<i>p</i>	Species	<i>p</i> ^b	Species	<i>p</i>	Species	<i>p</i>
1	<i>Bromus japonica</i>	<i>Tamarix</i> spp.	26.6	<i>Cirsium arvense</i>	49.9	<i>Glyceria grandis</i>	38.6	<i>Glyceria grandis</i>	24.3	<i>Glyceria grandis</i>	30.8	<i>Calamagrostis montanensis</i>	36.2	<i>Glyceria grandis</i>	37.6		
2	<i>Hordeum jubata</i>	<i>Bromus japonica</i>	17.1	<i>Bromus japonica</i>	19.8	<i>Bromus inermis</i>	13.9	<i>Bromus inermis</i>	19.7	<i>Bromus inermis</i>	19.4	<i>Glyceria grandis</i>	16.0	<i>Salix boothii</i>	16.9		
3	<i>Cirsium arvense</i>	<i>Cirsium arvense</i>	15.4	<i>Chenopodium album</i>	6.6	<i>Agropyron dasytachyum</i>	13.8	<i>Tamarix</i> spp.	18.9	<i>Tamarix</i> spp.	10.6	<i>Alopecurus arundinaceus</i>	15.4	<i>Tamarix</i> spp.	11.8		
4	<i>Agropyron dasytachyum</i>	<i>Medicago lupulina</i>	12.8	<i>Agropyron dasytachyum</i>	4.6	<i>Elaeagnus angustifolia</i>	8.8	<i>Populus deltoids</i>	9.0	<i>Populus deltoids</i>	10.2	<i>Salix boothii</i>	12.4	<i>Calamagrostis montanensis</i>	11.5		
5	<i>Populus deltoids</i>	<i>Bromus tectorum</i>	6.9	<i>Conyza canadensis</i>	2.5	<i>Populus deltoids</i>	8.6	<i>Poa pratensis</i>	6.3	<i>Poa pratensis</i>	7.9	<i>Spartina pectinata</i>	6.4	<i>Spartina pectinata</i>	6.9		
6	<i>Medicago lupulina</i>	<i>Descurainia sophia</i>	4.8	<i>Poa pratensis</i>	2.3	<i>Poa pratensis</i>	8.4	<i>Elaeagnus angustifolia</i>	5.0	<i>Elaeagnus angustifolia</i>	6.3	<i>Elaeagnus angustifolia</i>	5.6	<i>Ambrosia psilostachya</i>	4.1		
7	<i>Bromus inermis</i>	<i>Agropyron dasytachyum</i>	4.8	<i>Kochia scoparia</i>	2.3	<i>Cirsium arvense</i>	2.9	<i>Cirsium arvense</i>	3.8	<i>Cirsium arvense</i>	4.2	<i>Agropyron dasytachyum</i>	2.6	<i>Carax arvensis</i>	3.3		
8	<i>Bromus tectorum</i>	<i>Populus</i>	3.0	<i>Lactuca serriola</i>	2.2	<i>Chenopodium album</i>	1.6	<i>Rosa woodsii</i>	3.1	<i>Solidago canadensis</i>	3.7	<i>Solidago canadensis</i>	1.1	<i>Bromus inermis</i>	2.3		
9	<i>Penstemon albidus</i>	<i>Artemisia absinthium</i>	1.5	<i>Bromus inermis</i>	1.9	<i>Tamarix</i> spp.	1.0	<i>Solanum dulcamara</i>	2.5	<i>Cirsium arvense</i>	1.6	<i>Cirsium arvense</i>	1.0	<i>Euphorbia esula</i>	1.5		
10	<i>Lactuca serriola</i>	<i>Poa pratensis</i>	1.2	<i>Hordeum jubata</i>	1.7	<i>Convolvulus arvensis</i>	0.8	<i>Carax stenophylla</i>	1.7	<i>Poa pratensis</i>	1.5	<i>Verbasum thaspus</i>	1.0	<i>Aster campestris</i>	0.8		

^a BR Bighorn River (regulated); FP Fort Peck Reservoir; YR Yellowstone River (unregulated); M not occupied by *Tamarix*; SC occupied by *Tamarix*; TR treated via herbicide

^b *p*=proportional abundance

or diversity ($F_{2,16}=1.43$, $P=0.27$) between sites, but vegetative cover was less at Fort Peck, where vegetation was sparse compared to Bighorn or Yellowstone ($F_{2,16}=14.00$, $P<0.001$). Differences in richness ($F_{1,17}=1.52$, $P=0.24$) and Simpson's diversity ($F_{1,17}=3.77$, $P=0.07$) were not significant at microsites that were treated with herbicide compared to all untreated microsites, but species abundance was greater at untreated sites ($F_{1,17}=6.15$, $P=0.024$). When herbicide treated sites were compared only to other untreated sites where *Tamarix* was present, there was no difference in diversity ($P=0.12$), but richness ($P=0.07$) was nearly lower and species abundance ($P=0.001$) was lower at treated sites. There was minimal difference in species rank abundance between *Tamarix*-occupied and unoccupied microsites at each of the overall sites (Table 6). Likewise, differences in species rank were minimal between untreated and herbicide treated microsites. While the most abundant species at the occupied microsites differed slightly, the top five species at microsites generally did not change.

Hierarchical clustering analysis indicated that, as a general rule, microsites within a sub-site were more related to each other than those from other sub-sites, regardless of the presence or absence of *Tamarix* or of past herbicide treatment (Fig. 3). At the Bighorn River, plant communities at *Tamarix*-occupied microsites at both the General Custer and Arapooish sub-sites were closely related to their respective unoccupied microsites. This relationship was also true at the Yellowstone River Isaac Homestead sub-site. At Fort Peck, the Bone Trail unoccupied and treated microsites clustered together. Other Fort Peck sub-sites clustered together on the same branch of the dendrogram, but the respective microsites did not cluster. Other Bighorn and Yellowstone River sub-sites had similar, but weaker clustering patterns, with two Yellowstone River sub-sites clustering with two Bighorn River sub-sites, and two Bighorn River sub-sites clustering with the Fort Peck sub-sites.

Table 6 Mean plant species richness and Simpson's diversity values at microsites that differed in the presence of *Tamarix* spp, location, and herbicide application. Standard deviations are in parentheses

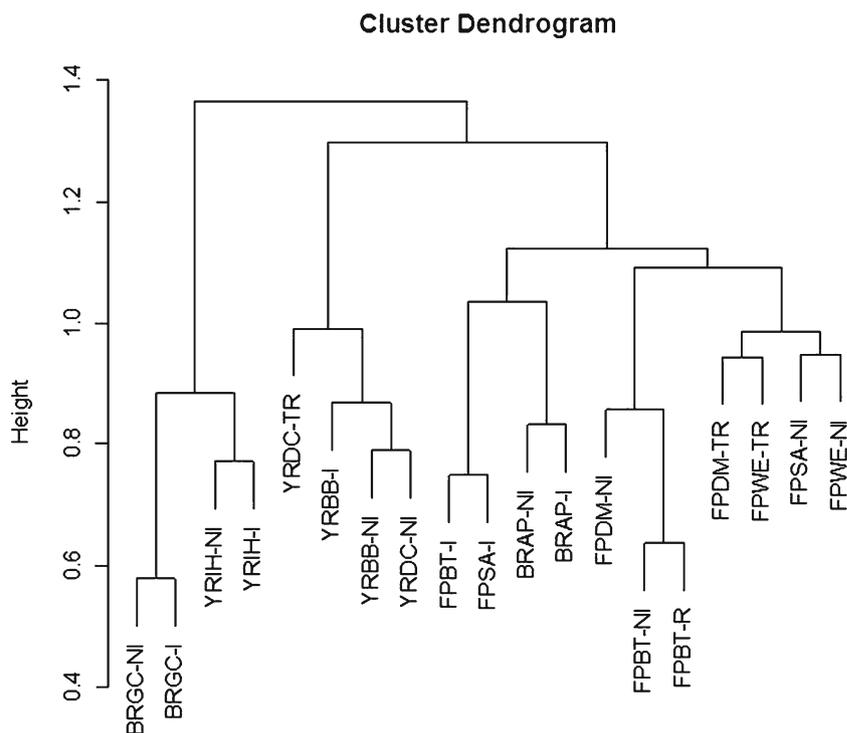
Site	Richness	Cumulative Cover	Simpson's Diversity
All unoccupied	9.7 (3.0)	108.4 (50.5)	0.70 (0.15)
All <i>Tamarix</i> -occupied	11.3 (4.3)	112.4 (52.5)	0.66 (0.12)
Fort Peck Reservoir	10.8 (2.9)	71.0 (31.3)	0.69 (0.11)
Bighorn River (regulated)	12.3 (5.7)	163.65 (18.0)	0.75 (0.09)
Yellowstone River (unregulated)	9.0 (3.5)	134.4 (39.3)	0.61 (0.18)
All untreated	11.1 (3.9)	123.5 (47.5)	0.71 (0.12)
Untreated <i>Tamarix</i>	13.2 (4.4)	146.2 (34.8)	0.73 (0.07)
All herbicide treated	8.5 (2.6)	61.8 (23.3)	0.57 (0.15)

Discussion

Our results suggest that *Tamarix* may alter soil conditions in the northwestern U.S., especially on water bodies without regular flooding. Mean Ca^{2+} , Mg^{2+} and K^{+} levels were two to three times higher at *Tamarix*-occupied Fort Peck (reservoir) microsites compared to unoccupied ones. However, these increases are likely periodically mitigated by leaching via the fluctuating reservoir water level. High water in the reservoir, which was at full pool and consistently inundated all of the sub-sites for over 60 days in the spring and summer of 2011, may leach these cations from the soil (Ladenburger et al. 2006). EC was two times higher in *Tamarix*-occupied sites than in non-occupied ones, but the mean (1.01 dS m^{-1}) was still well below the recommended upper (detrimental) limit values of 2 dS m^{-1} and 2.5 dS m^{-1} for cottonwood and willow establishment, respectively (Taylor and McDaniel 1998). Additionally, these EC levels are considerably lower than the 15 dS m^{-1} observed on *Tamarix*-occupied sites in north-central Utah (Carman and Brotherson 1982) and the 12.8 dS m^{-1} on the Colorado River (Busch and Smith 1995). These results are consistent with findings at Fort Peck by Lesica and Miles (2004) who suggested low impact of *Tamarix* on soils in Montana. In contrast with Ladenburger et al. (2006), who documented decreased pH and elevated EC in the Bighorn Basin, we found no soil impacts from *Tamarix* on the Bighorn (regulated) or Yellowstone (unregulated) Rivers. The lack of soil impacts from *Tamarix* along these rivers suggests that the flood regime may serve to curtail the buildup of salt in the soil (Ladenburger et al. 2006).

We found significantly elevated concentrations of N, P and K^{+} at *Tamarix*-occupied microsites on the Bighorn River and these values were generally higher, but not statistically significantly, to all other *Tamarix*-occupied sites. The accumulation of OM and nutrients resulting from *Tamarix* invasion may lead to increased plant growth if nitrogen or phosphorus was previously a limiting growth factor. Higher nutrient concentrations were also observed by Xu et al. (2006) and Yin et al. (2010), who found *Tamarix* clusters in the deserts of China to be "islands of fertility" with higher total N, available K and OM than in surrounding unoccupied areas. Bagstad et al. (2006) also showed elevated levels of nitrate under *Tamarix* stands on the San Pedro River of Arizona. This buildup of OM and total nutrients may have been associated with leaf litter accumulation. *Tamarix* litter has been shown to degrade slower than litter of some native vegetation (Pomeroy et al. 2000), although Ellis et al. (1998) found no difference between degradation rates of litter at *Tamarix ramosissima* and *Populus deltoids* dominated sites in New Mexico. The trend of increasing *Tamarix* leaf litter and nutrients may continue in Montana. The lack of herbivory from biological control insects, which are not established in Montana, may lead to litter with slower decomposition rates

Fig. 3 Hierarchical cluster analysis with grouping based on Ward's minimum variance method. BRGC=Bighorn River General Custer site. YRIH=Yellowstone River Isaac Homestead site. YRDC=Yellowstone River Duck Creek site. YRBB=Yellowstone River Bundy Bridge site. FPBT=Fort Peck Bone Trail site. FPSA=Fort Peck Sand Arroyo site. BRAP=Bighorn River Arapooish site. FPDM=Fort Peck Dam site. FPWE=Fort Peck West End site. NI=site not occupied by *Tamarix*. I=site occupied by *Tamarix*. TR=*Tamarix* at site treated via herbicide



than *Tamarix* litter in the southwestern U.S. where biological control insects are present (Uselman et al. 2011). This may be mitigated by periodic flooding at the Bighorn and Yellowstone River sites as high annual flows wash away litter.

Phosphorus and K^+ concentrations and pH had significant relationships with stand age, suggesting that time since *Tamarix* establishment may be an important factor in determining soil chemistry. Soil properties commonly change with stand age so this relationship is not unique to *Tamarix*; Stromberg (1998) showed that several soil properties changed with age in both *Tamarix* and *Populus fremontii* populations. *Tamarix* has been present in the southwestern U.S. for over 150 years and has been considered problematic there for at least 50 years (DiTomaso 1998), whereas it has only been present in Montana for approximately 50 years, indicating the potential for further soil modifications over time. The growing season in Montana is much shorter than in the southwest though, so the accumulation of cations would be expected to be slower in comparison to accumulation in the southwest U.S. These findings suggest that while *Tamarix* may alter soil salinity on some water bodies in the northwest U.S., the ecological significance is currently minimal and future changes will likely be slow to occur.

Mycorrhizal propagules in the soils were reduced in areas with *Tamarix* invasion on the Bighorn River microsites. This is consistent with results indicating that *Tamarix* is non-mycotrophic (Beauchamp et al. 2005), although Yang et al. (2008) showed high mycorrhizal infectivity in *Tamarix* in Northwest China. While the reduction of mycorrhizae

was not consistent across all three sites, and mycorrhizal propagules are not currently limiting, an extended and denser *Tamarix* presence could impact mycorrhizal propagule abundance leading to ecological change. If native plants that are potential competitors with *Tamarix* are mycorrhizal-dependent, this could favor *Tamarix* over native species. Propagule density could be relatively high in *Tamarix* soils if flood plain dynamics along the river sites serve as a source of propagules, although other studies suggest that these sites would have only patchy distribution of mycorrhizal propagules from sediment deposition (Harner et al. 2009).

Our results are contrary to many studies from the southwestern U.S. (but similar to Stromberg (1998)), and indicate that *Tamarix* in Montana has very little, if any, impact on plant communities, regardless of flow regime. Rather, our results are similar to Johnson et al. (2010) who showed that *Tamarix* simply occupied sites that were well-suited for all riparian plants. In the relatively free-flowing upper Verde River in Arizona, the authors found that sites with *Tamarix* had greater abundance of all riparian vegetation, including native understory species, graminoids and native trees. Also, based on the ratio of native to non-native species at the studied *Tamarix*-occupied versus unoccupied sites, our results indicate that *Tamarix* may simply be occupying sites that are more disturbed and suitable for early successional weedy species. The abundance of *Tamarix* at the study sites was much less than has been reported for other areas (Engel-Wilson and Ohmart 1978, Howe and Knopf 1991, Egan et al. 1993, Lovich et al. 1994, Weeks et al. 1997, Friedman et al. 2005, Birken and Cooper 2006). At our sites, *Tamarix*

was rarely the dominant species (the exception being one microsite at Fort Peck) and did not affect species richness or diversity when compared with unoccupied sites. The studied plant communities were structured more by site, which was a surrogate for flow regime, than by the presence or absence of *Tamarix*. In accordance, other research (Shafroth et al. 1998, Lite et al. 2005, Stromberg et al. 2005, Stromberg et al. 2007) has shown the importance of hydrology in determining plant community composition. Flow in the Bighorn River is dam-regulated and the Yellowstone River is free-flowing, and vegetation differences would be expected as a result of these differences. The vegetation in the drawdown zone at Fort Peck was reflective of a mix of the local upland plant communities and early seral species that colonize as the water level recedes (Lesica and Miles 2004).

Our results do not preclude the possibility that *Tamarix* could become problematic in Montana, especially if the regional climate warms. Currently, the non-native tree Russian olive (*Elaeagnus angustifolia*) is a more dominant woody riparian species than *Tamarix* in Montana, and it can tolerate lower mean annual minimum temperatures (Friedman et al. 2005). Cold sensitivity in *Tamarix* may limit its northern expansion (Friedman et al. 2008), however, the mean annual minimum temperature at which *Tamarix* becomes more dominant than *E. angustifolia* is -9.4 C (Friedman et al. 2005). Mean annual minimum temperatures at Billings, MT (near the Bighorn and Yellowstone River sites) and Glasgow, MT (near Fort Peck) are -9.8 C and -18.8 C, respectively (Western Regional Climate Center 2010). If long-term changes in climate elevate the minimum temperatures, *Tamarix* could potentially progress past its current lag phase and become the dominant riparian woody species and thus have greater impacts (Hellmann et al. 2008). Additionally, genetic changes in plants can lead to greater invasiveness (Dietz and Edwards 2006), and hybridization of *Tamarix* species in Montana may facilitate its further invasion (Gaskin and Kazmer 2009).

Under current conditions in its northern U.S. range, however, *Tamarix* seems to have little, or very slowly accumulating impact on soils. Likewise, plant communities are not negatively affected by *Tamarix* presence, nor does herbicide treatment result in positive shifts in plant communities. Rather, at our herbicide treated sites, the total amount of plant cover was greatly reduced compared to untreated sites, which could negatively affect the ecology of the sites. Specifically, riparian vegetation, provides habitat for insectivorous and ground or shrub nesting birds (Kelly and Finch 1999), and the lack of vegetation resulting from management may adversely affect birds. While the habitat quality of *Tamarix*-dominated sites is generally not as good as other woody riparian vegetation (Brand et al. 2010, Brand and Noon 2011), it is better than at sites where vegetation has been diminished through treatment or removal (Sogge et al.

2008). These results indicate that a change from active management to monitoring of *Tamarix*-occupied plant communities may be appropriate in this region. Under such a scenario, *Tamarix*-occupied sites could be monitored to determine population invasiveness (Lehnhoff et al. 2008) and impacts, with treatment initiated only when invasiveness or impacts are documented.

These results have implications for management of non-native plant species at their current distributional limits. It is important to recognize that their invasiveness and impacts may be considerably less at their range limits as compared to locations where conditions are more favorable for growth. Therefore, management may not be warranted for populations at their range limits, and management may have more adverse than positive effects (Rinella et al. 2009). However, while impacts may be minimal during the early phases of invasion at their range limits, this could be the result of a lag phase, after which impacts and rapid population expansion could occur. It is also possible that species in these less optimal ranges may not be invasive until some other process such as climate change or evolution (Clements and Dittommaso 2011) occurs. This underscores the importance of a monitoring program to evaluate spread and impacts of non-native plant species at their range limits.

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