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Climatic and hydrologic effects on the establishment of Tamarix ramosissima in the cold desert of northern Wyoming (Bighorn Lake)

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CLIMATIC AND HYDROLOGIC EFFECTS ON THE ESTABLISHMENT OF *TAMARIX RAMOSISSIMA* IN THE COLD DESERT OF NORTHERN WYOMING (BIGHORN LAKE)

by

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Climatic and hydrologic effects on the establishment of *Tamarix ramosissima* in the cold desert of northern Wyoming (Bighorn Lake) (38 pp.)

Director: Dr. Paul B. Alaback

Saltcedar (*Tamarix ramosissima)* is an exotic phreatophyte of the *Tamaricaceae* family, and is native to Eurasia and the Mediterranean regions. *Tamarix* has become widely established throughout the southwestern United States, particularly along rivers where natural flow regimes have been altered. Previously, field studies on establishment patterns of *Tamarix* were undertaken in the hot, xeric scrub communities of the Southwest. In this study, I address effects of climate and flooding on rates of mature *Tamarix* shrub recruitment in the cold, semi-arid desert environment of northern Wyoming at Bighorn Lake. Study results suggest that cooler temperatures ($p=0.041$), lower potential evapotranspiration ($p=0.054$), and high peak lake elevations ($p=0.031$) were potentially constraining rates of *Tamarix* recruitment. I found slower seedling growth, lower initial densities, later flowering, and a shorter growing season in northern Wyoming when compared to seedling studies in the Southwest. These results indicate that rates of recruitment by *Tamarix* may be somewhat slower, and invasive potential less certain in colder environments.

Resource managers may find it beneficial to concentrate control efforts on newer *Tamarix* invasions in the north where initial seedling mortality appears to be very high, growth slower, and flowering later, leaving fewer and smaller shrubs to treat. In addition, an integrative model on hydrologic requirements for successful establishment of *Tamarix* seedlings should be developed. This prescriptive model could provide resource managers with specific lake parameters, both magnitude and timing, which would allow for manipulation of reservoir releases to control future invasions.

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1. Introduction

Biological invasions by plants rank with the world's most intractable ecological problems (Vitousek et al., 1996; Williamson, 1996). The first ever international workshop for weed risk assessment was held in South Australia in February, 1999. Many of these invasive plants have brought about significant changes in landscape function, with riparian habitats being especially prone (Brock, 1994). Lack of knowledge on the biology, ecology, and environments of riparian invasive plants has become a major concern for land managers throughout the U.S. (Everitt, 1980). A recent U.S. Executive Order (February, 1999) recognized the need for all federal agencies to address invasive species as a major management concern. The genus *Tamarix* (only the deciduous species), a native of Eurasia and the Mediterranean regions was introduced into the U.S. as an ornamental in the late 1800's, and has been associated with declines in native biodiversity and water availability along desert rivers in the Southwest (Horton, 1960). Great Britain and southeastern England have reports of *Tamarix gallica* beginning to invade semi-arid, riparian areas (Brock, 1994). Eight species of *Tamarix* have been identified in U.S. and Canadian riverways (Brock, 1994). These riparian ecosystems are regional hot spots of biodiversity. It was presumed that *Tamarix* would not move northward due to its apparent preference for arid and semi-arid riparian environments (Baum, 1967), yet establishment is becoming more widespread in northern Wyoming, especially along Bighorn Lake (Swenson and Hendricks, 1982; Knight et al., 1987; Akashi, 1988; Knight, 1994). *Tamarix* is known as a drought tolerant species (Tomanek and Ziegler, 1960; Robinson, 1965; Van Hylckma, 1970, 1974, 1980; Brooks, 1971;

Broadfoot, 1973; Everitt, 1980; Brotherson and Winkel, 1986; Sedgwick and Knopf, 1989; Smith,1989; Shafroth et al., 1995; Cleverly et al., 1997; Devitt et al., 1997), yet it is unclear to what extent rates of establishment may be limited in arid regions of northern latitudes by colder temperatures. Previous field studies of *Tamarix* have only addressed establishment patterns in the relatively hot and xeric scrub communities in the southwestern U.S.

Another key question is to what extent are rates of *Tamarix* establishment affected by certain hydrologic regimes. *Tamarix* appears to be particularly well adapted to colonizing floodplains of artificially controlled reservoirs and rivers (Tomanek and Ziegler, 1960; Robinson, 1965; Everitt, 1980; Fenner et al., 1985; Stevens and Waring, 1985; Akashi, 1988; Knight, 1994; Busch and Smith, 1995; Di Tomaso, 1998). Altered flow regimes (peaks changed from spring run-off to summer and fall releases) and irregularly timed flood events appear to provide a suitable environment for successful *Tamarix* establishment (Horton, 1977; Everitt, 1980; Stevens and Waring, 1985; Di Tomaso, 1998). Rapid *Tamarix* invasion in the southwestern U.S. coincided with the building of many large dams (Brock, 1994). *Tamarix* invasion in Britain is apparently indirectly caused by global warming and lower flow conditions (Brock, 1994). The arrival of *Tamarix* in northern Wyoming appears to coincide with the installation of the Yellowtail Dam on Bighorn Lake (Swenson and Hendricks, 1982; Akashi, 1988). Reductions in water table or drawdown has been shown to cause mortality to established *Tamarix* stands (Van Hylckama, 1970; Horton, 1977; Devitt et al., 1997). On the other hand, *Tamarix* seedlings can survive and grow in inundated conditions from two to six weeks

(Horton et al., 1960 Gary, 1963; Graf, 1978; Bradley and Smith, 1986; Gladwin and Roelle, 1998), but extended inundation over six weeks or complete submergence for several weeks can kill mature shrubs (Everitt, 1980; Stevens and Waring, 1985; Kerpez and Smith, 1987; Brock, 1994).

In addition to questions of climatic and hydrologic effects on *Tamarix* establishment, it is unknown how rates of seedling recruitment in northern Wyoming contrast with sites in the southwestern U.S. Previous research on *Tamarix* seedlings found that a moist soil substrate, placid waters, lack of competition, and a sunny site (shade intolerance) was needed for successful germination (Tomanek and Ziegler, 1960; Warren and Turner, 1975; Kunzman et al., 1989). Also, seed viability was found to be up to five weeks (longer in controlled nursery environments), seed germination was generally within 24 hours, flowering occurred within the first year, and a lengthy seed dispersal period commonly occurred between late April through October (Tomanek and Ziegler, 1960; Campbell and Dick-Peddie, 1964; Everitt, 1980; Warren and Turner, 1975; Gladwin and Roelle, 1998). Other traits of *Tamarix* include being a facultative phreatophyte, a halophyte, fire tolerant, and the ability to layer, sprout, and develop adventitious roots (Merkel and Hopkins, 1957; Tomanek and Ziegler, 1960; Gary, 1963; Campbell and Dick-Peddie, 1964; Wilkinson, 1966; Brooks, 1971; Regehr et al., 1975; Warren and Turner, 1975; Horton, 1977; Everitt, 1980; Fenner et al., 1985; Bradley and Smith, 1986; Brotherson and Winkel, 1986; Kunzman et al., 1989; Busch and Smith, 1995; Shafroth et al., 1995; Gladwin and Roelle, 1998). In the Southwest, studies have found very high first year seedling density, which is reduced dramatically by the third year (Tomanek and

Ziegler, 1960; Warren and Turner, 1975 Kunzman et al., 1989). In their first year, seedlings grow slower than any other riparian species, but by their second year shrubs can grow up to 3m with root length dependent on the water table (Merkel and Hopkins, 1957; Tomanek and Ziegler, 1960; Horton, 1977; Everitt, 1980; Goldsmith and Smart, 1982; Di Tomaso, 1998; Gladwin and Roelle, 1998).

1.1. Study objectives

The combination of the second highest lake level ever recorded at Bighorn Lake in July of 1997, resulting in seedling quantities never seen before by resource managers, set up ideal conditions to develop and answer research questions in the field on *Tamarix ramosissima* invasions in northern Wyoming. The first two objectives of this study are to determine the effects of (1) climate – temperature, precipitation, and potential evapotranspiration, and (2) hydrology – peak lake levels and length of inundation on the rate and success of *Tamarix* recruitment in the cold desert environment of northern Wyoming. The final study objective is to collect baseline information on (3) *Tamarix* seedling growth, density, mortality, first flowering, and length of growing season for the 1997 cohorts noted above. This data will be compared to similar studies in the Southwest to provide a context for assessing growth rates and invasion rates of *Tamarix* in these northern sites. Research findings should aid resource managers in developing better management strategies for control of *Tamarix* in colder climates.

2. The study area

2.1. General description of study area

Bighorn Lake in northern Wyoming is a controlled reservoir situated in a semi-arid cold desert environment near the northern geographic limit of *Tamarix*, thus providing an ideal research location to address issues of climatic and hydrologic effects on *Tamarix* invasions as well as to document patterns of seedling dynamics.

Study sites are located on the south end of Bighorn Canyon National Recreation Area (National Park Service) and the Yellowtail Wildlife Habitat Management Area (Wyoming Game and Fish) in northern Wyoming, USA (44°45'N, 108°8'W; Fig.1). The total land area is 22,490ha. The confluence of the Bighorn and Shoshone Rivers is located on the south end of the lake with the current flowing northward into Montana, the Yellowstone River, and eventually into the Missouri River. Bighorn Canyon encompasses the reservoir known as Bighorn Lake formed in 1966 by the Yellowtail Dam located at Ft. Smith, Montana. Bighorn Lake is 113km long and only a few kilometers at its widest point. The water level of the reservoir fluctuates considerably. The highest lake level (1115m) occurred in July of 1967 when the reservoir was being filled to capacity, and the lowest lake level (1089m) occurred in October of the same year (U.S. Bureau of Reclamation). Not only do the lake levels fluctuate, but the timing of reservoir releases are very unpredictable based on spring run-off and agricultural needs in the surrounding farmlands.

2.2. Study area climate

The Bighorn Basin is cool-temperate and semi-arid, but with an extreme continental climate. Bighorn Basin provides a pocket for cold air drainage at night. Daily temperatures are lowest in January, averaging –18°C with the lowest temperature recorded at –37°C (National Climatic Data Center). Bighorn Basin is also the hottest part of Wyoming in the summer, averaging 33°C in July with the highest temperature recorded at 46°C (National Climatic Data Center). Warming spells and chinooks in the winter are also common in the Bighorn Basin. Average relative humidity is quite low, averaging 25%, with lows of 5 to 10% in both the summer and winter. The frost-free period begins around mid-May and lasts an average of 125 days in the basin. Bighorn Basin is the driest part of the state with annual average precipitation from 127 to 203mm (Martner, 1986). Snow is very light in the Bighorn Basin with annual averages from 381 to 508mm. About two-thirds of the total precipitation occurs as rainfall in the spring and early summer and one-third coming as snow (Knight, 1994). Bighorn Canyon's close proximity to the eastern slopes of the Northern Rocky Mountains places it within a significant rain shadow.

2.3. Study area vegetation

Encompassed within the park is a diversity of vegetation that is characteristic of the foothills in north central Wyoming. The Great Basin element is most prevalent toward the drier southern portion where the study sites are located. Dominant species include greasewood (*Sarcobatus vermiculatus*), sagebrush (*Artemisia tridentata*), saltbush (*Atriplex heterosperma),* curlleaf mountain mahogany (*Cercocarpus ledifolius)*, and Utah juniper *(Juniperus osteosperma*) (Knight et al., 1987). Riparian vegetation mosaics along Bighorn Lake includes mudflats and floodplain shrubland and woodlands. Plains cottonwood *(Populus deltoides)* and saltcedar (*Tamarix ramosissima)* are the most conspicuous vegetation type along the floodplains of Bighorn Lake (Knight et al., 1987; Akashi, 1988). Fluctuations of water level due to flood control create an ideal environment for the invasion of weedy species such as *Tamarix*. With the introduction of controlled flows in 1966, it appears that *Tamarix* may be dominating the reservoir mudflats along Bighorn Lake as the older cottonwoods are dying off (Akashi, 1988).

3. Methods

3.1. Study site selection

On July 14th, 1997, the second highest lake level (1113m above sea level) was recorded at Bighorn Lake (U.S. Bureau of Reclamation). Waters did not begin to recede significantly until mid-September. In late September, study areas were selected along the narrow band or "bathtub ring" of *Tamarix* seeds that were deposited after high waters receded. Only bands with obvious new seedlings were selected. Study sites were established along the "bathtub ring" of new seedlings at Crooked Creek north (NCC) and south (SCC) banks (44°52'5"N, 108°15"W and T58,R95,S36) and Kane Causeway east (EKC) and west (WKC) banks (44°45'N, 108°8'W and T56,R94,S15). Elevations were similar for all four study sites (1113-1114m). Each site has the opposite facing aspect than their labels (i.e. NCC has a south facing aspect) (Table 1). Site vegetation communities include greasewood desert shrubland (*Sarcobatus vermiculatus/ Artemisia tridentata*), floodplain shrubland (*Populus deltoides/ Artemisia tridentata*), and sagebrush desert (*Artemisia tridentata/ Chrysothamnus nauseosus)* as defined and delineated on vegetation cover maps for Bighorn Canyon NRA (Knight et al. 1987).

Table 1
General information and study site characteristics.

Study site	Geographic location	Township & Range	Elevation (m)	Aspect	Vegetation (Knight et al., 1987)	Soil Textures (Akashi 1988; Lebruska 1996)
North Crooked Creek (NCC)	44°52'5"N, 108°15"W	T58, R95, S36	1113	S-SE	Greasewood desert shrubland	Sandy-loam/clay
South Crooked Creek (SCC)	44°52'5"N, 108°15"W	T58, R95, S36	1113	N-NW	Greasewood desert shrubland	Sandy-loam/clay
East Kane Causeway (EKC)	44°45'N, 108°8'W	T56, R94, S15	1113	West	Floodplain shrubland	Sandy-loam/loam
West Kane Causeway (WKC)	44°45'N, 108°8'W	T56, R94, S15	1113	East	Sagebrush desert shrubland	Loam/sandy-loam

3.2 Climate

Data on daily precipitation and temperatures from 1951 to present were collected from the National Climatic Data Center and the National Oceanic and Atmospheric Administration at the climate observation station for Western Sugar in Lovell, Wyoming (www.ncdc.noaa.gov). The weather station is located 16km west of the study sites (44°50'N, 108°10'24"W) at an elevation of 1169m. Vegetation is comparable to the study sites with floodplain woodland species including sagebrush (*Artemisia tridentata*), saltbush (*Atriplex heterosperma*), Plains cottonwood (*Populus deltoides),* Russian olive (*Elaeagnus angustifolium),* and saltcedar (*Tamarix ramosissima).*

3.3. Hydrology

Daily lake elevations from 1966 to present were collected for Bighorn Lake from the U.S. Bureau of Reclamation, Yellowtail Dam Unit, Montana Area Office (http://www.gp.usbr.gov).

3.4. Mature shrubs

Representative stands of mature *Tamarix* shrubs were chosen within 10m from the four seedling study sites (NCC, SCC, EKC, WKC) to maintain similar site characteristics for comparison. Plots were located in four floodplain terraces from low (1109-1111m), mid (1111-1113m), high (1113-1114m), to highest (1114+m) elevations, to represent several obvious established "bathtub rings" of mature *Tamarix* shrubs. One plot was installed for each elevation on each of the four sites (N=16). Plot size was chosen (10 x $10m^2$) to be inclusive of variable shrub sizes and densities within each floodplain category. Within each plot, individual shrubs were cut below ground level (the deepest was 0.6m) to find the root crown, and rhizome rings were counted to determine shrub age (Brotherson et al., 1984). A maximum of 15 shrubs were sampled from each of the four elevation plots at each of the four locations. Some plots had fewer than 15 shrubs to sample, thus the total sample size was N=178. Shrubs were sampled by standing at the center of the $10m^2$ plot, turning a Silva compass index pointer three times, laying out a measuring tape in the direction of the index pointer arrow, selecting the first three shrubs encountered, then starting again at plot center until a total of 15 shrubs maximum were sampled. Density was determined for each elevational plot (4 floodplain terraces) at each of the four study sites (N=16).

3.5. Seedlings

Seedling density and mortality were measured by installing line transects (2 - 15m long, 1m wide, 30m total coverage) on each of the four study sites (NCC, SCC, EKC, WKC) parallel with the water's edge on the newly formed "bathtub ring" at 1113.2m above sea level. At each study site, 10 - (20 x 20cm^2) density plots were systematically located every 3 meters starting at 1.5m on these line transects (Fig. 2). All seedlings were counted inside the plot frame to measure density. In each plot frame, four seedlings were tagged on the inside corners of a grid to measure growth and mortality, except where four seedlings could not be found, thus N=154. One meter long lines, perpendicular to the main line transect, were systematically located at 0, 3, 6, 9, 12, and 15m for each study site. On these 1m perpendicular lines, three seedlings were tagged at 30, 60, and 90cm to measure growth and mortality, except where three seedlings could not be found, thus N=142. Density and mortality were measured from a total of 296 tagged seedlings and 40 - (20 x 20cm^2) plots. Growth (height of the tallest stem for each tagged seedling) was measured weekly from October 2, 1997 to May 16, 1998. Final growth and mortality data was collected September 16, 1998. Soil temperatures were taken next to the main line transect, on each of the four study sites, biweekly at noon regardless of weather from October to November 1997, then resumed in April to May 1998 to determine length of growing season. Depths of 5, 10, and 25cm were chosen based on average root length observations, and potential root lengths into the second year. When soils dropped at or below freezing (0°C), I observed no more seedling growth and the aboveground plant stems turned a yellow-brown.

4. Analysis

4.1. Climate and Hydrology

First, linear regressions were used to determine the amount of variation in mature *Tamarix* shrub recruitment associated with each of the following independent variables: temperature (GDD), precipitation, potential evapotranspiration (PET), peak lake levels, and length of inundation. Site effects were assessed using covariate analysis in which each site was coded into an independent binary variable for the regression. Site effects were judged significant if the site variables were significantly associated with residual variation in the regression model after accounting for variation associated with the main independent climate/hydrology variable (e.g. GDD, precip, PET, peak lake level, and length of inundation) at $p \leq 0.05$.

Second, climatic and hydrologic observations were divided into two subgroups to examine general differences in mature *Tamarix* shrub recruitment with respect to extremes in climatic and hydrologic variation. These subgroups were formed by sorting each climate and hydrology variables from low to high (30 year) and split into two equal sized (15 year) subgroups. Then, for each subgroup, mean number of shrubs established for each study site was compared with mean climate and hydrology variables for each year, thus $n=60$ for each subgroup. Mean number of established shrubs in each subgroup were compared using a Two-sample independent *t*-test ($p \leq 0.05$). For the Two-sample *t*-test analysis, subgroups included:

1) annual mean temperature (GDD) years = (cool) and (warm)
2) annual mean precipitation years = (dry) and (wet)
3) annual mean potential evapotranspiration (PET) years = (low) and (high)
4) annual peak lake level years = (low) and (high)
5) annual length of inundation years post-peak = (short) and (long)

For growing degree days, annual mean temperatures were calculated from daily temperature averages (minimum and maximums). Daily temperature averages were then converted to growing degree days. Growing degree day (GDD) is calculated from daily mean temperatures for each month of each year based on a 5°C baseline; anything below 5°C is equal to zero (Lewis, 1978; Martner, 1986; Knight, 1994). The GDD lower limit of 5°C was chosen based on the standard temperature above which a plant becomes active in the Bighorn Basin of Wyoming (Lewis, 1978; Martner, 1986; Knight, 1994).

For potential evapotranspiration (PET), annual mean potential evapotranspiration was calculated using Thornthwaite's equation which incorporates air temperature as an index of the energy available for evapotranspiration (Thornthwaite and Mather, 1957; Dunne and Leopold, 1978; Brooks et al., 1991). The empirical formula developed by Thornthwaite is ($E_t = 1.6 [10T_a / I]^a$); where, E_t = potential evapotranspiration in cm/month, T_a = mean monthly air temperature (°C), I = annual heat index adjusted for number of days per month and length of day (a function of latitude at 44°N), and $a = 0.49 + 0.0179I - 0.0000771I^2 + 0.000000675I^3$.

Length of inundation was calculated by using the annual peak lake level as the baseline and determining the number of days post-peak lake level the lake receded by 13cm, 30cm, 60cm, 150cm, 300cm, and 450cm. These number of days were then compared to total number of mature *Tamarix* shrubs for each year. The length of inundation categories were chosen assuming that, if moisture was a requirement for successful *Tamarix* recruitment in the first year, there might be some length of time and water table depth that would be detrimental to successful establishment. My field observations showed that root lengths tended to be about double the size of the aboveground stems during the first year, thus the average root length, based on an average stem height of 5.0cm, would be 10.0cm. The first category at 13cm was chosen to reflect the first loss of contact with the water table.

4.2. Mature shrubs and seedlings

Mature shrub age distributions and stand densities were analyzed for differences between the four study sites (NCC, SCC, EKC, WKC) and the four elevational categories (low, mid, high, highest) using Analysis of Variance and Tukey's multiple range comparison test *(n=4;* $p \leq 0.05$*)*.

A survivorship curve was developed for seedlings using weekly seedling counts (percent survival) from October 2 to November 23, 1997. Then, counts started up again on April 18 to May 16, 1998. And, a final count was done on September 16, 1998 for all four study sites. Average growth (total stem growth based on first and last height measurements or mean annual height increments) were analyzed for differences between the four study sites. Analysis of Variance and Tukey's multiple range comparison test was used to determine if there were any site differences for mean seedling growth *(n=4;* $p \leq 0.05$*)*.

5. Results

5.1. Climate and Hydrology

Linear regression analysis found only one of the independent variables (peak lake level) to be a significant predictor of mature *Tamarix* shrub recruitment ($r=0.219$, $F=5.9$, $df=1,118$, $p=0.016$). Covariate analysis for site effects found no significant association of site variables with residual variation in the regression equation. The resulting regression equation is:

[Expected Seedlings = *217.595 – 0.195*(peak lake level)]

Two-sample independent *t*-test analysis found significant differences between the mean number of mature *Tamarix* shrubs recruited in each subgroup for three of the independent variables (Fig. 3):

- Low vs. high peak lake levels (*t=2.183, df=118, p=0.031*)

Average number of established individuals was significantly higher during low peak lake level years (*mean=1108.3m, SE=1.3*) than during high peak lake level years (*mean=1110.8m, SE=1.4).*

- Cool vs. warm temperatures - GDD (*t=-2.064, df=118, p=0.041*)

Average number of established individuals was significantly higher during warmer temperature years *(mean=2220 growing degree days, SE=83.7)* than during cooler temperature years *(mean=2030 growing degree days, SE=85.8)*

- Low vs. high potential evapotranspiration – PET (*t=-1.945, df=118, p=0.054*)

Average number of established individuals was significantly higher during high potential evapotranspiration years *(mean=60.9cm, SE=1.3)* than during lower potential evapotranspiration years *(mean=57.6cm, SE=1.4).*

5.2. Mature shrub age distribution and density

Mature shrub age distributions for each site revealed uneven-aged stands despite obvious "bathtub rings" or terraces of *Tamarix* shrubs (Fig. 4). Average *Tamarix* stand density for all four study sites from all four elevation plots totaled 2 shrubs/m^2. It appears that long-term establishment, though small in number, was successful every year (except 1996) since the Yellowtail Dam was installed in 1967 to form Bighorn Lake. There were no significant site or elevation differences for mature stand density or age distribution.

5.3. Seedling survivorship and growth

Seedling density results indicate averages were much less in their first (224/m^2) and second year (15/m^2) at this northern location as compared to the Southwest. First-year density was found to be as high as 170,000/m^2 in Arizona (Warren and Turner, 1975) and 897/m^2 in Kansas (Tomanek and Ziegler, 1960). In Arizona, Kunzman et al. (1989) found self-thinning very rapid in the first three years with 8,000/m^2, then 200/m^2 on year 3, then 2/m^2 by year 15, with only 1/m^2 by year 30. It appears that at this northern location, there are some initial density and mortality differences, but over the long-term, all regions may experience similar high mortality.

Seedling survivorship curves for each site indicated the highest mortality occurring late into the second year (Fig. 5). Average survivorship was 100% at the end of the first year (November 1997), then dropped to 18% by the end of the second year (September 1998).

Seedling survivorship at this northern location was similar to first-year survivorship of 90% in Kansas (Tomanek and Ziegler, 1960).

The average seedling stem height for the first year (5cm) at Bighorn Lake was very similar to average heights recorded in the Southwest. In Kansas, Tomanek and Ziegler (1960) recorded growth of August seedlings as 4mm at 3 weeks, 6mm at 6 weeks, up to 5cm in 2 months. However, the average stem height in the second year (14cm) was much less for this northern location than found in the Southwest. Observations from Arizona, Kansas, and Texas found that seedlings can grow anywhere from 1 to 3m in their second year (Merkel and Hopkins, 1957; Tomanek and Ziegler, 1960; Horton, 1977; Everitt, 1980; Goldsmith and Smart, 1982; Di Tomaso, 1998; Gladwin and Roelle, 1998). In addition, flowering in *Tamarix* has occurred as early as the first year of growth in the Southwest (Merkel and Hopkins, 1957; Di Tomaso, 1998), but no flowering was observed on these northern sites during the study period.

Mean annual height increments for the 72 tagged seedlings that survived from October 2, 1997 to September 16, 1998 were found to be significantly different between site WKC and the other three study sites (Fig. 6). The highest average growth was 18.2cm at WKC and the lowest average growth was 4.0cm at NCC. The average growth for all four sites for the study period was 9.75cm. Using ANOVA and Tukey's multiple range comparison test analysis, average seedling growth between the four study sites (NCC, SCC, EKC, and WKC) was found to be significantly different (Table 2).

Table 2
Statistical analysis results on site differences and average seedling growth from October 2, 1997 to September 16, 1998 using Tukey's multiple range comparison test.

Seedling Growth (*p-values*)	N = 72, Mean = 9.75cm, SE = 1.974			
	NCC	SCC	EKC	WKC
NCC	1.000			
SCC	0.141	1.000		
EKC	1.000	0.201	1.000	
WKC	**0.000**	**0.008**	**0.000**	1.000

5.4. Growing season

Growing season was estimated to be 118 to 124 days based on soil temperatures taken during the study period from October 2, 1997 through May 1, 1998. Pochop (1977) and Martner (1986) found the average growing season to be 125 days for the Bighorn Basin of Wyoming. This average growing season of 125 days at this northern location is almost half the length of several southwestern states. In Arizona, New Mexico, and Texas, lower desert valleys sometimes have 2 to 3 years in succession without freezes (Garwood, 1996). First-year seedling growth appeared to end sometime between November 6 and 11, 1997 when soil temperatures consistently remained below freezing (0°C) at all depths. Bud burst and new stem growth began to reappear the following spring sometime between April 18 and 21, 1998 when soil temperatures remained above freezing (0°C) at all depths. No frost heaving was observed on these study sites during the two-year period. The majority of new growth in the second year was observed as basal sprouting with only a few of the taller stems surviving over the winter.

5.5. Weeds and seedling establishment

Due to the extreme high waters of 1997, study sites were exposed and sunny, and seedlings germinated on minimally vegetated areas. However, other weed species appeared to be germinating on these study sites as well. Field observations found weeds twice as tall as *Tamarix* and very dense at the WKC site on September 16, 1998. Weed species found on this study site included pigweeds (*Amaranthus sp.*), which can grow up to 2 meters. Other exotic competitors nearby included cocklebur (*Xanthium strumarium*), halogeton (*Halogeton glomeratus*), and Russian thistle (*Salsola iberica*). It is important to note that WKC was the only study site with very high densities of other weed species. And, even though all four study sites had similar densities (15/m^2), WKC had significantly taller *Tamarix* seedlings (19.3cm) than the other three sites (6.6cm).

6. Discussion

6.1. Potential climatic effects on successful recruitment

Selection of climate variables for analysis was based on the assumption that seed germination and survival of seedlings are most influenced by growing season length, temperature, and precipitation (Hulett and Tomanek, 1961; Rathcke and Lacey, 1985). To utilize temperature as a environmental variable affecting plant germination and establishment, a growing degree day (GDD) measurement unit was chosen. This unit represents one degree declination from a standard temperature in the average temperature of one day and provides an index of the amount of heat energy which plants have received from the air (Martner, 1986). Theoretically, below the 5°C threshold, the plants will not grow, which agrees with my study observations on growing season. Also, air temperature was used to calculate potential evapotranspiration (PET) even though we know that actual ET differs substantially from PET, where the latter only considers climate (Rosenberg et al., 1983). The greatest annual average values of PET (61cm/yr) are found in the Bighorn Basin of Wyoming where the study sites are located (Martner, 1986; Knight, 1994). And, since evapotranspiration is an important component of the water balance and controls soil moisture content, groundwater recharge, and streamflow, it also directly affects germination and distribution of phreatophytes (Dunne and Leopold, 1978).

It has been argued that meterological data, such as those chosen for this study, have limits in explaining successful establishment and distribution of vegetation (Lindsey and Newman, 1956; Barbour et al., 1987; Stephenson, 1990). However, my study results suggest that warmer years with higher potential evapotranspiration appear to favor the establishment of *Tamarix* at Bighorn Lake. This suggests that there could be a certain climatic regime which may limit the rate of *Tamarix* recruitment. Seedling differences found between these northern study sites and other southwestern locations also suggests that climate may be mildly limiting to *Tamarix* establishment based on lower initial seedling densities, slower stem growth, and delayed flowering (Merkel and Hopkins, 1957; Tomanek and Ziegler, 1960; Warren and Turner, 1975; Kunzman et al., 1989; Di Tomaso, 1998). And, as a characteristic cold desert environment, minimal precipitation in the Bighorn Basin may be of lesser consequence to *Tamarix* establishment than temperature. My study found that precipitation was not significant. Similar arid conditions can be found in southwestern states, thus other measurements involving the water table may reveal more about moisture stress than precipitation.

It has also been suggested that *Tamarix* has evolved a general purpose genotype (Brotherson and Winkel, 1986) which would allow it to invade different climatic zones. For example, in severe drought, *Tamarix* can drop its leaves, thus reducing evapotranspiration rates (Brock, 1994). In the Southwest, stem growth rates were found to be the lowest for *Tamarix* relative to other phreatophytes; a stress tolerant strategy found in the Mojave Desert (Cleverly et al., 1997). However, this strategy could also limit successful establishment in colder regions, especially for seedlings germinating late in the summer. It is possible that significant correlations between climate and successful *Tamarix* establishment in northern latitudes may be difficult to discern based on their ability to adapt to colder environmental conditions, even in the relatively short period of time they have been recorded this far north. Yet, these study results appear to support the potential for a lower temperature limit threshold and a slower rate of invasion in more northern locations.

6.2. Potential hydrologic effects on successful recruitment

Alterations of naturally flowing rivers into controlled reservoirs has led to an increase of *Tamarix* in many riparian areas (Everitt, 1980; Di Tomaso, 1998). In addition, there are strong correlations between base flows and river band vegetation (Everitt, 1980). Everitt (1980) found that peak discharge and high water bands make ideal locations for *Tamarix* germination due to lack of competition. Warren and Turner (1975) found fluctuations in river flow occurring during peak flowering resulted in establishment or destruction of *Tamarix* seedlings, depending on either an increased or decreased flow. Kerpez and Smith (1987) found seedling survival depended on mild currents and slowly receding flows, not frequent or severe flood events. Once established, absence of saturation was less important and resistance to inundation increased with plant age (Stevens and Waring, 1985). Flood stage or period of inundation was found to be significantly correlated with *Tamarix* mortality, even though colonization was extremely high after peak flooding events (Johnson et al., 1985). Gladwin and Roelle (1998) found that *Tamarix* seedlings had lower survival rates in fall flooding events, although Everitt (1980) suggested that a shift from natural spring run-off to controlled summer releases promotes *Tamarix* establishment.

Despite the complexities of research on hydrologic effects on seedling establishment, peak lake level appears to be an important factor in successful establishment of *Tamarix* at Bighorn Lake (Fig. 7). Lower annual peak lake elevations had a significant positive effect on the number of established shrubs, but length of inundation did not. It should be noted that the significance of lower peak lake levels could be confounded by warmer temperature and higher potential evapotranspiration years where increased reservoir withdrawals for agricultural needs would be assumed. However, Bighorn Lake was built specifically for back-up electricity and is not used as a main agricultural water source by local farmers. Lower annual peak lake elevations could also be an artifact of warmer years where overall lake evaporation is much higher.

Length of inundation most likely was found to be insignificant because of the high rate of *Tamarix* seed production and the extended period of seed dispersal. This allows germinating seedlings to take advantage of various hydrologic conditions over the entire summer and into the fall (Everitt, 1980; Di Tomaso, 1998), including spring and summer rains (Horton, 1977). The fact that lower peak lake levels enhanced *Tamarix* establishment is reasonable when considering that moisture is a requirement for successful seedling germination. Thus, seedling mortality would most likely increase if lake levels were to drop dramatically after a high peak event, which was often the case at Bighorn Lake. A recently developed hydrologic model found a certain rate of stream stage decline favored cottonwood seedling recruitment (Mahoney and Rood, 1998). An integrative model such as this one would be ideal in narrowing down specific requirements for *Tamarix* seedling establishment.

6.3. Interspecies competition and other potential site differences

Germination requirements for *Tamarix* seedlings generally require an open, sunny site and lack of competition or sufficient disturbance of natural vegetative cover to permit establishment (Everitt, 1980; Brotherson and Winkel, 1986). A potential limiting factor to successful *Tamarix* establishment could be interspecific competition, shade intolerance, and slow growth rate (Everitt, 1980). Riparian weeds, not just *Tamarix*, are invading altered and disturbed floodplains throughout the U.S. Due to the high levels of exotic species in the Bighorn Basin region, it is likely that competition for space and sunlight will effect future survival and successful establishment of *Tamarix* on these study sites. Successful germination and survival of seedlings seems to be severely affected by the density of weeds. Tomanek and Ziegler (1960) found seedling densities of $2/m^2$ on plots with over 100 weeds as compared to $6/m^2$ on sites with 0-50 weeds. *Tamarix* seedlings may be growing taller on site WKC, as compared to the other three sites, to successfully compete with the other weeds for space and sunlight. However, it is also possible that this site may be more fertile for some reason, thus the increased growth of all species. Long-term survival of *Tamarix* seedlings in this competitive situation will require further research.

Another potential limiting factor could be site aspect and prevailing winds. Warren and Turner (1975) found differing densities based on site aspect with higher density on the south facing site compared to the north site. He suggested that prevailing winds, subsequent wave action, and solar exposure may explain these aspect differences. The north and south facing sites on this study (NCC, SCC) did show some site differences in seedling growth and density, but not in mature shrub density. This could suggest that prevailing northwesterly winds in the Bighorn Basin may be limiting to seedling establishment. This cold desert basin is known for its high velocity, desiccating winds, especially during the winter months. Other factors including soil type, slope, and microsite topography were not considered to be distinctly different on these study sites based on a soil survey done at Bighorn Canyon (Lebruska, 1996). Another study in Utah, found no relationship between *Tamarix* distribution and seventeen soil factors (Brotherson and Winkel, 1986). It is interesting to note that site differences found for seedlings during this study were not found when analyzing mature shrubs. Thus, it is important to keep in mind that internal controls may be stronger than external influences on long-term survival.

6.4. Conclusions

Obviously, it is difficult to unravel the network of relationships most likely involved in the successful establishment of *Tamarix. Tamarix* does exhibit many characteristics of an "ideal weed" such as continuous seed production for as long as growing season permits and vigorous vegetative reproduction (Brotherson and Winkel, 1986), but is not necessarily an aggressive invader at Bighorn Lake. On the contrary, *Tamarix* still seems to be a slow starter that requires a specific niche for successful establishment. It invades distinct, previously disturbed, moist floodplain habitats. It is not creeping up hillsides and actively destroying occupied sites which is sometimes assumed when using the word "invasive". It might even be considered "naturalized" in some areas, but further research would be required to determine this status. Adding the colder climate into the equation, *Tamarix* may continue to invade and evolve adaptations over time, but this process of invasion may be at a slower rate than found in the Southwest.

Study results suggest that there are subtle climatic limitations on *Tamarix* establishment in northern Wyoming, and high peak lake levels appear to limit successful seedling establishment at Bighorn Lake. The uneven age distribution of mature *Tamarix* stands and high seedling mortality over time suggests minimal long-term survival. In addition, competition from other weed species and site specific variables such as wind and aspect may also affect population dynamics. Yet, despite all of these limitations, there appears to be a minimal number of individuals who succeed each year. And, since these "stronger" individuals are surviving to reproductive age, successful physiological adaptations to colder temperatures may become more prevalent over time.

7.0. Management Implications

Based on these study results from northern Wyoming, resource managers who are dealing with *Tamarix* invasions this far north may not find it necessary to treat (spray or remove) new seedlings right away. It appears that natural mortality occurs rapidly for new seedlings. Their growth rate appears to be slower and flowering age appears to be later. Especially in areas where *Tamarix* is just beginning to invade, the shrubs that are left by the third year will be minimal and easier to eradicate. Yet, it would still be important to remove shrubs prior to first seed dispersal. When first flowering occurs is still unknown at this time, but it did not occur during the second year of this study. For resource managers, this would prove to be much less expensive, less labor intensive, and less impacting to surrounding vegetation. Ideally, now is the time to address new invasions along northern rivers where *Tamarix* is just beginning to take hold.

In addition, an integrative model on hydrologic requirements for successful establishment of *Tamarix* seedlings should be developed. Mahoney and Rood (1998) was able to design a model for cottonwood recruitment in Canada. Also, Baker (1990) explained successful cottonwood forest development based on flood events and interannual climatic fluctuations. A similar prescriptive model could provide resource managers with specific lake level parameters, both magnitude and timing, which would allow for manipulation of reservoir releases to control future invasions.

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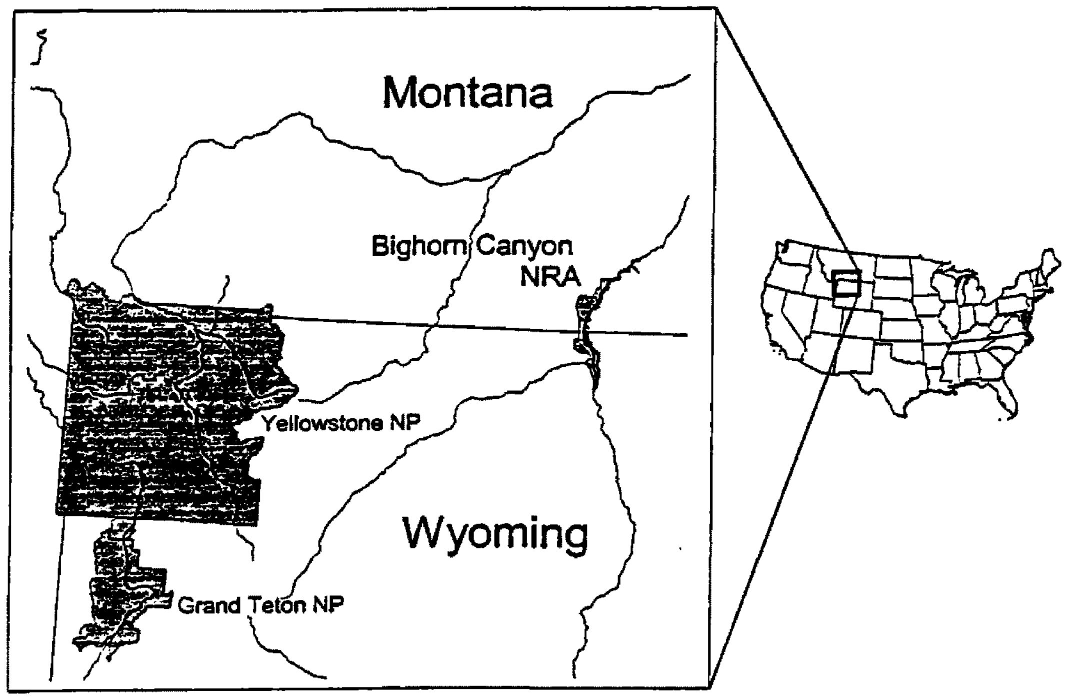

Fig. 1 Geographic region of study area in Bighorn Canyon National Recreation Area, Wyoming.

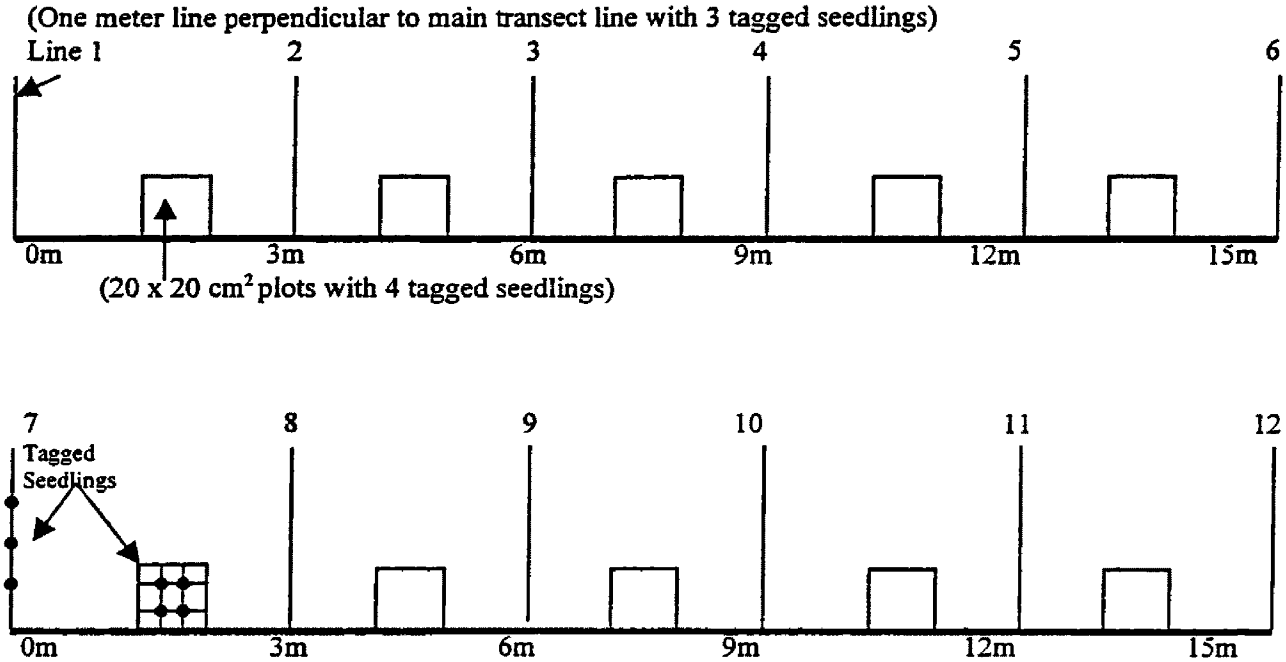

Fig. 2 A descriptive map of one study site's transect, plot, and tagged seedling locations. On each site there are 2 – 15m main line transects, 12 – 1m lines perpendicular to main line transects with 3 tagged seedlings on each line, and 10 – 20x20cm^2 plots with 4 tagged seedlings in each plot.

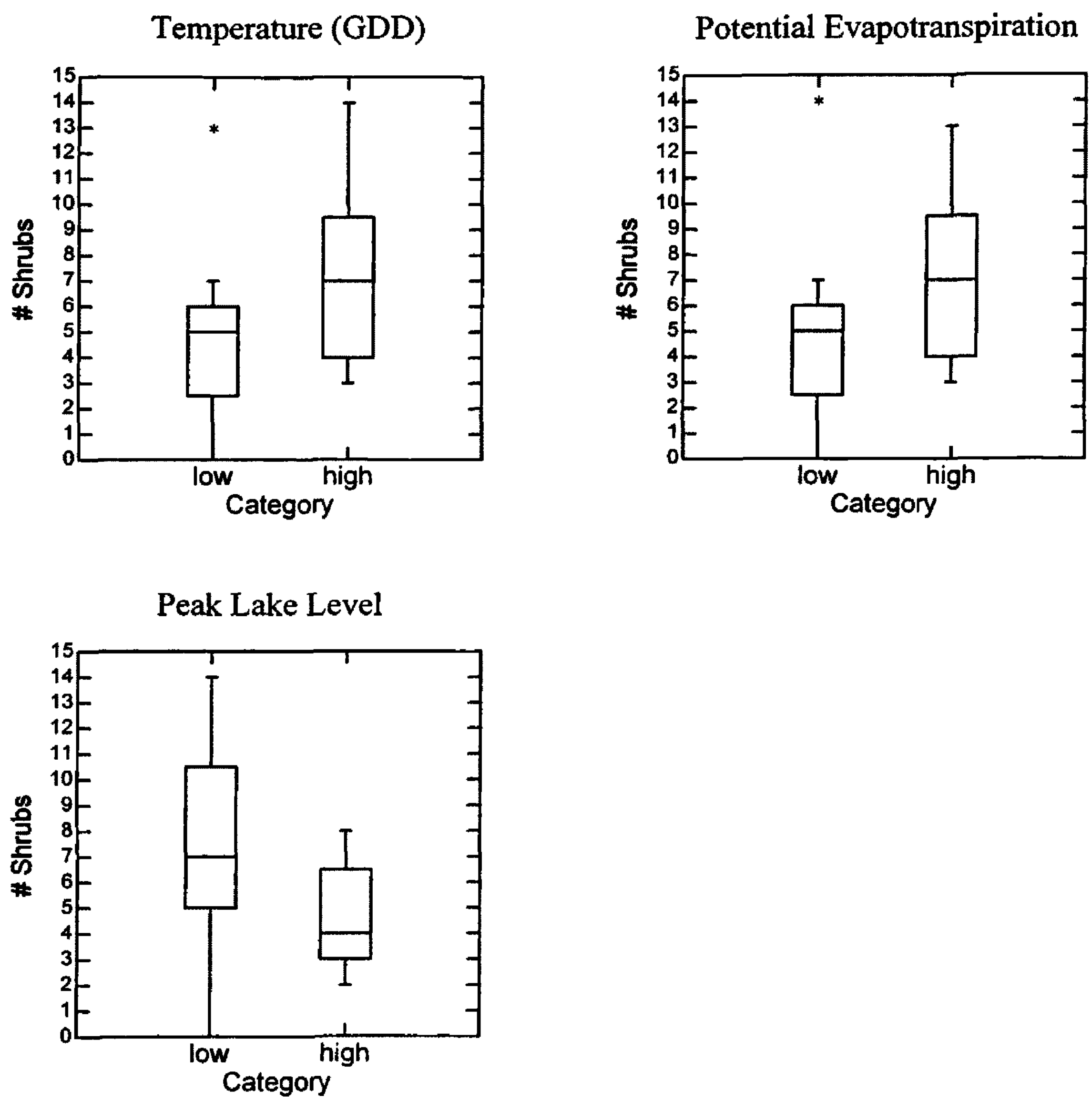

Fig. 3 Effects of low and high extremes of temperature (growing degree days), potential evapotranspiration, and peak lake levels on *Tamarix ramosissima* recruitment between 1967 and 1996 using mean number of mature shrubs belonging to each of these age classes at Bighorn Lake, Wyoming.

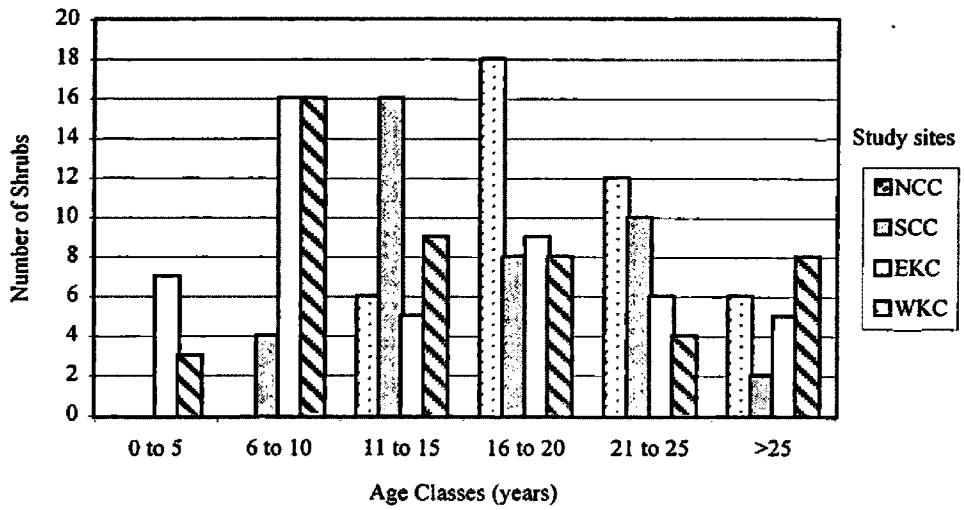

Fig. 4 Sampled *Tamarix ramosissima* shrubs were aged and grouped into six age classes to examine site differences and age distributions.

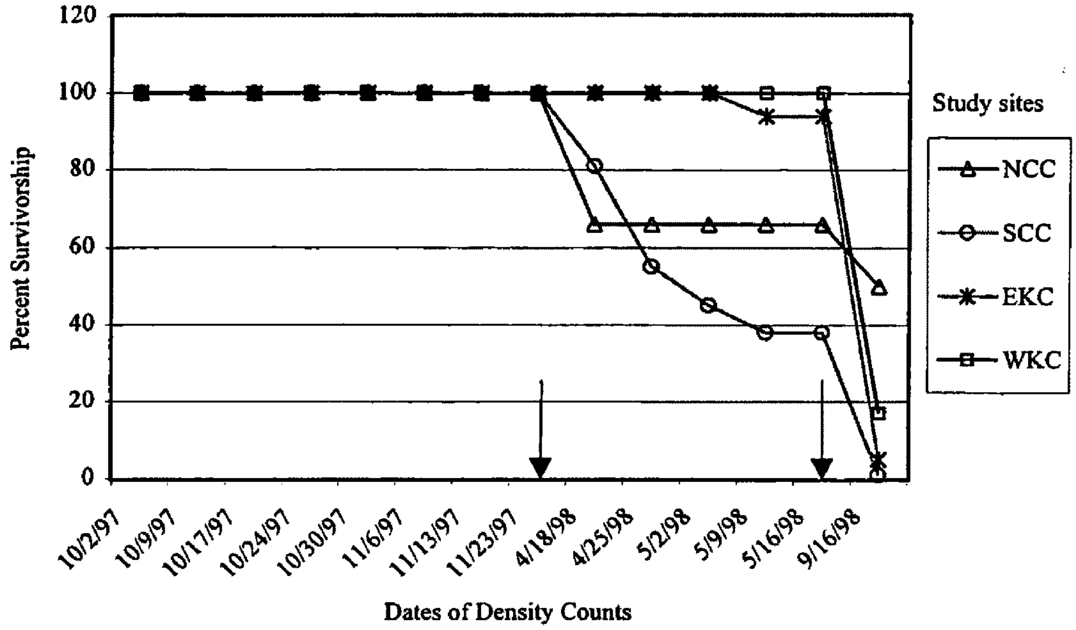

Fig. 5 Mean survival of *Tamarix ramosissima* seedlings from October 2, 1997 to September 16, 1998 at Bighorn Lake, Wyoming. Arrows indicate the two principle gaps in weekly sampling during study.

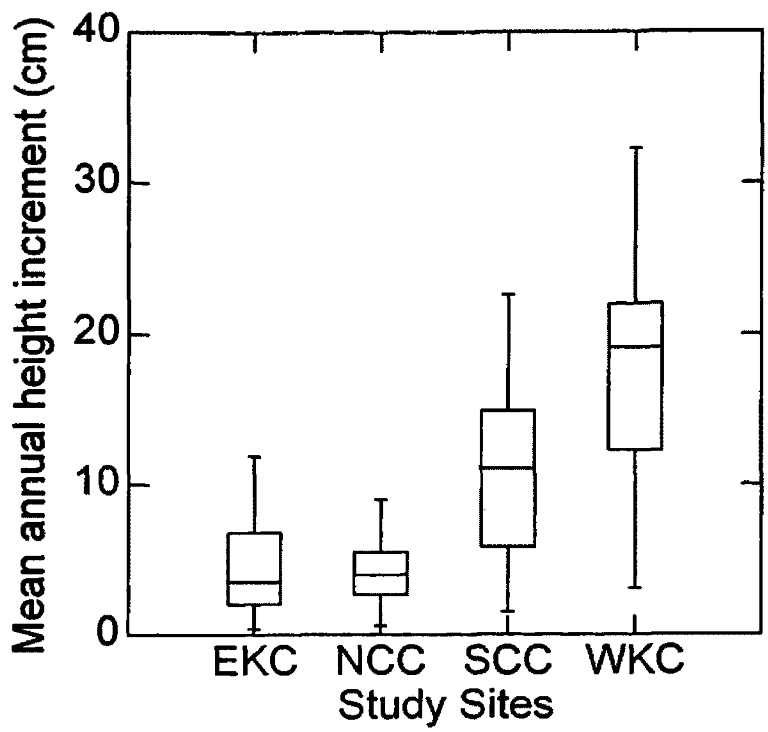

Fig. 6 Mean annual height increments of 72 *Tamarix ramosissima* shrubs from October 1997 to September 1998 compared across the four study sites at Bighorn Lake, Wyoming. The horizontal line within each box is the median.

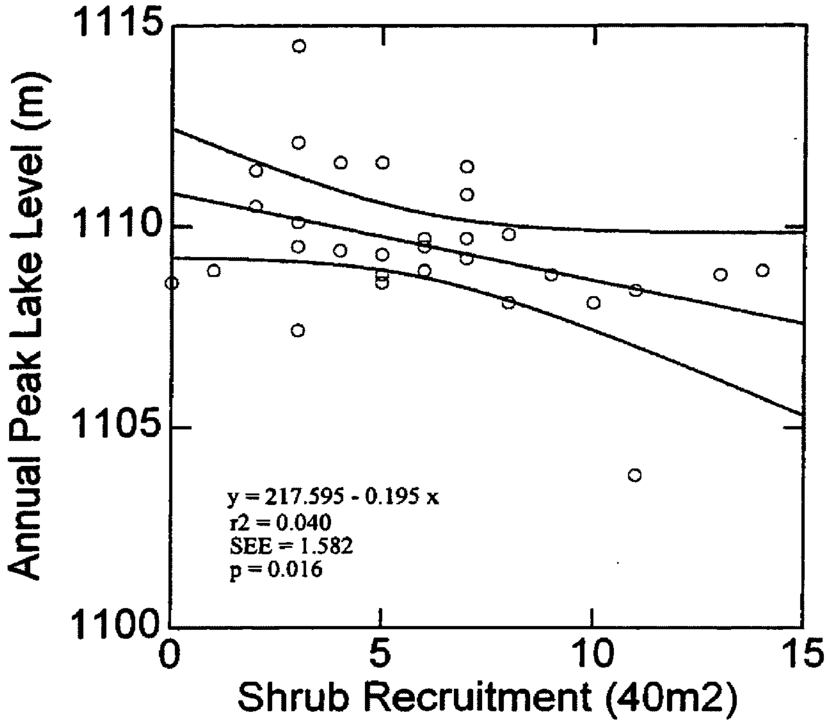

Fig. 7 Relationship between annual peak lake level and sampled *Tamarix ramosissima* shrubs recruited from years 1967 to 1996 at Bighorn Lake, Wyoming.