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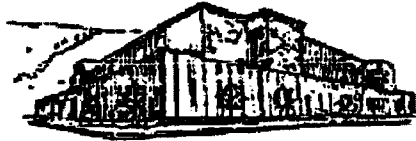
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INVASIVE POTENTIAL OF *TAMARIX RAMOSISSIMA* (SALT CEDAR) IN
CONTINENTAL CLIMATES OF NORTH AMERICA

by

Jason Patrick Sexton

B.S. Humboldt State University

presented in partial fulfillment of the requirements

for the degree of

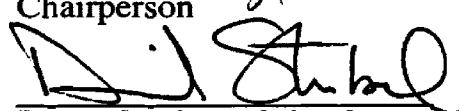
Masters of Science

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Invasive potential of *Tamarix ramosissima* in dry, cold climates of North America

Director: Anna Sala

AS

Tamarix ramosissima (saltcedar), a shrub or tree native to Eurasia, has heavily invaded many wetland and riparian systems of the southwestern United States. Since its first reports in the 1960's, saltcedar has spread throughout dry areas of most of the northern, colder states of the U.S. where its invasive potential is thought to be low. This study examines the invasive potential and spread of saltcedar in eastern Montana. *T. ramosissima* seeds from Arizona and eastern Montana, the extremes of its latitudinal range within the U.S., were grown together under high and low temperatures (representing Arizona and Montana climates respectively) to investigate growth, phenotypic plasticity, and genetic differentiation in response to temperature (Chapter 1). Low temperature significantly decreased gas exchange and biomass, and increased relative biomass allocation to roots in all populations. Montana seedlings had significantly shorter shoots than Arizona seedlings under high and low temperatures and invested more biomass into roots but only under cold temperatures. Shorter stature and increased plasticity in biomass allocation to roots for *T. ramosissima* ecotypes of eastern Montana may help overcome winter mortality and is possibly an adaptive response to climate variability. Phenotypic plasticity, ecotypic differentiation and high genetic variability for all traits measured, indicate that *Tamarix ramosissima* has the potential to spread and to evolve in response to climate. Saltcedar's dispersion patterns and dynamics over time were investigated in the field in eastern Montana (Chapter 2). Riparian communities where saltcedar was present were aged according to the oldest saltcedar individual and were sampled for plant community and abiotic changes over time. Data showed multiple infection origins along the Greater Yellowstone and Missouri River drainages. Saltcedar patches (or stands) increased in area and cover with time, and showed high proportions of young stems, indicating substantial vegetative recruitment. Further, native tree and shrub cover declined over time in communities where saltcedar was present. Soil pH decreased with saltcedar age and cover, and was the only abiotic factor that changed over time. Disturbances such as grazing and vegetation clearing in eastern Montana appear to greatly enhance saltcedar.

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CHAPTER 1

Genetic and phenotypic responses to temperature in seedlings of *Tamarix ramosissima* Ledeb., an invasive, woody species.

INTRODUCTION

The ability of introduced species to become invasive and occupy broad geographic areas depends on two main strategies: tolerance to growing conditions via phenotypic plasticity and local adaptation (Schlichting 1986, Williams and Black 1993). Under strong environmental selection and given enough genetic variation, invasive organisms may adapt to local conditions by first differentiating ecotypes (Allard 1965, Barret 1986). In native plant populations ecotypic differentiation has been shown to increase plant performance along biotic and abiotic gradients (Jain and Bradshaw 1966, Ramakrishnan and Gupta 1973, Hancock and Bringham 1978, Silander 1979, Waser and Price 1985, McGraw 1987, Geber and Dawson 1990, Dudley 1996) and is thought to be an important mechanism for rapid spread into multiple environments (Baker 1974, Antonovics 1976, Rapson and Wilson 1988). For example, the invasive *Spartina alterniflora* in San Francisco Bay, California, has rapidly evolved a new ecotype which appears to be adapting to high intertidal zones (Daehler et al. 1999). Despite constraints of founder effects non-native weeds exhibit substantial genetic variation (Barret and Richardson 1986), and ecotypic differentiation along biotic and abiotic gradients is common (Jain 1969, Jain and Martins 1979, Teramura and Strain 1979, Martin and Harding 1981, Hume and Cavers 1982, Schmidt and Levin 1985, Lacey 1988). However, it is rarely proven to be adaptive (but see Rice and Mack 1991, Rice et al. 1992) and is sometimes unexplainable (Hume and Cavers 1982).

Phenotypic plasticity is an additional or alternative mechanism to local adaptation by which species can tolerate wide environmental variation (Marshall and Jain 1968, Schlichting 1986, Williams and Black 1993, Via 1994, Williams et al. 1995) as well as preserve genetic variation (Bradshaw 1965, Baker 1974, McGraw 1987, Sultan 1987). The relative contribution of phenotypic plasticity and adaptation to invasiveness has received little attention. Plasticity may initially allow an introduced species to become naturalized across a range of environments (Figure 1.1). Once naturalized, recombination of introduced genetic variation may lead to a range of heritable phenotypes that can respond to local selection pressures and evolve distinct ecotypes (including those differing in plasticity). This hypothetical time lag, or naturalization phase, has been described as a stage of building up “infection pressure” (Salisbury in Baker 1986) during which apparently benign introduced species may be developing strong invasive potential.

The Eurasian *Tamarix ramosissima* Ledeb. (saltcedar) became an aggressive invasive plant in the 1920's in riparian ecosystems of the arid southwestern United States (see Chapter 2). This deciduous shrub/tree is known to spread quickly by producing large crops of airborne seeds throughout the growing season (Robinson 1965). Its facultative phreatophytic nature (i.e. capable of surviving when the water table drops below the rooting zone), vigorous resprouting, high water use and stress tolerance confer *Tamarix ramosissima* competitive advantage over native woody riparian species, particularly after disturbances such as fire, grazing and alteration of the flood cycle (Busch and Smith 1995, Sala et al. 1996, Cleverly et al. 1997, Smith et al. 1998). Consistent with its broad native distribution (Baum 1978), *T. ramosissima* has spread through a wide variety of habitats within western North America (Robinson 1965),

including the northwestern U.S. (Rice 1999). While *T. ramosissima* has rapidly spread throughout the northern states since the 1960's, its invasive potential in these colder areas is thought to be lower (Dixon and Johnson 1999) relative to the Southwest. This is partly based on the assumption that low temperature limits the dispersion of *T. ramosissima* (Brock 1994) even though in its native range it extends into cold climates (Baum 1978).

This study assesses the invasive potential of *Tamarix ramosissima* from a functional perspective. In particular, I studied how *T. ramosissima* seedlings from contrasting climatic regimes in the U.S. (Arizona and Montana; Table 1.1) responded to changes in temperature. I focused on seedling establishment, a crucial life stage for the long distance spread of this exotic plant. Because the airborne seeds of *T. ramosissima* are very small with little nutritive value (Merkel and Hopkins 1957) seedlings in colder climates that emerge late in the growing season will overwinter in an underdeveloped stage under harsh conditions. In this scenario, seedling mortality could be high and perhaps limit long distance colonization. Functional adjustments to cold temperatures in seedlings may be crucial for their survival and consequently the long distance spread of introduced species. I addressed the following questions: (1) How do seedlings of *T. ramosissima* respond to decreases in temperature relative to those in southwestern climates where it is invasive? (2) Do temperature responses in seedlings differ based on geographic origin? (3) Because local adaptation requires genetic variation I also asked whether there is significant within-populations genetic variation (family differences) in functional traits.

MATERIALS AND METHODS

I chose two dry regions at the extremes of the latitudinal range of *T. ramosissima* in the western United States (Table 1.1). Seeds were collected on plants in newly split seed capsules in late May and mid July 1998 in each of three riparian populations in southern Arizona and eastern Montana, respectively. Populations within states were delineated as stands of *T. ramosissima* at a minimum distance of 10 km from each other. Seeds were collected randomly from 5 plants at each population for a total of 15 families from each state. A family consisted of a seed set derived from a single plant in the field.

Arizona populations were sampled along the Gila River, a drainage historically dominated by *Populus fremontii*, *Salix goodingii*, and *Prosopis velutina* (Haase 1972). This portion of the Gila River, now dominated by monospecific stands of *T. ramosissima*, has been subjected to a myriad of human disturbances including clearing for agriculture, water diversion and flood control (Minckley and Brown 1994). Seed production at these sites can occur over half the year, from May to October (Warren and Turner 1975). Seeds were collected near the towns of Buckeye and Santa Cruz, and near the Phoenix International racetrack. See Chapter 2, Table 2.1, Arizona populations 1, 2 and 3 for latitude/longitude of seed collection sites.

Montana populations were sampled along the Yellowstone and Bighorn Rivers at similar elevations within a distance of 50 km. These sites are dominated by *Populus deltoides*, *Salix exigua*, *Shepherdia argentea* and *Symphoricarpos occidentalis* (Hansen et al. 1995, pers obs.). At these sites, *T. ramosissima* occurs mostly in discrete patches or stands within 100 m of the main channel and on river channel islands. *T. ramosissima* commonly occurs at these sites where disturbance is apparent (grazing, construction,

heavy flooding). Plants may suffer high mortality due to freezing effects and are sometimes found dead within the canopies of native vegetation. Seed production at these sites may occur from late June through September (pers obs.). Seeds were collected on the Bighorn River at the Manuel Lisa and Grant's Marsh fishing access sites, and on the Yellowstone River at Myers Bridge access site. See Chapter 2, Table 2.2, Sites 2, 3 and 22 for latitude/longitude of seed collection sites. Seed source populations from Arizona and Montana will hereafter be referred to as AZ and MT, respectively.

Growth chamber

Seeds were germinated in water for 2 days then transferred to mesh-bottom PVC plastic pipes on 28 October 1998. Pipes were capped with transparent plastic cups during the first two days after planting to avoid desiccation of seedling roots at the soil surface. These long pipes with a volume of 2.0 L (5 cm diameter x 1 m height) were used to accommodate the tap root of *T. ramosissima*. Pipes were filled with fine coarsity (70 mesh) silica sand in the upper 5 cm to maximize water retention. The rest of the pipe was filled with moderate coarsity (30 mesh) silica sand to minimize soil binding effects on roots. Soil moisture was held near saturation during seedling onset (two weeks) and sand was kept moist during the remainder of the growth period. Plastic pipes were kept partially submerged in plastic tanks (experimental blocks) in order to maintain soil moisture throughout the soil column. Plants were watered daily and fertilized every two weeks with 50 ml (1/2 strength first time then full strength) of Peters 20-20-20 (WR Grace And Co., Fogelsville, Pennsylvania) throughout the experimental period.

Plants were arranged within two controlled environmental chambers (EGC Plant Growth Chambers) in a randomized block design (5 blocks per chamber). Each of the

temperature environments (chambers) contained 2 states x 3 populations per state x 5 families per population x 10 replicates per family for a total of 300 plants (600 for the experiment). Each block contained two randomly positioned representatives of each of the 30 families for a total of 60 plants per block. Growth chamber temperature environments were representative of AZ (high-temperature) and MT (low-temperature) seed collection sites during their respective growing seasons (Table 1.1). Average night/day thermoperiods (10/14h) were 20/37 and 11/25°C throughout the bulk of the experiment. Seeds were germinated at 12/20 and 15/20°C night day thermoperiods in the low- and high-temperature chambers, respectively, then gradually brought to experimental temperatures within two weeks to reduce vapor pressure deficit (VPD) and desiccation.

Light levels from incandescent and fluorescent sources were kept at a photosynthetic photon flux density (PPFD) of 400-550 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ at the soil surface. Temperature and relative humidity at plant canopy height were continuously monitored throughout the experiment with a datalogger (CR10X, Campbell Scientific Inc., Logan, Utah). Daytime vapor pressure deficits of the air in the chambers were 1.3 and 3.36 kPa in the low- and high-temperature chambers, respectively.

Gas exchange

One block from each chamber (120 plants in total) was chosen for gas exchange measurements on February 1-2 1999. Mean air temperatures during gas exchange measurements were 23.4 and 31.1°C in the low- and high-temperature chambers, respectively. Net photosynthetic rate (A_n) and stomatal conductance (g) measurements were taken with a Licor 6200 portable photosynthesis system (LICOR Inc. Lincoln, NE).

Transpiration rates (E) were calculated from g and independent measurements of air temperature and relative humidity, assuming similar air and leaf temperatures.

Instantaneous water-use efficiency (WUE_{inst}) was calculated from measurements of A_n and E. Gas exchange estimates were calculated on a dry leaf mass basis.

Growth and biomass and allocation

Harvesting occurred after 12 weeks, between January 19 and February 9, 1999. Blocks were removed one at a time from the two growth chambers. Roots and shoots were washed, separated then oven dried for a minimum of 48 hours at 60°C. Dried roots and shoots were weighed separately and total plant weights were calculated for each individual. Shoot and root lengths were measured at time of harvest. Root mass ratio (RMR), the root mass divided by total mass, was calculated.

Statistics

Data were analyzed using an hierarchical (nested) analysis of variance (Proc GLM SAS Institute). Effects of population, block and harvest date were initially included in the analysis. However, since they did not improve model fit, population and block were excluded from the analysis. Because whole blocks were harvested at once, the effect of block is confounded by the effect of harvest date. Harvest date was used as a covariate, and the effects of treatment, state, and family nested within states was tested. Family was the only random factor. Where necessary, data were transformed to meet the assumptions of parametric analysis.

RESULTS

Gas exchange

All gas exchange variables (means \pm SE reported here) differed significantly between the high- (measured at 35 °C) and low- (measured at 23 °C) temperature environments (Table 1.2). Higher temperature increased A_n by 21.5 % ($P = 0.008$), E by 122.6 % ($P < 0.001$), and g by 189 % ($P = 0.02$), and decreased WUE_{inst} by 33.3 % ($P < 0.001$). No significant amount of variation in A_n , E , g , or WUE_{inst} could be attributed to the effect of state or family (Table 1.3).

Growth and biomass allocation

Total biomass and biomass allocation responded significantly to temperature environments (Table 1.2, Figure 1.2). Mean plant dry mass increased in the high-temperature environment by 67, 136 and 106% for roots, shoots and total mass, respectively ($P < .001$). Mean shoot length increased in the high-temperature environment by 86% ($P < .001$). Root length was not included in the analysis because it could not be accurately measured due to breakage during harvest. RMR decreased by 22.9 % with increased temperature ($P < .001$).

Total biomass and biomass allocation varied significantly between families ($P < .001$; Table 2.4). Shoot, root or total mass did not vary between states nor was there a state x temperature interaction. Shoot length varied significantly between states ($P = .02$) with longer shoots for AZ seedlings in both temperature environments (Figure 1.2). MT seedlings had higher RMR than AZ seedlings, but only in the low-temperature chamber ($P < .001$ for the effect of the state x temperature interaction).

DISCUSSION

In this experiment, I focused on seedling establishment, an important life stage for long distance spread of invasive species and a period when climatic selection might be most severe (Bradshaw 1960). My results show that *T. ramosissima* exhibits phenotypic plasticity for functional traits (gas exchange) and that ecotypes exist at the extremes of its distributional range in the U.S. I found a genetically determined increased plasticity in root investment in seedlings from colder areas (Montana) relative to those from warmer environments (Arizona) (i.e. a genotype by environment interaction; -Via 1994), which may be of adaptive value in highly variable, continental climates. These results and the fact that the distribution of *T. ramosissima* in North America is comparable to its native range (Baum 1978) suggest that the invasive potential of this introduced species is significant.

Consistent with generalized plant responses, physiological activity (gas exchange) and growth of *T. ramosissima* seedlings decreased in response to decreasing temperatures (Berry and Raison 1981, Korner & Renhardt 1987, Friend and Woodward 1990). In a common garden study, Williams and Black (1993) also found no differences in gas exchange and growth among populations of *Pennisetum setaceum*, and invasive species found along a broad altitudinal range in Hawaii. They attributed the altitudinal ubiquity of *P. setaceum* to phenotypic plasticity. The invasive potential of saltcedar in cold climates would decrease if reductions of growth due to low temperature were greater than for dominant native plants. However, comparisons of annual wood increment rates of adult *T. ramosissima* and the co-occurring native *Salix exigua* from California to

Montana, indicated that growth of saltcedar is less limited by low temperatures relative to natives (Chapter 2).

Cold temperature increased RMR and decreased plant height of *T. ramosissima* seedlings. Heritable increases in below-ground investment and plant dwarfism are common and have been related to decreased temperature, water, nutrients and light (Chapin 1980, Ollerenshaw and Baker 1981, Wardlaw et al. 1983, Komer and Renhardt 1987, Friend and Woodward 1990). In cold climates, relative increased investment in roots allows increased below-ground storage of reserves while minimizing heat transfer to the environment (Friend and Woodward 1990).

Results of this study also show that *T. ramosissima* exhibits morphological ecotypes: Montana seedlings were shorter regardless of temperature and invested more in roots, but only when grown at low temperature (i.e. higher plasticity in root investment). A caveat of this study, however, is that seeds were collected in the field rather than from pure-bred family lines which allow maximum separation of genetic and environmental factors (Hiesey and Milner 1965). However, the controlled growth chamber experimental approach allowed precise measurements during the seedling stage, particularly of relative investment in roots, a fundamental trait during seedling establishment that would be very difficult to measure in the field. While seedling growth is influenced by seed size and consequently by environmental conditions of the parent plant (Schaal 1984), seed size of *T. ramosissima* is extremely small (Warren and Turner 1975) and seedling growth appears to be dependent on carbohydrates produced early during seedling development (chlorophyll synthesis occurs within hours of imbibition with water; pers obs.) rather than on seed size.

Although a reciprocal transplant would be necessary to test whether the ecotypes found are truly adaptive (i.e. they increase seedling survival; Rice and Mack 1991), ecotypic responses reported here appear to be advantageous in cold environments and, thus, adaptive. If seeds from cold environments (Montana) germinate late in the season, developing seedlings may undergo high mortality due to above-ground freeze damage during harsh winters. Increased relative allocation to roots in cold environments in MT seedlings would minimize above ground tissue losses due to freezing while maximizing resource storage in roots for subsequent growth during the generally shorter growing season. Under hot weather, however, higher investment in above-ground structures would minimize overshadowing by neighbors. Both in AZ and eastern MT, neighbor competition is particularly important if seeds germinate early in the growing season when natives species also germinate (Horton et al. 1960, Everitt 1980). Rice et al. (1992) found that increases in shoot biomass in arid steppe populations of *Bromus tectorum* sped development and allowed life-cycle completion during opportune periods when soil moisture was available. Sultan (1992) also discusses how small adjustments of root biomass can dramatically increase plant performance.

It is not known whether these ecotypes evolved in its native habitat or in the U. S. However, they exist and potentially contribute to the invasive potential if this species. Further, *T. ramosissima* populations in the U.S. exhibited significant genetic variation in all traits measured. This genetic variability is consistent with preliminary data showing significant variation in haplotypes in populations from the western U.S. (Gaskin pers comm.). The history and source of this genetic variation is yet unknown. Levels of genetic variation found in immigrated populations depends on the number of

introductions, initial population variation, population size, varying selective pressures due to large-scale landscape heterogeneity, and the breeding system of the invader (Barret 1982, Barret and Richardson 1986, Bazzaz 1986, Novak and Mack 1993). In the case of *T. ramosissima* variation was likely imported via multiple introductions (Christensen 1962, Robinson 1965, Everitt 1980, Brock 1994) from different regions in its native distribution. However, genetic mutation and differentiation in *T. ramosissima* may have occurred in naturalized populations and perhaps continues to occur, increasing its genetic variation and potential to locally adapt in North America. That *T. ramosissima* is sexually reproductive (self- and outcrossing) and persists into late successional stages contributes to its potential to maintain high levels of genetic variation (Hamrick et al. 1979). High selection for increased plasticity of root allocation in *T. ramosissima* seedlings in cold environments may quickly affect future generations (Antonovics 1976) with minimal disruption from effects of population distance and outside gene flow (Jain and Bradshaw 1966). Phenotypic plasticity for an adaptive trait is expected to increase under selection (Marshall and Jain 1968). Small environmental changes and differences may be sufficient to alter “adaptive peaks” and trigger significant phenotypic changes (Whitlock 1997), although seedling-scale environmental heterogeneity can sometimes override genetic determinants of fitness (Hartgerink and Bazzaz 1984).

If *T. ramosissima* is experiencing selection for phenotypic plasticity in the northern distribution of its new range, its invasive potential could increase, and thus surpass the lag phase of the invasion process. As Barret (1982) states, “the evolution of genetic differentiation in weed species is favored if populations can persist in an area long enough to enable adaptation to the local environment”. Field observations in eastern

Montana (Chapter 2) indicate that *T. ramosissima* is persisting in this cold region. The results of this study indicate that this species exhibits phenotypic plasticity, ecotypic differentiation and substantial genetic variation available for future selection and local adaptation, and therefore has the potential to become invasive.

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TABLES

Table 1.1. Geographic and climate characteristics of cities near collections sites of *Tamarix ramosissima* seeds in western United States. Information from Garwood (1996).

Location	Latitude	# Frost-free days	Jun.-Aug. air Temp.(°C)	
			Mean	(Min/Max)
Buckeye, Arizona	33° 22' N	344	32.1	22.4/41.9
Hysham, Montana	46° 18' N	191	20.7	11.6/29.8

Table 1.2. Biomass, allocation and gas exchange for *Tamarix ramosissima* plants grown in high- (20/37 °C) and low- (11/25°C) temperature environments. Data are means \pm 1 SE. * $P < .05$; ** $P < 0.01$; *** $P < 0.001$.

Trait	High	Low	Significance
Shoot length (mm)	180.5 \pm 5.4	97.3 \pm 2.1	***
Shoot mass (g)	0.52 \pm 0.02	0.22 \pm 0.006	***
Root mass (g)	0.20 \pm 0.009	0.12 \pm 0.004	***
Total mass (g)	0.72 \pm .03	0.35 \pm 0.009	***
Root mass/Total mass (RMR)	0.27 \pm 0.003	0.35 \pm 0.004	***
A_n ($\mu\text{mol CO}_2 \text{ g}^{-1}$)	469.2 \pm 20.0	386.1 \pm 21.7	**
E ($\text{mmol H}_2\text{O g}^{-1}$)	691.5 \pm 39.6	310.7 \pm 15.8	***
g ($\text{mmol H}_2\text{O g}^{-1}$)	41.9 \pm 7.0	14.5 \pm 0.70	*
WUE_{inst} (photo./trans)	0.8 \pm 0.03	1.3 \pm 0.06	***

Table 1.3. Summary of analysis of variance for temperature responses of net photosynthesis on a dry mass basis (A_n), stomatal conductance (g), transpiration (E) and instantaneous water-use efficiency (WUE_{inst}). In this mixed model randomized block design family is a random factor nested within state. Data for g , E , and WUE_{inst} were log transformed before analysis.

Source	Dependent Variable	Type III SS	df	Mean Square	F-value	Sig.
Temperature	A_n	214441.415	1	214441.415	7.474	.008
	g	7.811	1	7.811	30.594	.000
	E	13.658	1	13.658	78.430	.000
	WUE_{inst}	5.268	1	5.268	33.998	.000
State	A_n^*	29073.926	1	29073.926	1.194	.281
	g^*	.204	1	.204	1.623	.208
	E^*	.361	1	.361	3.781	.058
	WUE_{inst}^*	.06878	1	.06878	.665	.419
Family	A_n	685748.867	29	23646.513	.824	.715
	g	3.048	29	.105	.412	.995
	E	2.407	29	.08299	.477	.986
	WUE_{inst}	2.762	29	.09526	.615	.928
State x Temperature	A_n	20744.449	1	20744.449	.723	.398
	g	.03798	1	.03798	.149	.701
	E	.007872	1	.007872	.045	.832
	WUE_{inst}	.02869	1	.02869	.185	.668

*Error was calculated with family as a random factor: Error = .862MS(FAM(STATE)) + .138MS(Error).

*Error was calculated with family as a random factor: Error = .864MS(FAM(STATE)) + .136MS(Error).

Table 1.4. Summary of analysis of variance for temperature responses of biomass and allocation variables in *Tamarix ramosissima*. In this mixed model randomized block design family is a random factor nested within state. Data for root mass ratio (RMR) and total mass were log transformed before analysis.

Source	Dependent Variable	Type III SS	df	Mean Square	F-value	Sig.
Harvest time (Covariate)	RMR	6.743E-02	2	6.743E-02	28.063	.000
	Total Mass [‡]	3.340	2	3.340	45.517	.000
	Shoot Length	69878.864	2	3639.138	19.202	.000
Temperature	RMR	.756	1	.756	314.824	.000
	Total Mass [‡]	12.320	1	12.320	167.879	.000
	Shoot Length	916600.58	1	3639.138	251.873	.000
State*	RMR	2.464E-02	1	2.464E-02	2.653	.115
	Total Mass [‡]	8.451E-03	1	8.451E-03	.039	.845
	Shoot Length	4.12E+04	1	4.12E+04	6.049	.020
Family	RMR	.243	28	8.672E-03	3.609	.000
	Total Mass [‡]	5.441	28	.194	2.648	.000
	Shoot Length	6836.008	28	3639.138	1.879	.005
State x Temperature	RMR	4.618E-02	1	4.618E-02	19.218	.000
	Total Mass [‡]	2.340E-02	1	2.340E-02	.319	.573
	Shoot Length	1048.812	1	3639.138	.288	.592

*Error was calculated with family as a random factor: Error = .993MS(FAM(STATE)) + 6.946E-

03MS(Error). [‡]Root Mass and Shoot Mass have the same significance as Total Mass and are not presented.

FIGURES

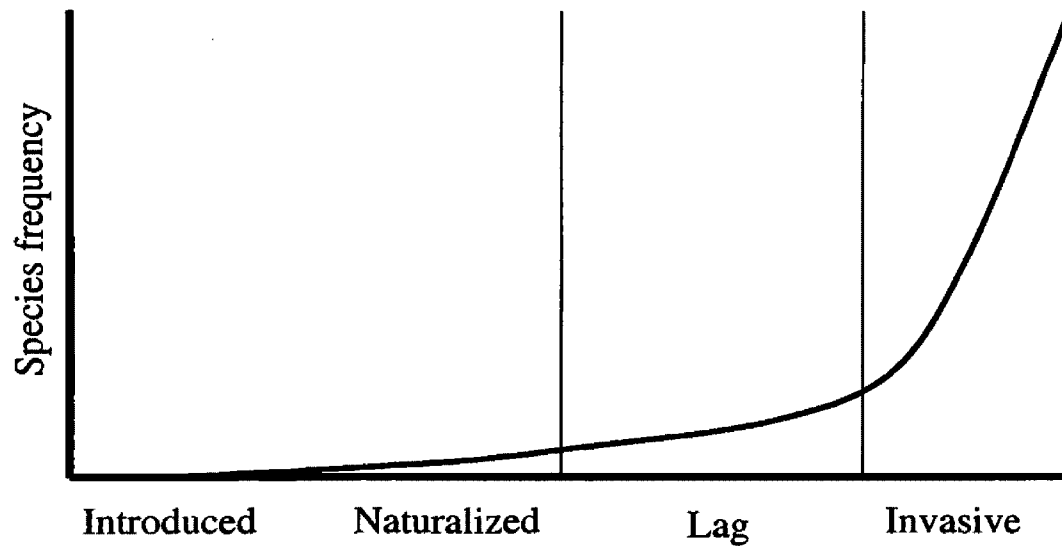


Figure 1.1. Hypothetical time course for the frequency of an invasive species. Initial frequencies are held stable during the “lag” phase as the species adjusts to its new environment.

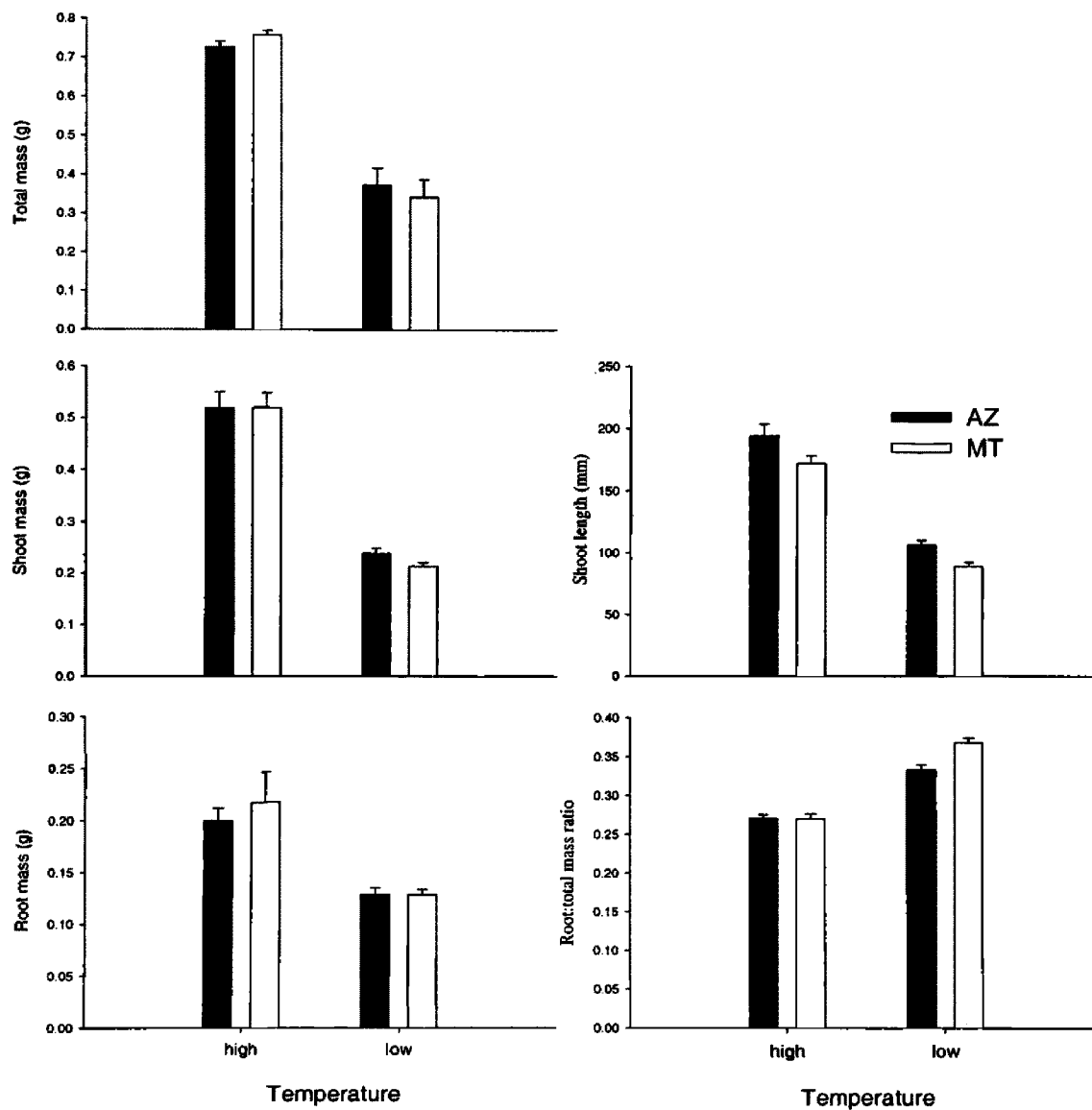


Figure 1.2. Biomass allocation and growth in response to temperature for Arizona (AZ) and Montana (MT) seedlings of *Tamarix ramosissima* grown in low- (11/25°C) and high- (20/37°C) temperature environments. Treatment means are given with vertical bars representing \pm SE of the means.

CHAPTER 2

Invasive potential of *Tamarix ramosissima* in northern climates: latitudinal growth responses and plant community changes in eastern Montana.

INTRODUCTION

Many life history traits may contribute to the invasive potential of exotic species, particularly in environments free from their natural competitors and predators (Baker 1974, Rejmánek and Richardson 1996). In order to make quick and effective conservation decisions it is important to assess the invasive potential of introduced species as early on in its invasion as possible (Kareiva et al. 1996). However it is very difficult to accurately do so (Crawley 1987, Roy 1990) and predictive models of spread and invasion have not been proven to be superior over ad hoc assessments (Roughgarden 1986). Studying the patterns of an introduced species' spread, as well as community changes since the introduction, may allow accurate predictions of invasive potential (Roughgarden 1986). In this chapter I describe the occurrence and spread of saltcedar (*Tamarix ramosissima* Ledeb.) in eastern Montana and discuss the status of its invasion in this semi-arid, northern climate.

Saltcedar is a deciduous shrub or small tree native to Europe and Asia that was introduced into North America in the 1800's to stabilize erodible soils and as an ornamental. It now exists naturalized within most of the western United States (Robinson 1965) and has become an invasive, dominant species along many riparian habitats in the southwestern U.S. (Everitt 1980, Brock 1994). Saltcedar meets most characteristics of the "ideal" invasive plant (Baker 1974, Newsome and Noble 1986, Rejmánek and Richardson 1996, Goodwin et al. 1999), having small, short-lived seeds that readily

germinate, early reproduction, frequent and large seed crops, large size, long flowering period, vegetative reproduction, plastic growth form, and perfect, self-compatible flowers. Saltcedar has a wide native distribution (Baum 1978), which is often an accurate predictor of invasiveness (Goodwin et al. 1999). High drought tolerance gives saltcedar great advantage in semi-arid to ephemeral riparian habitats (Cleverly et al. 1997, Smith et al. 1998). The saltcedar invasion has been aided by human-related ecosystem disturbances such as decreases in river discharges (damming) and heavy livestock grazing (Everitt 1980, Busch and Smith 1995, Stromberg 1997 and 1998b, Smith et al. 1998, Taylor et al. 1999). Alterations of ecosystem-level properties where saltcedar occurs in arid lands include an increase in the fire regime frequency (Busch 1995), increased evapotranspiration (Busch et al. 1992, Busch and Smith 1995, Sala et al. 1996), depletion of surface water (cf. Vitousek 1986), and soil salinization (Busch and Smith 1993).

The invasion of saltcedar in the Southwest began slowly, and became noticeable between 1925 and 1960 even though saltcedar had been present there possibly since the late 1700s (Christensen 1962, Brock 1994). By the 1960's saltcedar formed dense, monospecific stands on large southwestern watersheds such as the Colorado and Green Rivers (Christensen 1962). Within the past fifty years, reports of saltcedar occurrence in northwestern states have increased exponentially (Robinson 1965, Brock 1994, Dixon and Johnson 1999, Rice 1999). In spite of these reports little is known about the biology and invasive potential of this plant in the northern limit of its new range although it is assumed to be strongly limited by low temperatures (Brock 1994).

Saltcedar was naturalized in eastern Montana in the early 1960's and is known to

occur along the Yellowstone River and its major tributaries (Powder River, Tongue River, Bighorn River, Little Bighorn River), and along stretches of the Missouri River including Fort Peck Lake (Swenson et al. 1982, Hansen et al. 1995). It has not been determined whether it is displacing native vegetation and increasing in frequency in these riparian areas, or whether it is only a benign immigrant. The goal of this study was to provide a preliminary assessment of the spread and impacts of saltcedar on the riparian plant communities in Montana, and to predict its potential as a large-scale invasive species in colder, dry climates. Specifically, (1) Does saltcedar growth and morphology differ along a latitudinal gradient, from southern states where it is an aggressive invader, to northern, colder states? (2) How have northern plant communities changed over time with the introduction of saltcedar? (3) How have saltcedar populations in Montana changed over time? (4) Which environmental factors, if any, correlate with saltcedar occurrence in northern climates? To address these questions, wood increment rates and branching patterns of saltcedar individuals were compared along the western U.S. In addition, a detailed field survey of saltcedar-invaded riparian plant communities was conducted in eastern Montana.

MATERIALS AND METHODS

Taxonomy

The taxonomy of the deciduous species of *Tamarix* is complex. Both, *T. ramosissima* and *T. chinensis*, have been cited in the United States, although they are difficult to distinguish and are often regarded as the same species (Everitt 1980, Brock 1994). All saltcedar plants collected for this study were identified as *Tamarix ramosissima* at the University of Montana according to the criteria of Baum (1967, 1978).

Growth rates and branching along a latitudinal gradient

Saltcedar stem cross-sections at 50 cm were collected on low-gradient floodplains where saltcedar was prolific in Arizona, Nevada, Utah, Wyoming and Montana during June and July, 1997. Within each state, a minimum of 75 samples spanning the full range of stem diameters were collected at random along transects in three distinct populations (within 50 km of each other) within each state (Table 2.1). Fifteen additional samples were collected in California during the summer of 1998. Stem cross-sections of *Salix exigua* Nutt. (sandbar willow), a native shrub of analogous growth form, were also collected for comparison at sites where both species co-occurred. The diameter of each stem sample was measured and the number of annual growth increments were counted, assuming that one annual ring was equal to one year's growth. Stem growth rates were expressed in mm wood /year. Irregularly shaped or deformed stem samples were not included in the analysis.

The degree of branching of saltcedar was compared in Arizona and Montana. Isolated, individual saltcedar plants with heights of 2-3 meters and varying ages were cut

at a height of .5 m and the diameter of each stem as well as the number of stems were measured. The degree of branching was expressed as the number of branches per total added cross-sectional stem area (cm^2) at 0.5 m.

Eastern Montana field sampling

Riparian sites containing saltcedar in eastern Montana were located by searching roadside riparian areas. Thirty eight saltcedar stands were sampled during the summer of 1998 at 23 distinct sites along 5 major river systems and 3 isolated areas with ephemeral surface water (Figure 2.1, Table 2.2). In eastern Montana saltcedar stands occur mostly in discrete patches which are easily identified. Of the 38 stands in Montana, 7 were seedling beds where adult woody plants were absent. Depending on the stand size, one to three 10 m^2 ($2 \times 5 \text{ m}$) plots were positioned within the stand. The long axis of the plots were perpendicular to the flow of the water source. Within each plot the following parameters were estimated twice independently by ocular measurement and the mean recorded: % cover of each non-graminoid species, % graminoid cover, % bare ground, rock and litter cover, saltcedar condition (% stem mortality). The number of species found and the percentage of non-native species was calculated for each stand. Graminoid species (Cyperaceae, Juncaceae, Poaceae) were treated as a single functional group. Plot cover values were pooled to calculate mean stand values. At each stand, the following additional variables were recorded: stand area (m^2) as estimated from average stand length and width, minimum stand age, elevation (determined from topographic maps), disturbance type and level, and saltcedar seedling density. Each saltcedar stand was aged from root crown sections of the three largest saltcedars within the stand. Disturbance factors such as grazing, clearing, and flooding were qualitatively described as 0 (none), 1

(minimal), 2 (moderate) or 3 (heavy).

Demographics

To describe stand age structures, 2 m wide transects were extended through the long axis of the stand intercepting the highest number of saltcedar plants. Within these transects, all live saltcedar individual plants (clumps) were cut at ground level and aged from the largest stem. Basal stem sections were sorted into seven age classes and the proportion of individuals in each age class was calculated.

Soil sampling

Within each plot, 10 soil cores (0 - 7.5 cm depth) were collected at random and analyzed for texture (particle-size), electrical conductivity (EC), and pH. Samples from each plot were combined and mixed, air-dried, and sieved to 2 mm. Soil texture was determined by hydrometer using the particle-size analysis method outlined in Gee and Bauder (1986). EC and pH measurements were made by shaking 40 g of soil with 80 ml of distilled deionized water for 15 minutes. Samples were allowed to stand for 5 minutes before pH and EC measurements. pH was measured using an Orian 710 meter equipped with a combination gel-filled electrode. EC was determined using a Cole-Parmer conductivity meter. Texture, pH and EC values for each plot were pooled to obtain a stand average.

Statistical analyses

Data were screened for parametric assumptions and transformed when possible. Otherwise, non-parametric tests were used. Differences in wood growth rates between species and states were analyzed using Tamhane's T2 test (unequal variances). A two-

tailed, independent samples t-test was performed on branching data for saltcedar in Arizona and Montana. Correlations between soil, stand and vegetation variables were performed by pooling data from all stands in eastern Montana. Bivariate Pearson correlation coefficients (r) for normally distributed variables and Spearman's coefficients of rank correlation (r_s) for non-normal and categorical variables were computed. T test and correlation analyses were performed in SPSS (7.5 for Windows).

Detrended Correspondence Analysis (DCA, Hill 1979) was used to compare plant community composition in saltcedar stands (Carman and Brotherson 1982, Busch and Smith 1995, Gauch 1995). Mean species percent cover values (0-100) were placed into a species-by-samples data matrix (Gauch 1995) in which samples were represented by saltcedar stands. The species-by-samples data matrix was ordinated by DCA using PC-ORD (McCune and Mefford 1997). Spearman's coefficients of rank correlation (r_s) were computed between key environmental as well as species cover variables and axes 1, 2, and 3 of DCA to identify possible gradients of community organization. Rare species (species not occurring in at least 5 % of saltcedar stands) were omitted as recommended in Gauch (1995). Rare species were down-weighted and axes were rescaled in the DCA ordinations.

RESULTS

Stem growth rates and branching along a latitudinal gradient

Saltcedar stem growth rates (mm/year) decreased significantly from Arizona to California (Figure 2.2, $P = 0.002$) and remained constant with further latitudinal increase. Sandbar willow growth rates did not change significantly with latitude. The lowest stem growth for both species was in Utah where elevation was highest (Table 2.1). Saltcedar growth was similar to that of sandbar willow except in more northern latitudes (Wyoming and Montana) where saltcedar growth was significantly greater ($P < 0.05$ in both states). Saltcedar branching in Montana was significantly higher than in Arizona ($P = 0.011$, Figure 3).

Eastern Montana

Saltcedar was found along the Yellowstone River Drainage and its major tributaries as well as on the shores of Fort Peck Lake (Figure 2.1). Saltcedar stands were not found on the Tongue River with the exception of one inaccessible plant near Ashland, Rosebud Co. The oldest individual sampled in the state was 34 years old at Bighorn Access on the Bighorn River (Table 2.2). The majority of relatively old stands were found along the Bighorn River near Yellowtail Dam in Bighorn Co., with minor exceptions on the Powder and Yellowstone Rivers. Along the Bighorn River stand age decreased as elevation decreased ($r = .67$, $P = 0.05$, $n = 9$), indicating downstream spread along that watershed. The Yellowstone and Powder rivers did not show a clear pattern between saltcedar stand age and elevation, suggesting multiple sites of introduction along these rivers.

Average age class distributions for the Yellowstone, Bighorn and Powder Rivers,

and for isolated stands with ephemeral or intermittent surface water showed a high proportion of young individuals (≤ 15 years) suggesting population increase or frequent resprout (Figure 2.4; seedling beds excluded). Stands at Fort Peck Lake were relatively even-aged.

For all correlation-tested stand variables sample size was 38, except for stand area (square root) where saltcedar seedling bed and outliers values were removed and $n = 29$. Saltcedar SQRT stand area increased linearly with stand age ($r = .53$, $P = 0.003$) (Figure 2.5). Saltcedar % cover increased with stand age ($r = .40$, $P = 0.01$) while % mortality of saltcedar also increased ($r_s = 0.70$, $P < .001$) (Figure 2.5; Table 2.3). The cover of native Salicaceae tree and shrub species, plains cottonwood (*Populus deltoides* Marsh.) and sandbar willow decreased with the age of saltcedar stands (Figure 2.6), and were negatively correlated with saltcedar % cover (Table 2.3). The number of plant species (non-graminoids) and the proportion of native plants present during June and July in saltcedar stands did not change significantly with the age of saltcedar stands (Table 2.3). Disturbance level did not correlate with saltcedar variables, but did correlate with % non-native species ($r_s = 0.32$, $P = .049$) (Table 2.3). Non-native plants found in saltcedar stands included: *Ambrosia artemisiifolia* L., *Cirsium arvense* (L.) Scop., *Cynoglossum officinale* L., *Euphorbia esula* L., *Salsola iberica* Sennen and Pau and *Tanacetum vulgare* L.. Although the cover of individual graminoid species was not tallied, non-native grasses such as *Agropyron repens* (L.) Gould, *Phalaris arundinacea* L., and *Dactylis glomerata* L. were abundant near many areas where saltcedar was found.

Soil pH was the only soil factor found to significantly correlate with saltcedar variables (Table 2.3). Soil pH correlated negatively with saltcedar stand age ($r = -.546$, P

< .001) and saltcedar % cover ($r = -0.33$, $P = .04$) (Figure 2.7). In order to assure equal representation of each river from each saltcedar age class, soil pH data were subsampled from the eastern Montana data set. Subsampled data showed the same trend of decreasing soil pH with increasing stand age ($r = -0.52$, $P = 0.02$, $n = 19$). Thus, differences in soil pH over time are not driven by geographic (river of origin) trends.

The eigenvalues (variances accounted for by the hypothetical environmental gradients or axes) for DCA axes 1, 2 and 3 of the primary matrix were .32, .20, and .09, respectively. The only clear separation of plant communities within the DCA ordination based on watershed origin was for stands termed “Ephemeral”, which had moderate grouping (Figure 2.8).

Associations of environmental stand variables and DCA axes of the species-by-samples ordination revealed gradients along which plant communities, in the presence of saltcedar, may be separating in eastern Montana. The DCA axis 1 was negatively associated with gradients in elevation and stand age, and positively associated with soil pH (Table 2.4). Saltcedar stands tend to decrease in age along axis 1 with the exception of young (3-10 years old) stands (Figure 2.9).

Associations between species variables and DCA axes revealed trends in community organization within saltcedar stands. The cover of native Salicaceae species (sandbar willow and plains cottonwood) and saltcedar seedling density were positively associated with axis 1 of DCA while saltcedar cover, % mortality, and graminoid cover were negatively associated (Table 2.4). Sandbar willow and plains cottonwood were not found within mature saltcedar stands. Axis 2 was positively associated with saltcedar cover and % non-native species, but negatively associated with graminoid cover (Table

2.4). Axis 3 was negatively associated with plains cottonwood and graminoid cover, and positively associated with % non-native species (Table 2.4). Axis 3 accounted for only 9 % of the variation in the DCA ordination, and is not graphically represented.

DISCUSSION

Saltcedar populations appear to be expanding in the continental climates of eastern Montana, and now occupy many disturbed riparian areas in those ecosystems. Despite strong gradients of temperature climates, stem growth in saltcedar did not decrease with latitude (southern California to Montana). The stem growth of saltcedar in Montana, where temperatures are the lowest of the states sampled, is significantly greater than that in Utah ($p < .001$) where saltcedar is highly invasive (Christensen 1962). High elevation in Utah sites may explain growth differences (Table 2.1). Greater wood increments in Arizona are likely a result of growing season differences and much lower branching (see Chapter 1, Table 1.1). Increased branching in saltcedar in the North is perhaps a stress response to frost-induced stem mortality. Saltcedar crown damage and mortality was heavy where thick ice forms during the winter (Fort Peck Lake, Powder River). Superior stem growth over the native sandbar willow in colder, northern latitudes suggests that saltcedar growth is less limited by low temperature than native shrubs. Saltcedar is thought to be cold-limited because of sharp decreases in saltcedar abundance in high elevations in North America (Brock 1994); these results also showed increased mortality with increases in elevation (Table 2.3). Yet saltcedar persists in eastern Montana where winter temperatures can fall below -20° C. This apparent contradiction highlights a rift in our understanding of saltcedar's environmental limitations. The spread of saltcedar in continental climates of North America does not appear to be limited by growing season length or winter temperature. In its native lands, *Tamarix ramosissima* persists over a wide distribution in the cold, continental climate of northern Asia (Baum 1978).

In this study, saltcedar was found on all major watersheds in eastern Montana. In 1982, it had only been reported on the Yellowstone River (Swenson et al. 1982). Rapid regional spread of saltcedar in eastern Montana since its introduction in the mid 1960's suggests that saltcedar has spread mostly by sexual means along riparian corridors. In eastern Montana saltcedar has a pattern of scattering or satellite spread (Bazzaz 1986) as opposed to a continuous advance with an invasive front. Such a pattern suggests that there have been multiple introductions of saltcedar in this region. Little is known about the timing and circumstances of saltcedar's arrival in Montana. It is apparent that the Bighorn River is a major site of introduction due to old and abundant saltcedars found there. Yellowstone River saltcedar populations may be derived in part from the Bighorn River. Upstream increases in saltcedar age on the Bighorn River suggest introductions from Wyoming or perhaps construction of the Yellowtail Dam during 1961-1966 (the oldest stand found in Montana, 34 years old, could have recruited during that period). Saltcedar individuals as old as 51 years were found upstream from Yellowtail Dam at Wyoming Population #1 (Table 2.1).

Saltcedar seedlings were rarely found beneath the canopies of saltcedar or within thick ground cover such as grass. Seedlings were mostly found on newly deposited sandbars at low elevation sites. Shafroth et al. (1998) reported that recruitment success and establishment of saltcedar in central Arizona is dependent on a combination of factors including streamflow and discharge. They concluded that germination and establishment requirements do not necessarily differ between native and non-native tree and shrub seedlings. The fact that saltcedar seed production extends throughout late summer, when it may recruit in the absence of Salicaceae competitors, may confer it

recruitment advantage in eastern Montana.

The high proportion of young individuals (< 15 years old) in saltcedar stands in eastern Montana suggests that populations are increasing and/or that stands are kept young through resprout. Despite a large proportion of young plants found in most stands, saltcedar seedling density significantly decreased with stand age. Vegetative reproduction could not be separated from seed reproduction within transects due to the rhizomatous nature of saltcedar, therefore true sexual recruitment patterns are not known. Although saltcedar may live longer than fifty years (pers obs.), high stem mortality is seen in stands as young as fourteen years in eastern Montana. Everitt (1998) has pointed out that saltcedar stands are often kept young and vigorous by human control efforts such as cutting and burning. Young stand age structures coupled with high stem mortality found in eastern Montana may reflect vigorous resprout in response to frost damage.

Despite stem mortality, total stand area and the percent cover of saltcedar increases with stand age, supporting the contention of land managers that saltcedar is becoming invasive in eastern Montana. Roughgarden (1986) suggests that the square root of the area occupied by an invasive species increases linearly with time; such is the case on a local scale with saltcedar in eastern Montana.

In eastern Montana, soil pH decreased (more acidic) with both increased stand age and saltcedar cover. Detritus associated with saltcedar may acidify the soil as more organic matter is added to the soil surface. However, if saltcedar communities begin on bare substrates, decreases in soil pH over time may be caused by additions of organic matter from all species and may not be exclusively the effect of saltcedar. Salinity (EC) in eastern Montana was not associated with saltcedar presence even though saltcedar is

often described as having large effects on this environmental trait (Brock 1994). Carman and Brotherson (1982) found increased salinity levels in saltcedar-infested soils and reported a high tolerance of saltcedar to many edaphic variables in central Utah. Campbell and Dick-Peddie (1964) found no pattern between edaphic factors and dominant plant species (including saltcedar) on the Rio Grande in New Mexico. Similarly, in central Utah no patterns were found between biotic factors and abiotic factors in saltcedar stands, including soil pH (Brotherson and Winkel 1986). Soil texture, EC and organic matter did not differ between saltcedar and cottonwood stands in southern Arizona, although saltcedar stands did show an increase in EC with stand age (Stromberg 1998a). This lack of differences between stand types was attributed to frequent soil flushing by floodwaters; they did not measure soil pH. The positive correlation of soil pH with axis 1 of DCA suggests that plant communities in eastern Montana are influenced by changes in soil pH. Changes in soil chemistry have been reported following disturbance and the introduction of a new species, as with bracken fern in clear-cut forest types in northern Idaho (Johnson-Maynard et al. 1998).

The strong correlation of stand age with DCA axis 1 suggests that a community maturity gradient is affecting plant composition in riparian habitats of eastern Montana. Such plant community changes with time may be affected by saltcedar maturity, or may stem from the natural succession on deposited sand bars where saltcedar seedlings often begin (Gladwin and Roelle 1998). Although only correlative, decreases in *S. exigua* and *P. deltoides* cover with increases in saltcedar age and cover may indicate a negative effect of saltcedar on these woody competitors (Roughgarden 1986). Alternatively, saltcedar may be occupying disturbed sites where native plants are not successful.

Decreases in native woody plants with the introduction of saltcedar have been shown in southwestern communities as floodplain salinity increases and surface water flow decreases (Cleverly et al. 1997, Smith et al. 1998). However, little is known about long-term successional processes in saltcedar stands (Everitt 1998, Stromberg 1998a). In eastern Montana saltcedar does not appear to be highly competitive and often occurs adjacent to much larger stands of the invasive Russian olive (*Elaeagnus angustifolia* L.); mature saltcedar individuals were occasionally found dead within the canopies of younger native plants such as buffalo-berry (*Shepherdia argentea* (Pursh) Nutt.).

Although saltcedar is quickly spreading in eastern Montana its distribution there is patchy and resembles a gap filling or colonizing strategy typical of immigrants not able to invade intact, undisturbed communities (Bazzaz 1986, Newsome and Noble 1986). Indeed, most saltcedar stands in this study occurred in disturbed sites such as grazed, cleared or constructed river banks, or on newly deposited sandbars. Although no disturbance correlations with saltcedar variables were revealed in this study, the use of a coarse qualitative scale to measure disturbance may have masked a relationship between saltcedar and disturbance. Saltcedar has similarly been described on the Snake River in Idaho as abundant yet “non-aggressive”, with saltcedar frequently found in disturbed areas (Dixon and Johnson 1999). Disturbance by overgrazing increases ecosystem vulnerability to species invasion (Baker 1986, Orians 1986), and is thought to aid saltcedar in the Southwest (Hughes 1993). Within the DCA ordination, eastern Montana plant communities had the highest saltcedar cover where graminoid cover was lowest. Grazing pressure perhaps drives these patterns. It is note-worthy that very little saltcedar was found on the Tongue River where grazing appears minimal and the riparian

community has few breaks in plant cover. Saltcedar was very successful on islands in eastern Montana. Smaller areas and thus less complex communities (Orians 1986) as well as frequent scouring disturbance and inundation could explain heavy colonization of river islands by saltcedar. Decreasing disturbance pressures such as overgrazing may decrease the invasibility of saltcedar in northern regions.

As has been shown in other introduced species (Newsome and Noble 1986), saltcedar's tolerance of a wide range of climate (Chapter 1) may allow it to continue to invade more northern latitudes in North America. Northern ecosystems with continental climates such as eastern Montana appear highly susceptible to saltcedar invasion in the long term. Substantial wood growth, fast expansion, high proportions of young saltcedars within stands, increases in saltcedar cover and the area it occupies, and decreases in native species % cover in older saltcedar stands are strong signs of invasion. While the naturalization process for saltcedar in eastern Montana is still young (< 40 years), this plant is already found on most major river systems. Saltcedar in eastern Montana may be in a lag phase of invasion characteristic of many invasive organisms (Baker 1986, Bazzaz 1986, see Chapter 1).

The time it takes to become invasive in a new region varies between species (Bazzaz 1986). Seemingly mild community effects of saltcedar should not lead to complacency as long-term effects of invaders may be much more serious than initial impressions (Orians 1986). Saltcedar may have been naturalized where it is now invasive in the Southwest for over a century before it became a concern. The results from this study show that *T. ramosissima* is now found on most major river corridors of eastern Montana. They also show an increase of stand area and cover with time accompanied

with significant resprouting in stands of all ages. These results and correlated changes in community structure and soil properties (pH) suggest that *T. ramosissima* has the potential to invade continental climates of North America, particularly in disturbed sites. Prevention and control of this plant in the Northwest are likely to be more successful in the early phases of colonization of saltcedar as compared to the difficulty of removal of mature, well-established stands. Early assessments of invasive potential such as the one reported here are preventive tools, hopefully to be used in the conservation of biodiversity.

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TABLES

Table 2.1. Site information for collections of *Tamarix ramosissima* (saltcedar) and *Salix exigua* (willow) stems.

State and watershed	Population #	Latitude	Longitude	Elevation (m)
<u>Arizona</u>				
Gila River	1	33° 20.5 N	112° 37.5 W	271
"	2	33° 22.7 N	112° 19.5 W	274
"	3	33° 15.2 N	112° 09.7 W	280
California				
Big Morongo Canyon	1	34° 02.5 N	116° 34.5 W	800
<u>Nevada</u>				
Virgin River	1	36° 47.4 N	114° 05.8 W	517
"	2	36° 50.4 N	113° 59.0 W	528
"	3	36° 53.8 N	113° 55.1 W	546
Utah				
Green River	1	39° 11.5 N	110° 04.6 W	1245
Price River	2	39° 14.3 N	110° 15.2 W	1410
"	3	39° 27.0 N	110° 37.7 W	1450
Wyoming				
Bighorn River	1	44° 29.3 N	108° 02.9 W	1155
Shoshone River	2	44° 51.3 N	108° 19.8 W	1169
Creek	3	44° 41.2 N	108° 04.4 W	1331
Montana				
Fort Peck Lake	1	47° 37.3 N	106° 11.5 W	703
"	2	47° 33.7 N	106° 13.2 W	697
Hell Creek	3	47° 35.3 N	106° 54.8 W	710

Table 2.2. Characteristics of *Tamarix ramosissima* stands in eastern Montana.

Site #	Stand	Watershed	Latitude*	Longitude	Elev.(m)	Stand age (years)	Stand area (m ²)
1	BHBH1	Bighorn River	45° 25 N	107° 47 W	944.4	31	358
"	BHBH2	"	"	"	"	34	544
2	BHGM1	"	45° 50.553 N	107° 35.235 W	836.7	24	2,230
"	BHGM2	"	"	"	"	17	242
3	BHLM1	"	46° 08.436 N	107° 27.777 W	795	24	437
"	BHLM2	"	"	"	"	1	176
"	BHLM3	"	"	"	"	1	289
"	BHLM4	"	"	"	"	21	372
4	BHML	"	45° 31.5 N	107° 43.4 W	897	24	260
5	BHTL	"	45° 38.566 N	107° 39.492 W	880.8	30	1,696
6	BHTM	"	45° 20.668 N	107° 52.668 W	994.5	27	314
7	CYS	Clark's Fork, Yellowstone R.	45° 18.838 N	108° 54.639 W	1086	14	15
8	EX63	ephemeral	46° 12.130 N	107° 15.765 W	932.4	10	378
9	FPSP	Fort Peck Lake	47° 33.669 N	106° 12.716 W	690.6	17	105
10	HELL1	"	47° 35.178 N	106° 54.986 W	702.9	14	549
"	HELL2	"	47° 35.317 N	106° 54.817 W	"	19	10,000
"	HELL3	"	"	"	"	1	2,500
11	MPC1	Montana Power Co., ash pond	45° 53.2 N	106° 37.2 W	990	20	689
"	MPC2	"	"	"	"	5	91
12	PRBC	Powder R.	45° 11.863 N	105° 45.252 W	965.7	14	300
13	PRBLM1	"	45° 20.865 N	105° 31.827 W	903	20	246
"	PRBLM2	"	45° 20.788 N	105° 31.938 W	"	11	448
"	PRBLM3	"	45° 20.921 N	105° 31.387 W	"	4	147
14	PRF	"	45° 42.000 N	105° 10.693 W	855	31	1,024
15	PRGR1	"	46° 28.387 N	105° 18.521 W	681	13	125
"	PRGR2	"	"	"	"	1	155
16	PRT1	"	46° 44.409 N	105° 25.917 W	674.1	1	150
"	PRT2	"	"	"	"	10	100
"	PRT3	"	"	"	"	1	200
17	PRWY	"	45° 00.350 N	105° 53.993 W	1032.6	7	270
18	WC1	Wolf Creek	46° 32.009 N	106° 38.690 W	762	6	36
"	WC2	"	"	"	"	8	272
19	YSC	Yellowstone R.	46° 08.421 N	107° 32.821 W	840	17	198
20	YSDC	"	45° 41.622 N	108° 38.434 W	960	11	32
21	YSM	"	46° 30.225 N	105° 44.128 W	711.3	30	144
22	YSMB1	"	46° 15.429 N	107° 20.285 W	810	21	20,574
"	YSMB2	"	"	"	"	1	360
23	YSRR	"	46° 15.909 N	106° 41.915 W	758.7	19	115

* Unless given, GPS location was recorded at each site, not per individual stands within a site.

Table 2.3. Correlation matrix for *Tamarix ramosissima* (TARA) stands in eastern Montana ($N = 38$). Values are Pearson (\dagger) and Spearman rank correlation coefficients. PODE = *Populus deltoides*, SAEX = *Salix exigua*.

Stand properties	Stand age	TARA cover	TARA % mortality	TARA seedling density	PODE cover	SAEX cover	Graminoid cover	% non-native
Stand area	0.38*	0.35*	0.30	-0.11	0.02	-0.32*	0.19	0.26
Disturbance	-0.09	0.05	-0.14	0.26	0.19	-0.07	-0.19	0.32*
Elevation	0.27 [†]	0.07 [†]	0.41**	-0.52***	-0.33*	0.01	0.26 [†]	0.05 [†]
Species properties								
TARA cover	0.40**	1.00						
TARA % mortality	0.70***	0.41*	1.00					
TARA seedling density	-0.59***	-0.22	-0.48**	1.00				
PODE cover	-0.32*	-0.38*	-0.45**	0.36*	1.00			
SAEX cover	-0.43**	-0.46**	-0.51***	0.14	0.36*	1.00		
Graminoid cover	0.45*** [†]	0.02 [†]	0.38*	-0.38*	-0.19	-0.15	1.00	
% non-native species [‡]	-0.05 [†]	0.25 [†]	0.08	0.26	-0.27	-0.46**	-0.28 [†]	1.00
# of species [‡]	-0.01	0	-0.11	0.14	0.17	0.06	0.32*	-0.09
Soil properties, 0-7.5 cm								
EC	-0.05	-0.11	0.32	0.07	-0.18	-0.22	-0.07	0.28
pH	-0.55*** [†]	-0.33** [†]	-0.55***	0.31	0.34*	0.27	-0.47*** [†]	0.12 [†]
Clay	0.13	0.07	0.27	0.03	-0.11	-0.24	0.30	-0.14
Sand	0.05 [†]	0.10 [†]	-0.11	-0.13	-0.05	0.05	-0.16 [†]	0.30 [†]
Silt	-0.18 [†]	-0.15 [†]	0.03	0.24	0.04	0.09	0.06 [†]	-0.22 [†]

Statistical levels of significance for correlations are indicated by * ($P \leq 0.05$), ** ($P \leq 0.01$) or *** ($P \leq 0.001$).

[‡] Refers to non-graminoid species only.

Table 2.4. Spearman rank correlation coefficients (r_s) between detrended correspondence analysis (DCA) axes scores and variables from *Tamarix ramosissima* (TARA) stands in eastern Montana. PODE = *Populus deltoides*, SAEX = *Salix exigua*.

	DCA Axis		
	1	2	3
Saltcedar stand properties			
Elevation	-0.38**	-0.14	-0.07
Disturbance	0.09	0.28	0.14
Stand age	-0.53***	-0.06	-0.32
Stand area	-0.22	0.04	-0.03
Soil properties, 0-7.5 cm			
EC	-0.19	0.02	0
pH	0.41**	0.14	0.09
Clay	-0.11	-0.21	0.02
Sand	-0.03	0.22	-0.01
Silt	0.04	-0.16	0.1
Species properties			
TARA cover	-0.39*	0.6***	0.19
TARA % mortality	-0.61***	-0.02	-0.16
TARA seedling density	0.37*	0.15	0.2
PODE cover	0.73***	-0.07	-0.38*
SAEX cover	0.67***	-0.27	0.16
Graminoid cover	-0.38*	-0.67***	-0.4*
# of species [‡]	0.14	-0.16	-0.19
% non-native species [‡]	-0.29	0.36*	0.39*

Statistical levels of significance for correlations are indicated by * ($P \leq 0.05$), ** ($P \leq 0.01$) or *** ($P \leq 0.001$). [‡] Refers to non-graminoid species only.

FIGURES

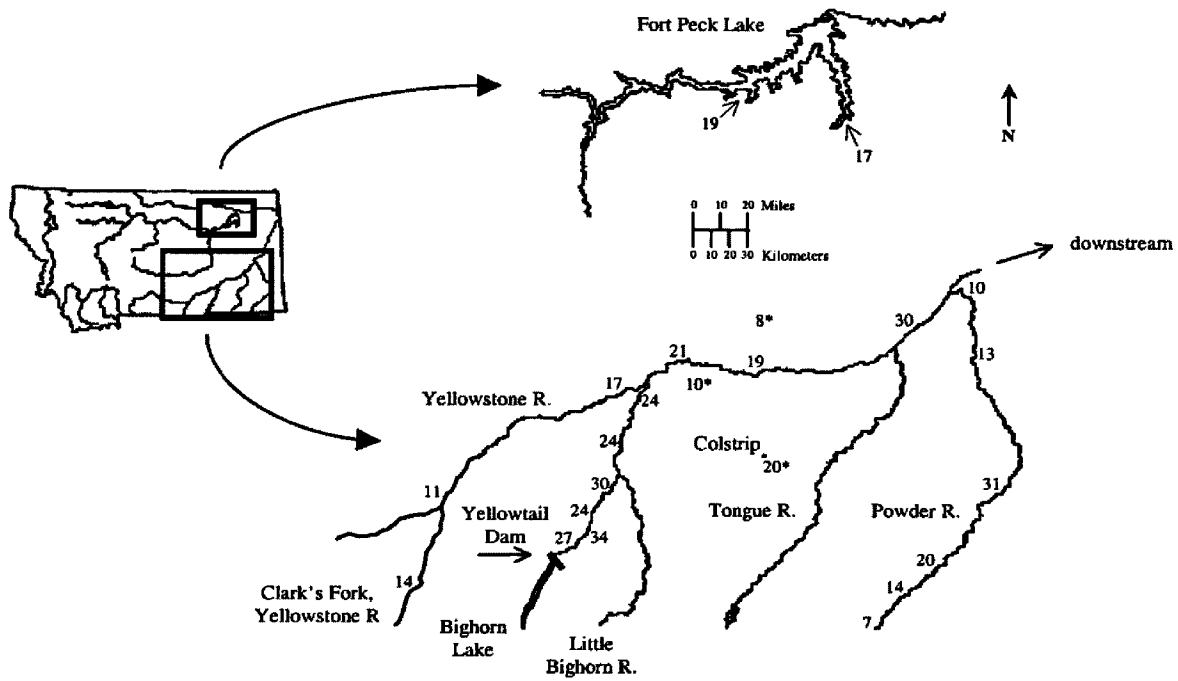


Figure 2.1. Saltcedar study area in eastern Montana showing sampling sites and maximum ages of saltcedar stands. * Isolated sites not along main rivers.

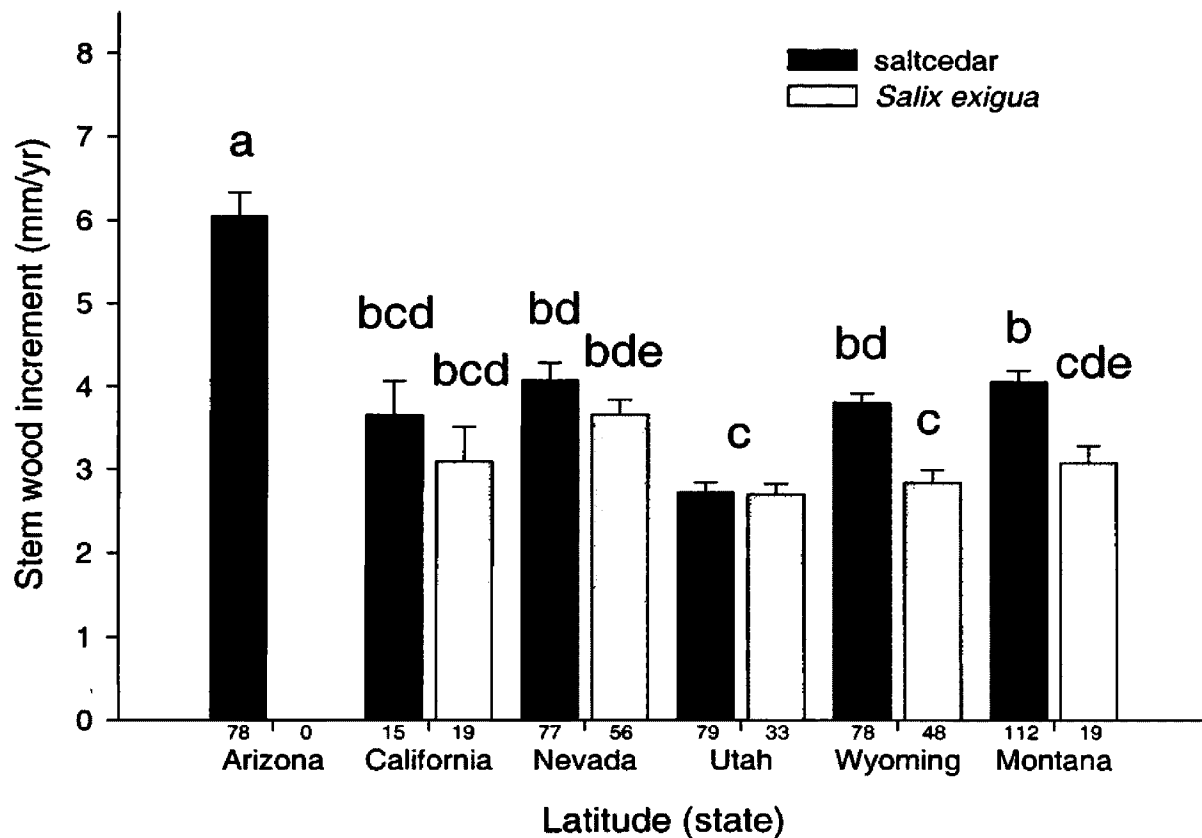


Figure 2.2. Stem growth rates of the non-native saltcedar (black) and native *Salix exigua* (grey) along a latitudinal gradient in western United States. Letters represent differences at the 95% significance level ($P = .05$). Bars represent ± 1 SE. Numbers under bars are sample sizes (n).

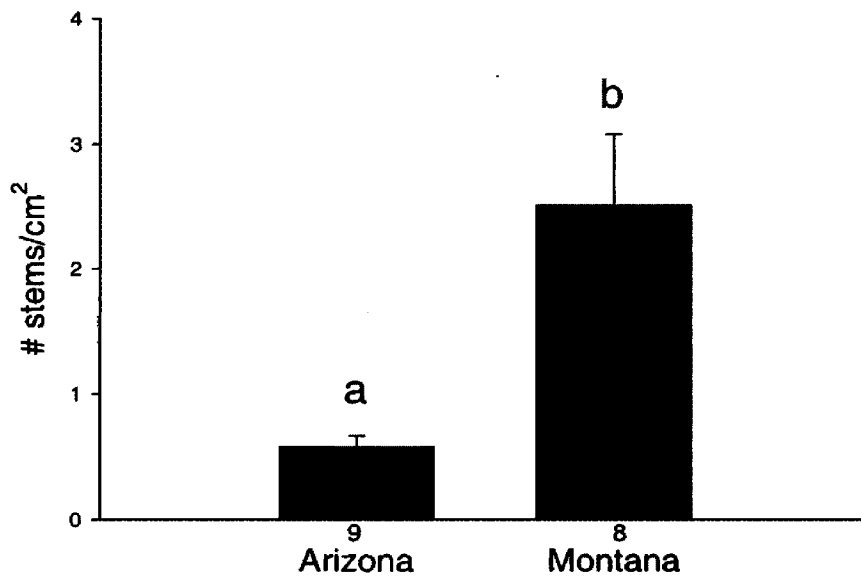


Figure 2.3. Degree of branching for *Tamarix ramosissima* from Arizona and Montana at .5 m above-ground level. Letters denote significant differences ($P = .011$). Bars represent ± 1 SE. Numbers under bars are plants sampled (n).

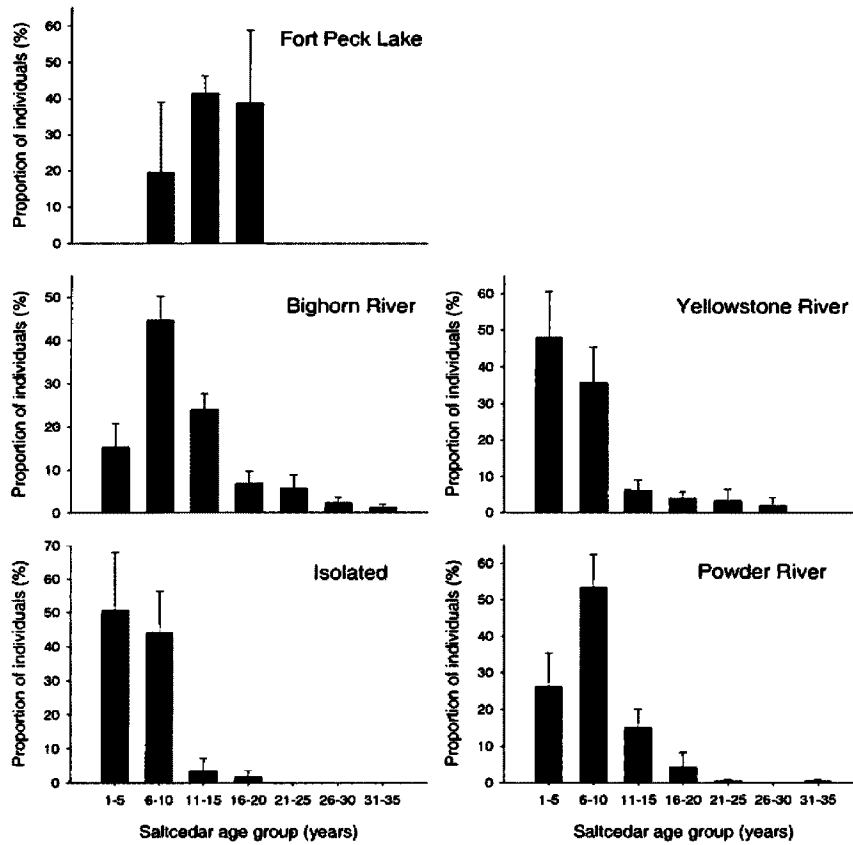


Figure 2.4. Age structure of *Tamarix ramosissima* (saltcedar) stands from 4 watersheds and “Isolated” saltcedar stands (ephemeral water sources) in eastern Montana. Bars represent ± 1 SE.

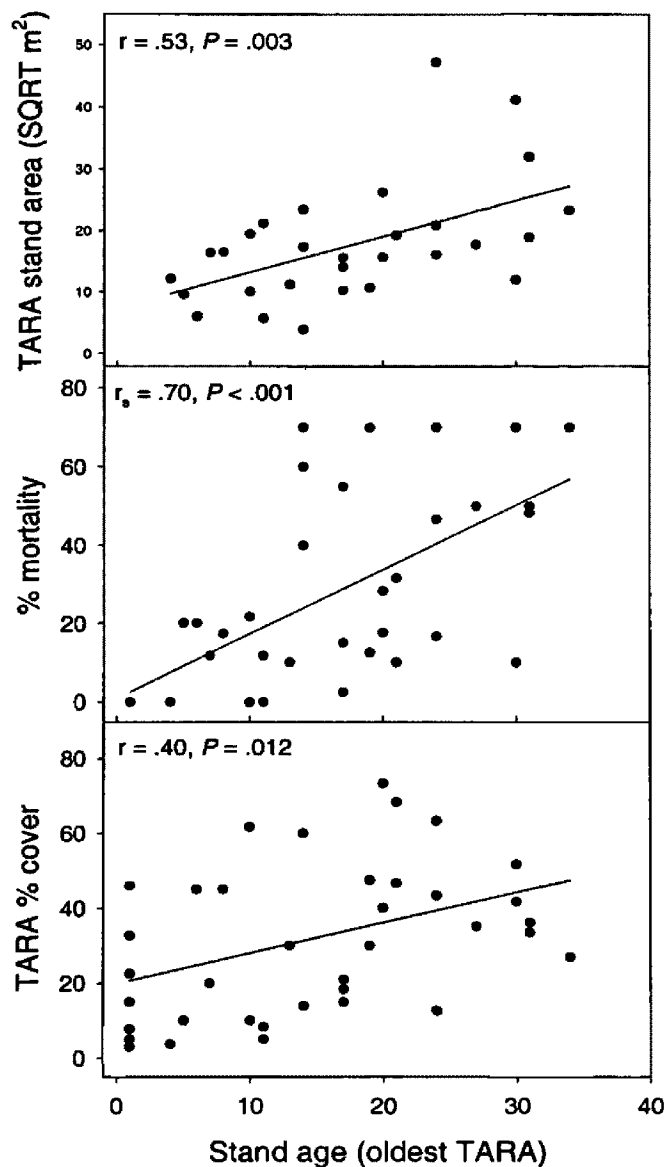


Figure 2.5. Correlations between *Tamarix ramosissima* (TARA) stand age, TARA % mortality ($n = 38$), saltcedar % cover ($n = 38$) and square root (SQRT) stand area ($n = 29$) in eastern Montana. Pearson (r) and Spearman (r_s) correlation coefficients are given along with significance values (P).

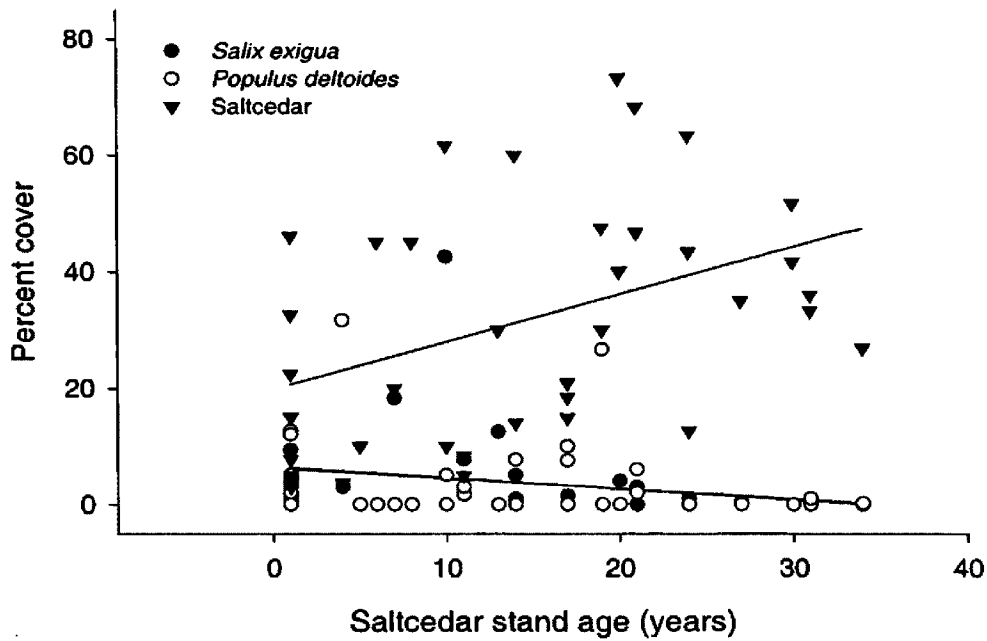


Figure 2.6. Pearson (r) and Spearman (r_s) correlations between *Tamarix ramosissima* stand age and percent cover of saltcedar, *Salix exigua* and *Populus deltoides*. Saltcedar percent cover increased with stand age ($r = .40$, $p = .012$), while SAEX ($r_s = -.427$, $p = .008$) and PODE ($r_s = -.322$, $p = .049$) decreased with stand age.

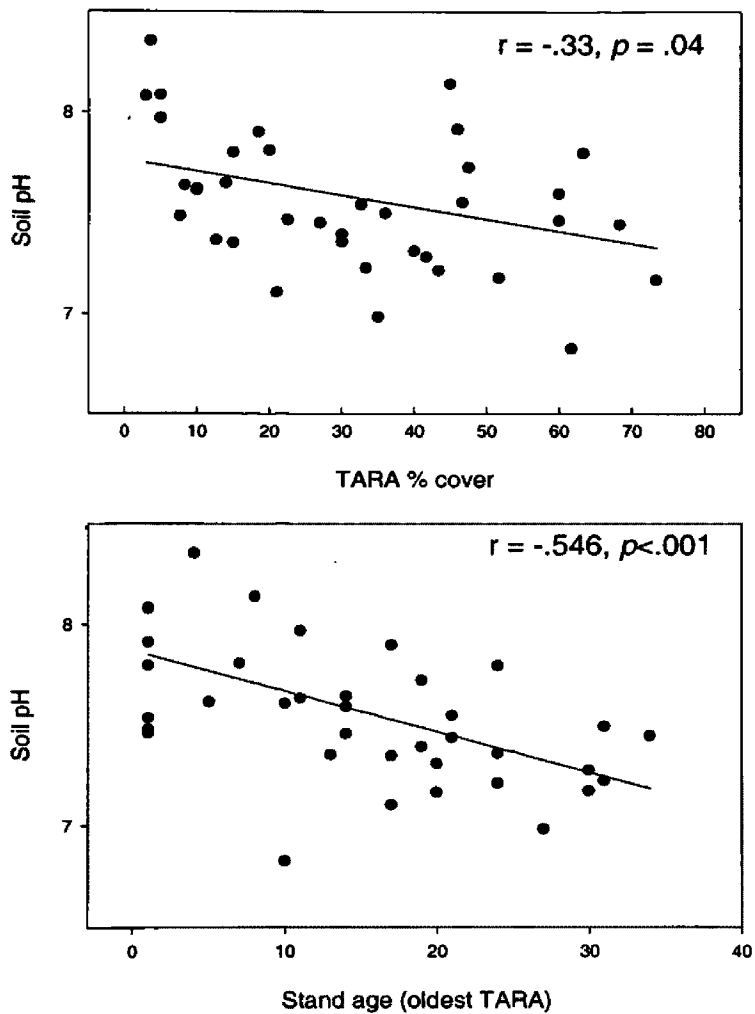


Figure 2.7. Correlations between soil pH and stand age and % cover of *Tamarix ramosissima* (TARA) in eastern Montana. Pearson (r) correlation coefficients are given along with significance values (P).

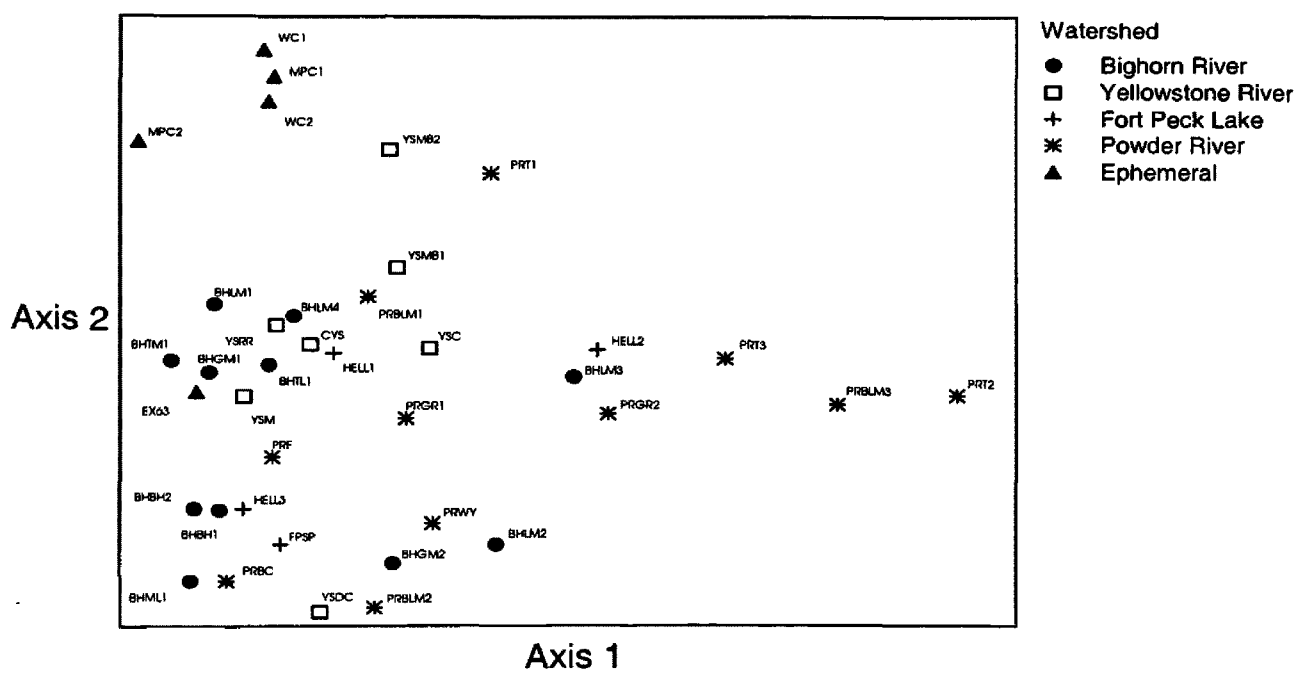


Figure 2.8. Detrended correspondence analysis (DCA) species-by-samples matrix ordination of *Tamarix ramosissima* (saltcedar) stands in eastern Montana with watersheds distinguished by symbol (see Table 2.2).

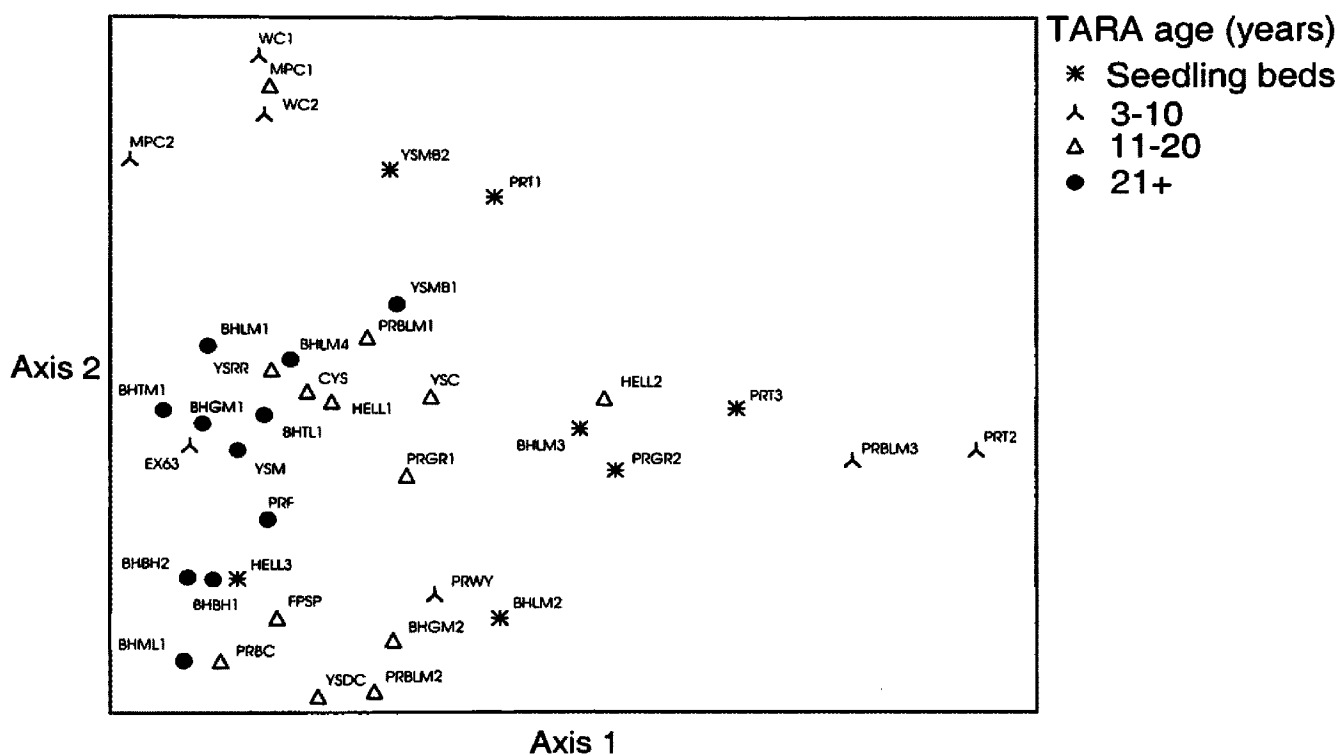


Figure 2.9. Detrended correlation analysis (DCA) species-by-samples matrix ordination of *Tamarix ramosissima* (saltcedar) stands in eastern Montana with stand ages distinguished by symbol.