DISSERTATION

COMPETITION AND SUCCESSION IN TAMARISK STANDS: TOWARDS BIOLOGICAL CONTROL USING NATIVE PLANTS

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JOHN DEWINE ENTITLED COMPETITION AND SUCCESSION IN TAMARISK STANDS: TOWARDS BIOLOGICAL CONTROL USING NATIVE PLANTS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

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Tamarisk species *(Tamarix ramosissima* Ledeb., *T. chinensis* Lour., *T. gallica* L. and hybrids), have invaded riparian areas throughout western North America to the detriment of native plants and animals. Tamarisk is a relatively recent addition to North American plant communities, thus competitive and successional processes are still developing. Box elder (*Acer negundo* L. var. *interius* (Britt.) *Sarg.*) is a potential native competitor found in mid elevation canyons throughout western North America. Competition was studied through neighborhood analysis and succesional trends were analyzed through dendrochronology in mixed stands of box elder and tamarisk in the canyons of Dinosaur National Monument (DNM), Colorado. The shade tolerances of both species were compared through field based and greenhouse experiments. Box elder was the superior competitor; the presence of canopy box elders within one and two meters was significantly related to tamarisk but not box elder mortality. The presence of canopy tamarisk trees was not related to box elder or tamarisk mortality. Tamarisk establishment predated or was concurrent with box elder establishment on newly formed surfaces. Tamarisk initially dominated the canopy, but box elder eventually overtopped and killed the tamarisk. Box elder had superior shade tolerance to tamarisk, and maintained positive growth and survived under higher shade than tamarisk. The shade generated by box elder canopies was capable of killing mature tamarisks. Box elder seedlings were planted under tamarisk canopies to determine if tamarisk facilitates box elder seedling survival. Tamarisk and box elder stands were mapped to determine where the distribution of the two species intersects in DNM. Box elder seedling survival was tested across a range of abiotic gradients found in the canyons of DNM. Tamarisk facilitated box elder seedling survival, the distribution of tamarisk and box elder intersected in many areas, and seedling box elders survived and grew under the range of litter depth, soil texture, groundwater depth and shade intensities found in DNM. The manipulation of competitive and succesional processes through the promotion of box elder and other native tree establishment is suggested as a means of bottom up tamarisk control to complement traditional control techniques.

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Chapter 1

Introduction

Riparian zones are highly productive and diverse ecosystems, which act as corridors for plants and animals and serve as a link between land and water (Gregory et al. 1991, Naiman et al. 1993, Naiman and Decamps 1997, Goebel et al. 2003). The high productivity, frequency of natural and human induced disturbance, linear nature, and heterogeneity of habitats intrinsic to riparian zones make these areas especially prone to invasion by non-native species (Planty-Tabacchi et al. 1996, Stohlgren et al. 1998, Hood and Naiman 2000). Semi-arid and arid riparian zones in the western United States have been extensively invaded by the non-native woody shrub, tamarisk (*Tamarix ramosissima* Ledeb., *T. chinensis* Lour., *T. gallica* L., and their hybrids) (Gaskin and Schaal 2002). Tamarisk has replaced native woody plants as the dominant species in many riparian forests (Campbell and Dick-Peddie 1964, Robinson 1965, Howe and Knopf 1991), reducing native plant and animal diversity (Brock 1994).

Tamarisk is a relative newcomer to western North American riparian vegetation communities, thus the potential for successional change in tamarisk stands is poorly understood. Interspecific differences in shade tolerance is a key mechanism for successional change in forested ecosystems (Shugart 1984, Glitzenstein 1986, Lin 2001). Tamarisk photosynthesis is light saturated only at high levels of irradiance (1100 μmol m^2s), and moderate shade reduces its photosynthetic rates (Anderson 1982). Therefore tamarisk may be susceptible to replacement by more shade tolerant species over time. (Stromberg 1998) observed mesquite establishment in the understory of tamarisk stands in Arizona and (Campbell and Dick-Peddie 1964) noted the apparent successional replacement of tamarisk by native species along the Rio Grande in New Mexico. In both observational field studies and controlled greenhouse experiments, tamarisk grows more slowly than native species and is a poor competitor when resources are abundant (Cleverly et al. 1997, Sher et al. 2000, Sher et al. 2002). Thus, shade tolerant species may be able to replace tamarisk through superior competitive ability.

Box elder (*Acer negundo* L. var. *interius* (Britt.) Sarg.) is a riparian tree with a range encompassing much of North America. It is a major component of the vegetation in mid elevation canyons throughout the upper Colorado River Basin, where it and tamarisk are potential competitors. Historically, box elder was the only abundant native woody species in canyons of the Green and Yampa Rivers in Dinosaur National Monument, Colorado (Powell 1875, Dellenbaugh 1908, Hillers 1972, Stephens and Shoemaker 1987). Tamarisk individuals in Dinosaur National Monument first established in the late 1930s through 1950s, with large numbers establishing in the 1960s and again in the 1980s (Cooper et al. 2003). Box elder is now a co-dominant with tamarisk and the two species often are found in mixed stands. Due to its larger potential height, high leaf area, and high shade tolerance, box elder may be a superior light competitor (Foster 1992).

In chapter 2, I investigated the characteristics of mixed box elder-tamarisk stands. I quantified the effects of neighboring plants of both species on the survival of tamarisk compared to box elder to determine the superior competitor. I then identified successional trends in mixed stands through an analysis of dendrochronological data, understory composition and understory light levels.

In Chapter 3, I compared the shade and drought tolerances of tamarisk and box elder. I used a field experiment to determine if the shade generated by box elder canopies is sufficient to kill healthy, mature tamarisks. I then used a greenhouse experiment to compare the shade tolerances of tamarisk and box elder with and without drought stress.

Invasive plant management is typically approached using chemical and mechanical removal or traditional biological control. These "top-down" eradication techniques are focused solely on the removal of the target organism. Bottom-up control limits the resources available to the undesired species by manipulating disturbance, competition, and succesional processes (McEvoy and Coombs 1999). In experimental settings, the addition of bottom-up control techniques to traditional top-down control has led to increased non-native species control and has enhanced native plant establishment (McEvoy et al. 1993, Wilson and Partel 2003). Bottom-up control has the potential to prevent reinvasion by altering the conditions that allowed the initial invasion, yet bottom-up invasive species management is rare (Sheley 2003, D' Antonio et al. 2004).

Current tamarisk control techniques include herbicide application, mechanical removal, and the introduction of an insect herbivore (Kerpez and Smith 1987, Duncan et al. 1993, McDaniel and Taylor 2003, Deloach et al. 2004). A major weakness of these techniques, with the possible exception of the traditional biological control, is failure to correct the situation which led to the initial invasion and thus prevent reinvasion. A bottom-up technique is clearly needed to augment top-down control. The use of native trees such as box elder to suppress and kill tamarisk is a promising technique with the potential to control tamarisk and prevent reinvasion while restoring native forest habitat.

Observational evidence indicates that tamarisk may facilitate box elder establishment in the semi-arid canyons of the Green and Yampa Rivers in Dinosaur National Monument. Facilitation generally increases in importance in stressful environments and gives way to competitive interactions in more benign environments (Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997, Brooker and Callaghan 1998). The semi-arid canyons of Dinosaur National Monument may initially represent a stressful environment for box elder establishment. Evapotranspiration rates are high, precipitation is low, and young plant roots do not yet reach the water table. Tamarisk may initially facilitate box elder establishment by providing shade, which reduces evapotranspiration rates and limits water loss. As box elder seedlings grow, their roots eventually reach the water table and a limiting resource, water, becomes perennially available. The interaction between box elder and tamarisk may then switch to a competitive interaction. The taller box elder may eventually kill tamarisk through light interception. If tamarisk facilitates box elder establishment in Dinosaur National Monument, the traditional top-down approach of clearing tamarisk may need to be reconsidered where the distribution of the two species intersect. The goal of Chapter 4 was to determine if tamarisk facilitates box elder establishment, then determine where the two species spatially intersect in Dinosaur National Monument by comparing the distribution of both species on the Yampa and Green Rivers by fluvial landform and floodplain position. The final goal was to fine tune bottom-up control recommendations by analyzing box elder seedling survival and growth across a range of litter type and depth, soil texture, shade intensity, and water table depths indicative of those found in Dinosaur National Monument.

Study Sites

The Colorado River Basin drains 629,200 km^2 of the western United States and Mexico. Much of the basin is semi-arid or arid with snowmelt from high elevation mountain regions contributing approximately 70% of the annual runoff (Christensen et al. 2004). The Yampa and Green Rivers are major tributaries of the upper Colorado River (Fig. 1.1).

The headwaters of the Green River are in the Wind River Range of western Wyoming. The Green River flows 1175 km through Wyoming, Colorado, and Utah to its confluence with the Colorado River in Canyonlands National Park, through alternating confined bedrock canyons and broad alluvial valleys. Flaming Gorge Dam, in northeastern Utah, was completed in 1962 for water storage and hydropower generation and regulates the flow of the middle and lower Green River. Lodore Canyon is located in the southeastern edge of the Uinta Mountains, approximately 90 km downstream from Flaming Gorge dam. It is 760 m deep and 28 km long. The channel is organized into fan-eddy complexes typical of canyon rivers on the Colorado Plateau (Grams and Schmidt 1999). The study sites are located at the pool and eddy margins associated with these complexes. Lodore Canyon riparian woody vegetation is dominated by senescent box elders on terraces inundated during rare pre-dam floods. Inset onto the pre-dam floodplain is a woody floodplain plant community, inundated by infrequent post-dam floods, dominated by tamarisk and box elder (DeWine 2005). Other woody riparian plants include isolated Fremont cottonwood individuals (*Populus fremontii* S.Wats.), netleaf hackberry (*Celtis laevigata* var. *reticulate* (Torr.) L.Benson.), and sandbar willow (*Salix exigua* Nutt.). Mean annual precipitation at Brown's Park, CO, located immediately upstream of Lodore Canyon on the Green River is 21.7 cm with 14.1 cm falling from March-September.

The relatively unregulated Yampa River originates in the Park Range and White River Plateau of northwestern Colorado and flows through alternating broad alluvial valleys and confined bedrock canyons. Yampa Canyon is located in Dinosaur National Monument, with canyon walls >500 m high and is 72 km long. Debris fan constrictions influence flow in many areas, but they are not as abundant as in Lodore Canyon. Other locally important geomorphic influences are entrenched meanders and wide alluvial parks (Larson 2004). The study sites are located in the alluvial parks and at a pool margin upstream of a large debris fan. The riparian woody plant community is dominated by tamarisk and box elder with sandbar willows common in mesic sites. Fremont cottonwood, netleaf hackberry, red-osier dogwood (*Cornus sericea* L.), and river birch (*Betula occidentalis* Hook.) are also present. Mean precipitation at Maybell, CO, located on the Yampa River, 25 km southwest of Yampa Canyon is 31.0 cm, with 18.5 cm falling from March-September. Echo Park is an inter-canyon opening immediately downstream of the Yampa and Green confluence.

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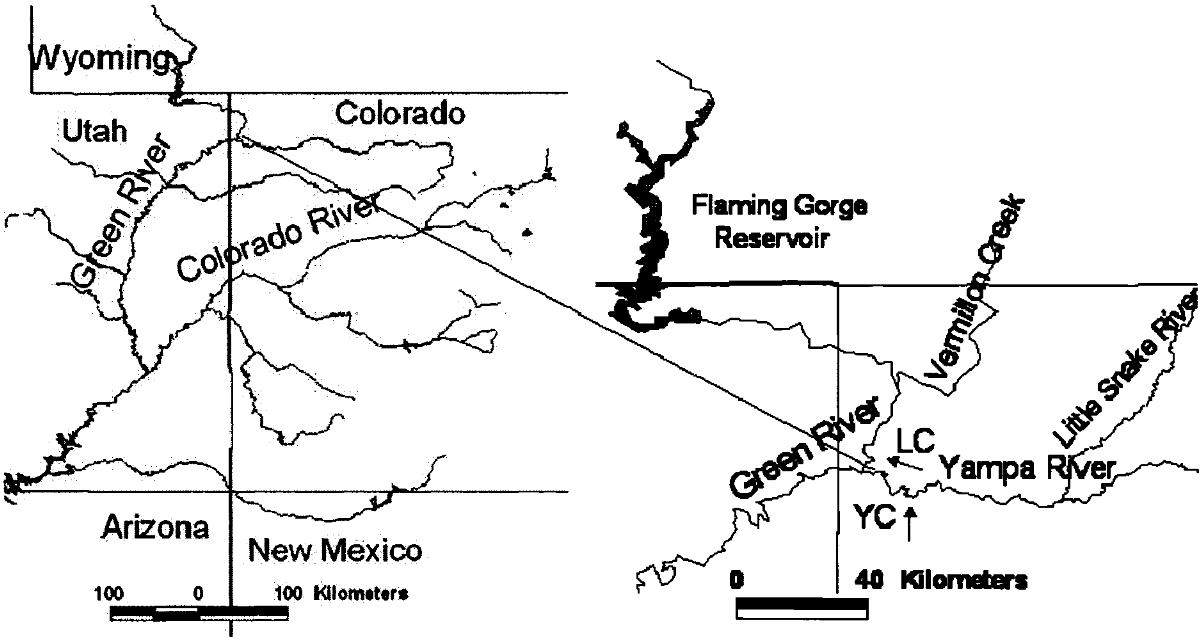

Fig 1.1 Study area location within the upper Colorado River Basin. Arrows indicate Lodore Canyon (LC) on the Green River and Yampa Canyon (YC) on the Yampa River

Chapter 2

Competition and Successional Trajectories in Mixed Tamarisk and Box Elder Stands

Introduction

Riparian zones are highly productive and diverse ecosystems, which act as corridors for plants and animals and serve as a link between land and water (Gregory et al. 1991, Naiman et al. 1993, Naiman and Decamps 1997, Goebel et al. 2003). The high productivity, frequency of natural and human induced disturbance, linear nature, and heterogeneity of habitats intrinsic to riparian zones make these areas especially prone to invasion by non-native species (Planty-Tabacchi et al. 1996, Stohlgren et al. 1998, Hood and Naiman 2000). Semi-arid and arid riparian zones in the western United States have been invaded by the non-native woody shrub, tamarisk, including *Tamarix ramosissima* Ledeb., *T. chinensis* Lour., *T. gallica* L., and their hybrids (Gaskin and Schaal 2002). Tamarisk has replaced native woody plants as the dominant species in many riparian forests (Campbell and Dick-Peddie 1964, Robinson 1965, Howe and Knopf 1991), reducing native plant and animal diversity (Brock 1994).

Tamarisk releases prodigious amounts of small wind and water dispersed seeds throughout the growing season, which germinate readily on bare moist soil, allowing it to rapidly exploit available habitat (Merkel and Hopkins 1957, Horton et al. 1960, Robinson 1965, Warren and Turner 1975). Tamarisk also has superior flood and drought tolerance compared with many co-occurring native woody plants (Horton et al. 1960, Tomanek and Ziegler 1962, Warren and Turner 1975, Anderson 1982, Brotherson and Field 1987, Kerpez and Smith 1987, Busch and Smith 1995, Cleverly et al. 1997, Pockman and Sperry 2000, Horton et al. 2001c, Sprenger et al. 2002). High stress tolerance and superior dispersal ability allow tamarisk to preferentially colonize harsh environments, but trade offs associated with these characteristics may give tamarisk a disadvantage when competing with native species.

Tamarisk was introduced to North America from Eurasia in the early to middle 1800s for use as an ornamental plant, and to stabilize stream banks (Horton 1964, Robinson 1965, Brotherson and Winkel 1986). Escapes from cultivation were first reported in the 1870s (Brotherson and Winkel 1986, Brotherson and Field 1987). Individuals were observed growing wild on the Virgin, Salt, Gila, and Colorado by the early 1900s (Bowser 1960, Robinson 1965, Graf 1978, 1982). The invasion occurred slowly until the 1920s, with observations limited to isolated individuals. The 1920s-1960s was a period of rapid invasion for tamarisk; dense tamarisk stands were common on major western drainages including the Rio Grande (Robinson 1965), the Salt and Gila (Graf 1982), and the Green (Birken 2004)6), by the 1950s and 1960s.

Tamarisk is a relative newcomer to western North American riparian vegetation communities, thus the potential for successional change in tamarisk stands is poorly understood. Succession, broadly defined as temporal changes in plant community composition following disturbance or site formation, is a central tenet of ecological theory (Warming 1895, Cowles 1899, 1911, Gleason 1917, Pickett and Thompson 1978). However, succession in tamarisk stands has not been studied and tamarisk monocultures are considered to be permanent features of invaded landscapes (Robinson 1965, Horton 1977, Brotherson and Winkel 1986, Di Tomaso 1998).

Dispersal processes largely determine the species composition of recently colonized sites, but resource competition increases in importance over time (Bazzaz 1996). Competition for light becomes more important as canopies close in forested ecosystems (Cowles 1899, 1911, Glitzenstein 1986, Lin 2001). Tamarisk photosynthesis is light saturated only at high levels of irradiance (1100 μmol m^{-2} s^{-1}), and moderate shade reduces its photosynthetic rates (Anderson 1982 82). Therefore tamarisk may be susceptible to replacement by more shade tolerant species over time. (Stromberg 1998) observed mesquite establishment in the understory of tamarisk stands in Arizona and (Campbell and Dick-Peddie 1964) noted the apparent successional replacement of tamarisk by native trees along the Rio Grande. These observations may indicate that many riparian plant communities invaded by tamarisk are adjusting to the invasion, and the endpoints of succession and competitive processes are unknown.

Box elder (*Acer negundo* L. var. *interius* (Britt.) Sarg.) is a riparian tree with a range encompassing much of North America. It is a major component of the vegetation in mid elevation canyons throughout the upper Colorado River basin. Historically, box elder was the only abundant native woody species in the canyons on the Green and Yampa rivers in Dinosaur National Monument, Colorado (Powell 1875, Dellenbaugh 1908, Hillers 1972, Stephens and Shoemaker 1987) . Tamarisk first established in Dinosaur National Monument in the late 1930s through 1950s, with large numbers establishing in the 1960s and again in the 1980s (Cooper et al. 2003). Box elder is now a co-dominant with tamarisk and the two species often occur in mixed stands. Due to its larger potential height, high leaf area, and high shade tolerance, box elder may be a superior light competitor (Foster 1992).

Understanding competition between box elder and tamarisk will provide critical information for tamarisk control and native plant restoration. Traditional tamarisk control methods can be costly and ineffective and typically do not prevent reinvasion (Stevens and Walker 1998). Using native species to control tamarisk could have the dual benefits of limiting the importance of an undesirable exotic and promoting the establishment of native plant communities. Closed canopies composed of native species could also prevent tamarisk reinvasion. An analysis of competition between tamarisk and box elder coupled with an investigation of the establishment chronology in mixed tamarisk box elder stands can quantify competitive interactions and lead to predictions of successional trajectories. The purposes of this study were to: (1) Determine if box elder or tamarisk is the superior competitor by analyzing species composition, plant size, mortality rates and neighbor densities in mixed species stands; and (2) identify successional trends in mixed species stands by analyzing dendrochronological data, understory and overstory species composition, and understory light levels.

Methods

Site Selection

Nine mixed box elder/tamarisk stands were chosen for analysis. Eligible sites had a population of both tamarisk and box elder dispersed throughout the site, and had an area >250 m^2. Sites were subjectively selected to represent potential competitive interactions and successional trajectories in stands with co-occurring box elder and tamarisk populations. Four sites used in a previous box elder study (DeWine 2005) were selected to avoid sacrificing additional box elders and to take advantage of existing dendrochronological information.

Four sites were analyzed in Yampa Canyon on the Yampa River, three in Lodore Canyon on the Green River, and two in Echo Park below the confluence of the two rivers. A total of 2,506 plants were analyzed. A 250 m^2 area was selected for study in the center of each site. In one site (Outlaw) a 750 m^2 stand was analyzed. In another site (Gates) a stand <250 m^2 was selected because box elder dendrochronological data were available.

Competitive Interactions

Interspecific and intraspecific competition in the mixed tamarisk/box elder stands was measured using a neighbor analysis which quantifies the effects of spatial distribution and neighbor size at the individual plant level (Mack and Harper 1977, Weiner 1982). Neighborhood models have been shown to be valuable tools for the study of competition in forest stands (Weiner 1984, Daniels et al. 1986, Wagner and Radosevich 1998).

At each site the species and mortality status (live or dead) of each woody plant was determined. The plant height and width was estimated to the nearest half meter using a measuring tape for smaller individuals and a survey rod for larger individuals. The diameter of each stem was measured to the nearest centimeter at the plant base using a tape. Each individual woody plant within one and two meters of the base of every canopy woody plant was recorded. Tamarisk individuals typically have a multiple stem growth form in the study area. Flood events can result in the burial of plants, and each stem may superficially appear to be an individual plant. Using knowledge gained from participating in the excavation of tamarisks in the study site and on other Green River sites, I differentiated tamarisk ramets and genets using proximity, growth patterns and stem orientation. The effect of understory woody plants was also studied at six sites, where every woody plant, within one and two meters of the base of every other woody plant was recorded. The effect of understory woody plants was not analyzed at three sites due to time constraints.

The relationship between mortality for both species and the cumulative live stem basal area of box elders or tamarisk within one and two meters of each tree was tested using stepwise logistic regression and correlation analysis. Multiple logistic regression was used because the response variable is binary (dead or alive), and assumptions of normality are not required. Explanatory variables were tested for associations with mortality using the maximum likelihood method. Regression models were selected using stepwise variable selection ($\alpha = 0.05$) and effects were tested using likelihood ratio chi-square tests. The predictor variables tested were total box elder canopy basal area within one and two meters, ($A1_{Bover}$, $A2_{Bover}$), total box elder understory basal area within one and two meters ($A1_{Bunder}$, $A2_{Bunder}$), total tamarisk canopy basal area within one and two meters ($A1_{Tover}$, $A2_{Tover}$), and total tamarisk understory basal area within one and two meters ($A1_{Tunder}$ $A2_{Tunder}$). Total basal area was calculated by measuring the diameter of each live stem at the ground surface and summing the stem area for each species. Separate tests were conducted for the two response variables (box elder mortality and tamarisk mortality) and for the two neighbor distances tested (one and two meters) for each site and for all sites pooled.

Mean canopy height was used to divide sites into early, middle, and late successional classes to facilitate analysis. Sites with mean canopy heights < six meters were termed early successional, six to nine meters were considered mid successional, and > nine meters were classified as late successional. The successional class does not necessarily denote stand age because growth rates and plant heights can differ depending on site conditions and species composition. Furthermore, disturbances such as flooding and beaver activity can reset a site to an earlier class.

Light Interception

A transect was installed through the center of each site parallel to the river. Photosynthetically active radiation (PAR) was measured at the ground surface at each meter, excluding the first and last meter (to avoid edge effects), within two hours of solar noon. The measurements were compared with full sun measurements taken adjacent to each site to determine the percent PAR intercepted, which is considered percent shade.

Establishment History

In an earlier study, box elders were excavated at several locations along the Yampa and Green Rivers, and the establishment date for each individual was determined using dendrochronological techniques (DeWine 2005). Four of these sites were used for tamarisk age analysis. Three of the sites were also used for neighbor analysis; however a DNM tamarisk removal project prevented neighbor analysis at one of the sites. Approximately ten tamarisk individuals per site were randomly chosen and excavated. The taproot and root crown were sectioned into five centimeter thick slabs and sanded to a smooth finish using sequentially finer sandpaper to 30 μm. The slab with the germination point, identified by the point where the pith originates (Scott et al. 1997, Cooper et al. 2003), was analyzed further. The center of each slab was polished with 150 μm paper and the rings were counted using a high power dissecting microscope. False rings were detected by the presence of an incomplete transition between early- and late-wood vessels through some portion of the stem. Partial and missing rings were detected by cross dating between the sections of each sample. The establishment dates and root crown burial depths for the excavated box elder and tamarisk samples were compared to determine the colonization chronology for the site.

Results

The study sites were dominated by box elder. Box elder canopy cover ranged from 40-95%, while tamarisk canopy cover ranged from 0-40% (Table 2.1). The live tamarisk to box elder ratio was 0.3:1 by basal area. Tamarisk mortality was high, 1037 (121.0 m^2) dead tamarisk were recorded for a 1.6:1 live to dead tamarisk ratio by basal area. Box elder mortality was comparatively low, 127 (152.9 m^2) dead box elders were found for a live to dead box elder ratio of 4.5:1.

The cumulative basal area of box elder canopy trees within one meter of each tamarisk ($A1_{Bover}$) was a significant predictor of tamarisk mortality (df = 1, $\chi^2 = 43.95$, $P < 0.0001$) (Table 2.2). An odds ratio of 1.31 indicates that a one square meter increase in $A1_{Bover}$ was associated with an increase in the likelihood of tamarisk mortality by 31%. Likewise, the cumulative basal area of box elder canopy trees within two meters ($A2_{Bover}$) was a significant predictor of tamarisk mortality (df = 1, $\chi^2 = 99.21$, $P < 0.0001$). A one square meter increase in $A2_{Bover}$ was associated with a 20% increase in the likelihood of tamarisk mortality. The cumulative basal area of canopy tamarisks within two meters ($A2_{Tover}$) was significantly related to box elder mortality (df = 1, $\chi^2 = 11.26$, $P = 0.001$). An odds ratio of 0.17 indicates that an increase of one square meter of $A2_{Tover}$ was associated with a decrease in the odds of box elder mortality by 83%. The effect of understory trees was included in the analysis at six sites. When these sites were pooled, the cumulative basal area of understory box elders within two meters ($A2_{Bunder}$) was significantly related to box elder mortality (df = 1, $\chi^2 = 5.11$, $P = 0.0238$). An odds ratio of 0.18 indicated that for an increase of 1 m^2 $A2_{Bunder}$ the likelihood of box elder mortality decreased by 82%.

Early Successional Sites

Characteristics

The two early successional sites were characterized by relatively low canopy heights (4 and 5 m), high live plant densities (1.90 and 1.28 live plants/m^2), and a mixed canopy of tamarisk and box elder (Table 2.1). Box elders comprised 40% and 50% of canopy cover, and tamarisks comprised 40% and 30% of canopy cover.

Both sites had large numbers of live tamarisk (126 and 308) and little tamarisk mortality (Fig 2.1). The ratio of live to dead tamarisk by basal area was 11.0:1 and 16.8:1 (Table 2.3). Live box elders were less numerous (44 and 11 plants present) with no dead individuals found. The ratio of live tamarisks to live box elders was 0.9: 1 and 1.8: 1 by basal area. Live tamarisks had higher total basal area in the understory at both sites (Table 2.3, Fig 2.1). In contrast, box elder plants had greater canopy basal area at both sites. PAR interception ranged from 0% to 99%, with means of 78.5% and 97.7% shade for the two stands (Table 2.1).

Dendrochronology

Box elder and tamarisk establishment, from initial site colonization to the mid 1980s, appeared to be concurrent at the Gates site. Two box elders and two tamarisks established in the 1960s and 1970s (Fig. 2.2A). The majority of sampled tamarisks (n = seven) and box elders (n = six) established during the mid 1980s. Two box elders established in 1997.

The Steamboat site appears to have been initially colonized by tamarisks which have been deeply buried in sediment. Due to poor root crown quality, only approximate minimum ages could be determined (Fig. 2.2B). However, the root crown burial depth (76-125 cm) of these individuals indicates that the tamarisks were established at the site before the box elders. Establishment dates could be determined for the shallowly buried

(4-22cm) tamarisks and box elders. The oldest box elder established in 1974, seven box elders and two tamarisks established in the mid 1980s

Statistical Analysis

The cumulative basal area of box elder canopy trees within one meter ($A1_{Bover}$) was a significant predictor of tamarisk mortality at the Gates site (df = 1, $\chi^2 = 10.83$, P = 0.001) (Table 3). An odds ratio of 2.95 indicates that an increase of one square meter $A1_{Bover}$ was associated with a 195% increase in the likelihood of tamarisk mortality. $A1_{Bover}$ was also a significant predictor of tamarisk mortality at the Steamboat site (df = 1, $\chi^2 = 7.34$, P = 0.007). An odds ratio of 1.67 indicates that an increase of 1 m^2 $A1_{Bover}$ was associated with a 67% increase in the likelihood of tamarisk mortality. The cumulative basal area of canopy tamarisks within 2 m ($A2_{tover}$) was significantly related to tamarisk mortality at the Steamboat site (df = 1, $\chi^2 = 4.14$, P = 0.04). However, an odds ratio of 0.24 indicates that an increase of 1 m^2 $A2_{tover}$ was associated with a 76% decrease in the likelihood of tamarisk mortality.

Mid Successional Sites

Characteristics

The four mid successional sites were characterized by canopy heights ranging from seven to nine meters (Table 2.1) and plant densities ranging from 0.20-0.84 live plants/m^2. Box elders completely or partially dominated the canopy. Canopy cover ranged from 60-95% box elder and 0-30% tamarisk. Species dominance by total live basal area varied widely, with the live tamarisk to box elder ratio ranging from 0.2:1 to 6.6:1 (Table 2.2).

The Laddie site had many canopy openings and was characterized by very low tamarisk mortality (live/dead tamarisk ratio = 140.8 by basal area), and no box elder mortality. Tamarisk mortality was higher at the other sites (Echo, Laddie 2 and Buster); live to dead tamarisk ratios by basal area were 0.7:1, 0.8:1, and 4.5:1. Box elder mortality was much lower at every site; live to dead box elder ratios ranged from 24.3:1-112.0:1 by basal area. PAR interception ranged 71%-99.6%, with means of 98.2%, 93.6%, 98.6% and 94.3% (Table 2.1).

Dendrochronology

All live and dead tamarisks were removed as part of a National Park Service tamarisk removal project from the mile 233 site on the upper Green River after dendrochronological analysis but before extensive site analysis were completed. The mean canopy height was seven meters and was dominated by box elders prior to tamarisk removal, thus the site was classified as mid successional. Tamarisk establishment appears to have predated box elder establishment at this site. Five tamarisks established during the 1960s and 1970s (Fig 2.2C). All of the six sampled box elders and two of the tamarisks established in 1983.

Statistical Analysis

The cumulative basal area of canopy tamarisks overstory basal area within one meter ($A1_{Tover}$) was significantly related to tamarisk mortality at the Laddie 2 site (df = 1, $\chi^2 = 10.86$, P = 0.001) (Table 2.3). An odds ratio of 0.13 indicates that an increase of 1

m^2 $A1_{Tover}$ was associated with an 87% decrease in the likelihood of tamarisk mortality. The cumulative basal area of canopy box elders within two meters ($A2_{Bover}$) was a significant predictor of tamarisk mortality at the Buster site (df = 1, $\chi^2 = 11.18$ P = 0.0008). An odds ratio of 1.08 indicates that an increase of 1 m^2 $A2_{Bover}$ was associated with an 8% increase in the likelihood of tamarisk mortality.

Late Successional Sites

Characteristics

The three late successional sites were characterized by tall canopies (11-12 m) comprised entirely or almost entirely of box elders, and live plant densities of 0.21-0.29/m^2 (Table 2.1). Tamarisk mortality was complete at the Echo2 (235 dead tamarisks) and Monkeypaw (77 dead tamarisks) sites (Table 2.2). Much of the Outlaw site was occupied by box elders which established prior to the introduction of tamarisk to the area. Relatively low numbers of both dead (75) and live (40) tamarisk at the large Outlaw site indicate that the established box elders limited tamarisk colonization to newly formed surfaces and canopy gaps. Box elder mortality was relatively low at the late successional sites (Fig. 2.1). Live to dead box elder ratios were 31.1:1, 1.9:1, and 74.5:1 by basal area for the Echo 2, Outlaw, and Monkeypaw sites respectively. Box elder canopy trees had the highest percent live foliage (76-84%), followed by understory box elders (48-78%), and understory tamarisk (21-26%) (Table 2.2). The only significant PAR detected was in canopy gaps at the Outlaw site. PAR interception at the Outlaw site ranged from 6%-99.8% with a mean of 86.5%. PAR interception at the other two sites ranged from 99.6%-99.9% with both means at 99.9% (Table 2.1).

Dendrochronology

Outlaw was the only Yampa River site used for dendrochronological analysis. Large mature, box elders were cored rather than excavated, thus only minimum ages were determined for these individuals. The oldest cohorts at the Outlaw site were large box elders on raised outer levees with minimum establishment dates ranging from 1917-1945 (Fig. 2.3). A younger box elder cohort in the site interior was represented by two samples with establishment predating 1962. One box elder and three tamarisks established in the 1960s -1970s, and 11 box elders and five tamarisks established in the mid 1980s. Throughout much of this site, box elder establishment predated tamarisk establishment.

Statistical Analysis

The cumulative basal area of canopy tamarisks within two meters ($A2_{Tover}$) was significantly related to tamarisk mortality ($df = 1$, $\chi^2 = 4.42$, $P = 0.04$) at the Outlaw site. An odds ratio of 0.03 indicates that an increase of 1 m^2 $A2_{Tover}$ was associated with a 97% decrease in the likelihood of mortality. Tamarisk mortality could not be statistically analyzed at the Echo2 and Monkeypaw site due to the absence of live tamarisks.

Discussion

Competition

Box elder was a superior competitor to tamarisk at each study site. Box elders dominated the site canopies and had much lower mortality rates than neighboring tamarisks. The presence of neighboring box elders was associated with an increased likelihood of tamarisk mortality, but the presence of neighboring tamarisks was either not associated with box elder mortality or was associated with a decreased likelihood of box elder mortality (Table 2.3). Early successional sites, with short mixed species canopies, had little mortality of either species. However late successional sites, with tall box elder canopies, had high tamarisk mortality and live box elders in both the understory and canopy (Fig. 2.1).

Researchers have suggested that tamarisk is able to dominate invaded North American riparian ecosystems through the competitive exclusion of native species (Campbell and Dick-Peddie 1964, Crawford et al. 1993, Busch and Smith 1995). However, with the exception of a study that linked tamarisk removal to increased *Salix* growth (Busch and Smith 1995) there is a dearth of supporting evidence for this theory. In fact, tamarisk seedlings were inferior competitors to *Populus deltoides* subsp. *wislizenii* (S. Wats.) Eckenwelder and *Salix exigua* seedlings in both an observational field study and a controlled greenhouse experiment (Sher et al. 2000, Sher et al. 2002). The present study offers additional evidence that adult tamarisks can be competitively inferior to native species and further refutes the theory of tamarisk dominance through competitive exclusion. The success of tamarisk in North America is more likely due to its high stress tolerance and superior dispersal ability, coupled with a release from the herbivores and other natural enemies found in its native range (Horton et al. 1960, Warren and Turner 1975, Brotherson and Field 1987, Brock 1994, Cleverly et al. 1997, DeLoach et al. 2000, Horton et al. 2001b).

Successional Trends

Box elder and tamarisk recruitment patterns at the Green River sites have been extensively modified by upstream dam operations. A senescent box elder population is located on high surfaces no longer inundated by flood flows. Younger tamarisk and box elder are found on a post-dam floodplain inset into the pre-dam floodplain (Cooper et al. 2003, DeWine 2005). Formation of the post dam floodplain was initiated and woody plant colonization began in the 1960s when both tamarisk and box elder seed sources were present (Grams and Schmidt 1999, Cooper et al. 2003, DeWine 2005).

Classical successional theory predicts that the establishment of species with higher shade tolerance tends to peak later after disturbance or site formation then in less shade tolerant species (Clements 1916, 1938). Establishment patterns at this site are in accordance with this prediction and indicate that box elder can invade established tamarisk stands. Tamarisk establishment appears to have peaked well before box elder establishment at two of the three Green River sites (Fig. 2.2). However, box elder now dominates the canopy (Table 2.1). The Yampa River sites differed from the Green River sites because recruitment of pre-1960s and post-1960s woody plant cohorts occurred on the same surfaces. At the Yampa River Outlaw site, box elder establishment predated the tamarisk invasion. Tamarisk establishment was limited to newly formed surfaces in the site interior and stand edges. Box elder and tamarisk establishment was largely concurrent on the newly formed surfaces, yet box elder dominates the site, and tamarisk only exists in canopy gaps. It is likely that tamarisk will largely be excluded as the box elders grow and further limit understory light levels.

Interspecific differences in mortality have been linked to successional change in forested ecosystems (Christensen 1977, Peet and Christensen 1980, Harcombe and Marks 1983, Glitzenstein 1986, Walters and Reich 1996, Lin 2001). Live tamarisks were abundant at the early succesional sites, but all or most tamarisks were dead at the late successional sites (Fig. 2.1). In contrast, box elders had much lower mortality rates compared to tamarisk throughout the study area. The status of *Acer* species as late successional canopy dominants may be attributed in part to high survival rates in low light conditions (Kobe et al. 1995, Walters and Reich 1996). High survival at low growth rates (Lin 2001) allows for the maintenance of future overstory recruits in the understory (Walters 1994, Kobe et al. 1995). Live box elder understory trees were found at all sites, including sites with 100% tamarisk mortality. However, live tamarisk understory trees were rare at late successional sites (Fig. 2.1). Thus, in the absence of a major disturbance box elders are likely to dominate these stands into the future.

Shade Tolerance

Each site had high levels of PAR interception (Table 2.1), indicating that light limitation may have caused tamarisk mortality. Differential shade tolerance is a key determinant of successional processes in forested ecosystems (Shugart 1984, Glitzenstein 1986, Lin 2001) and may be the mechanism for the superior competitive ability of box elder and the successional changes observed in mixed tamarisk and box elder stands. This hypothesis will be tested in Chapter 3. Box elder is a shade tolerant species (Foster 1992), but the current and previous analyses suggest that tamarisk is not. Researchers across the western United States have noted that tamarisk does poorly under *Populus* canopies (Campbell and Dick-Peddie 1964, Lesica and Miles 2001, Cooper et al. 2003). Box elder can survive and grow under dense tamarisk canopies (Chapter 4), grow taller than and overtop the tamarisk, reducing light to levels that may be too low for tamarisk growth and survival. The bottleneck for the box elder population appears to be seed dispersal and initial seedling establishment. A challenge for land managers trying to establish box elder will be to alleviate this bottleneck through managed flooding, seed introduction, and box elder plantings which could influence the course of natural successional processes. The use of directed successional processes to control non-native plants and promote native plant establishment may prove to be an extremely important and much needed tool in addressing the global problem of non-native species invasions.

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Table 2.1 Locations, mean canopy height, successional classification (Succ. Class), stand area, live plant density, % canopy (Can) cover for tamarisk (tam) and box elder (BE), and % PAR intercepted (PAR Int) for study sites.

Site	River	Height	Succ. Class	Stand Area m^2	Live Plant Density Plants/ m^2	BE Can %	Tam Can %	PAR Int. %
Gates	Green	4	Early	90	1.90	40	40	78.5
Steamboat	Green	5	Early	250	1.28	50	30	97.7
Echo	Green*	7	Middle	250	0.25	60	30	98.2
Laddie	Yampa	7	Middle	250	0.20	60	30	93.6
Laddie 2	Yampa	7	Middle	250	0.84	95	2	98.6
Buster	Green	9	Middle	250	0.78	95	0	94.3
Echo2	Green*	11	Late	250	0.26	95	0	99.9
Outlaw	Yampa	12	Late	750	0.29	80	5	86.5
Mpaw	Yampa	11	Late	250	0.21	95	0	99.9

* Below confluence.

Table 2.2 Results of stepwise forward logistic regression analysis relating tamarisk (Tam) and box elder (BE) canopy and understory basal areas within 1 and 2 m to tamarisk and box elder mortality. Values for entry and removal are 0.05. The significant variables in the final model are tabulated, along with Wald Chi-Square, the P value, and the odds ratio associated with each variable, and the direction (Sign) of the relationship. A positive relationship means the explanatory variable is positively related to survival probability, a negative relationship means the explanatory variable is negatively related to survival probability.

Site	Resp. variable	Explanatory variable	Distance	Wald χ^2	P	Odds Ratio	Sign
Gates	Tam	BE canopy	1 m	10.83	0.0010	2.95	_
Sboat	Tam	BE canopy	1 m	7.34	0.0067	1.67	_
		Tam canopy	2 m	4.14	0.0419	0.241	+
Laddie 2	Tam	Tam canopy	1 m	10.86	0.0010	0.13	+
Buster	Tam	BE canopy	2 m	11.18	0.0008	1.08	_
Outlaw	Tam	Tam canopy	2 m	4.42	0.0354	0.026	+
All	Tam	BE canopy	1 m	43.95	0.0001	1.31	_
			2 m	99.21	<0.0001	1.20	_
	BE	Tam canopy	2 m	11.26	0.0013	0.17	+
		BE Under*	2 m	5.11	0.0238	0.18	+

*Understory relationships tested for Gates, Laddie, Laddie 2, Echo, Outlaw, and Monkeypaw sites only.

Table 2.3 Number and summed basal area for live and dead plants by species and location (understory and canopy) for each study site. Site abbreviations are as follows: Sboat = Steamboat, Lad = Laddie, Lad2 =Laddie 2, Mpaw = Monkey Paw.

		Tamarisk				Box elder			
		Live		Dead		Live		Dead	
Site		Under	Over	Under	Over	Under	Over	Under	Over
Gates	N	117	9	46	0	38	6	0	0
	Basal Area (m^2)	7.5	4.6	1.1		4.8	9.3		
Sboat	N	301	7	41	0	4	7	0	0
	Basal Area (m^2)	17.1	3.1	1.2		0.4	10.7		
Echo	N	10	22	85	17	13	17	1	1
	Basal Area (m^2)	8.3	25.8	30.2	21.9	0.4	13.1	0.1	0.2
Lad	N	10	24	2	1	5	11	0	0
	Basal Area (m^2)	8.2	76.3	0.4	0.2	0.9	11.9		
Lad2	N	44	47	143	4	68	50	15	0
	Basal Area (m^2)	5.8	33.7	7.4	0.7	2.2	31.4	0.3	
Buster	N	128	0	293	0	34	34	11	0
	Basal Area (m^2)	5.9		7.2		17.0	12.2	1.2	
Echo2	N	0	0	253	0	37	28	14	0
	Basal Area (m^2)			30.9		5.0	116.4	3.9	
Outlaw	N	39	1	75	0	141	37	64	3
	Basal Area	2.2	0.6	1.2		94.6	165.4	128.3	8.9
Mpaw	N	0	0	77	0	15	38	17	1
	Basal Area (m^2)			18.9		6.8	157.1	1.4	0.8
Total	N	649	110	1015	22	355	228	122	5
	Basal Area (m^2)	55.0	144.1	98.3	22.7	132.0	527.4	135.1	10.0

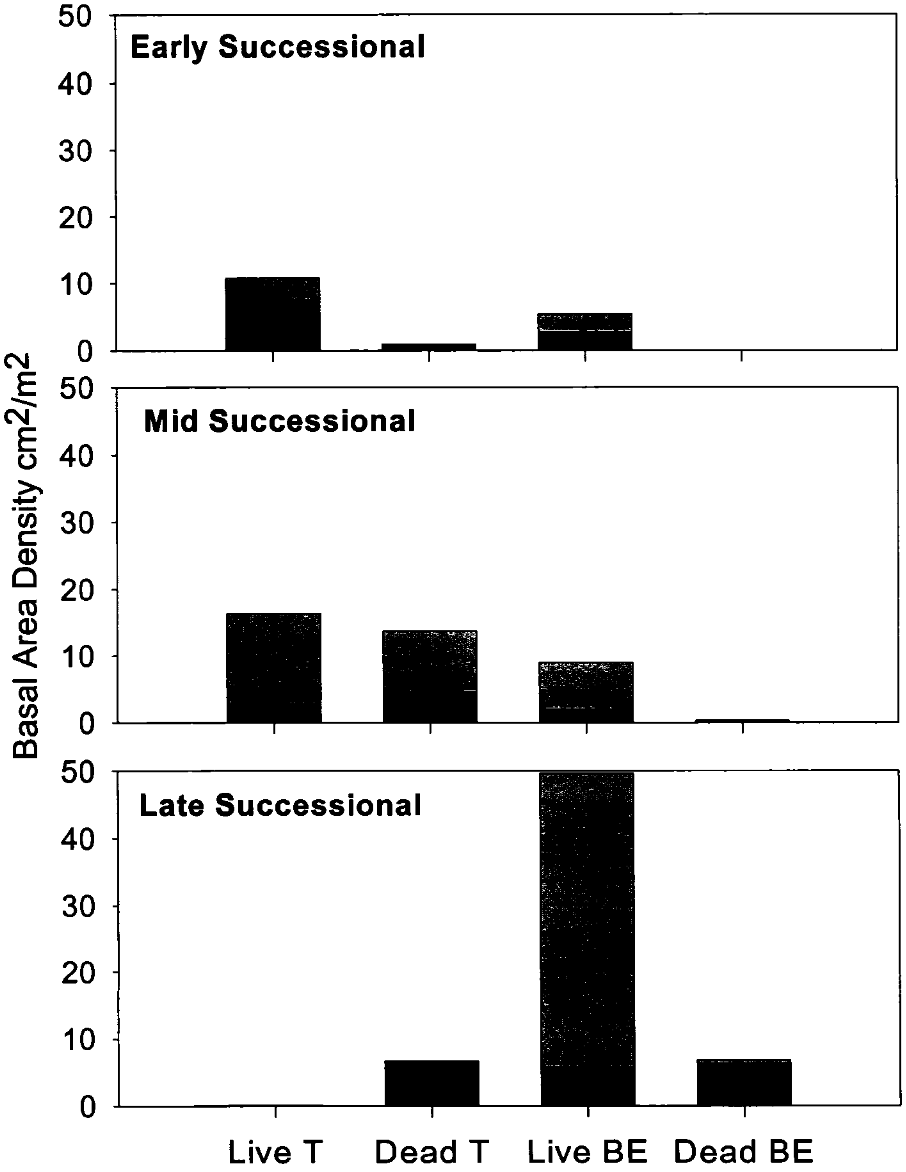

Figure 2.1 Mean basal area density (cm^2/m^2) for understory (black) and canopy (gray) live tamarisks, dead tamarisks, live box elders, dead box elders, at early, middle, and late successional sites.

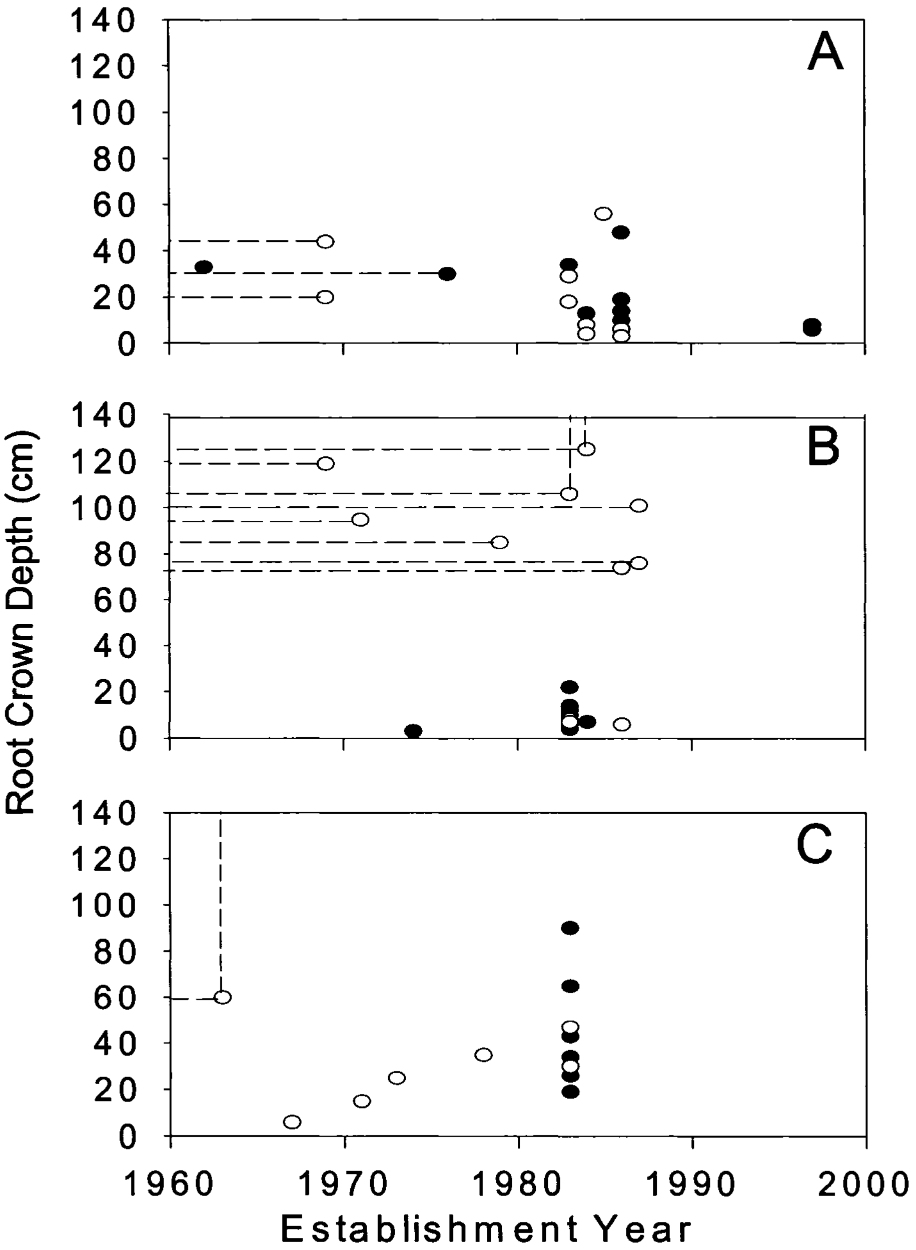

Figure 2.2 Root crown depth and establishment year for (A) Gates site, (B)Steamboat site and (C) Mile 233 site, on the Green River (Lodore Canyon). Solid circles indicate box elder individuals and hollow circles indicate tamarisk individuals. Dashed lines indicate uncertainty, where only minimum ages and/or depths could be determined.

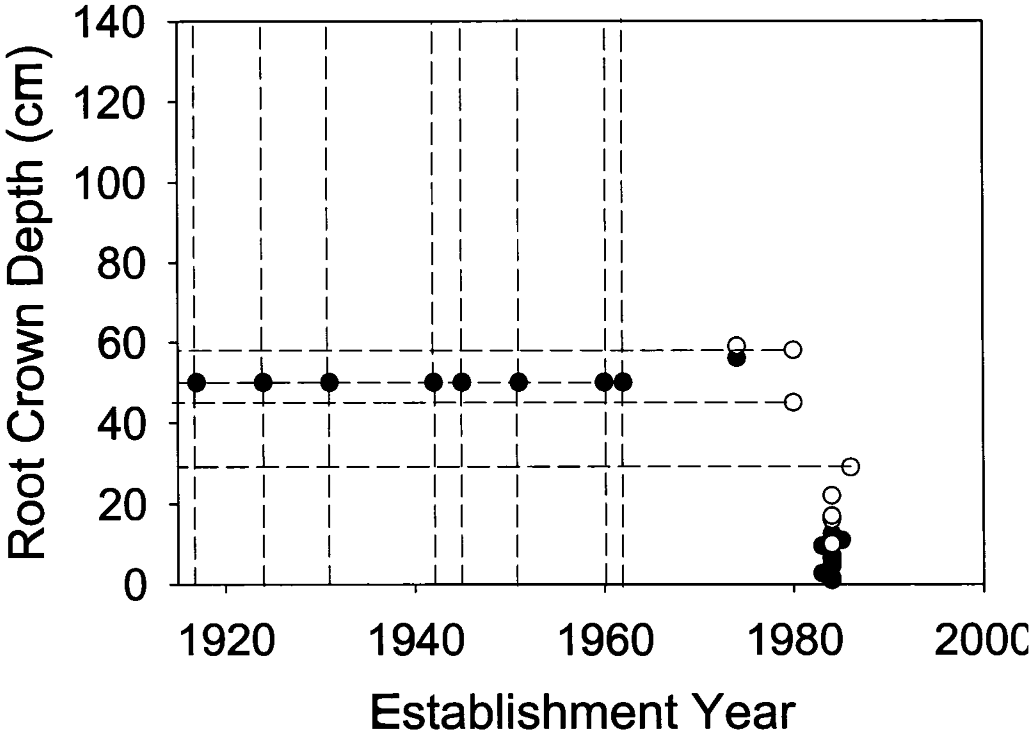

Figure 2.3 Root crown depth and establishment year for Outlaw site on the Yampa River. Solid circles indicate box elder individuals and hollow circles indicate tamarisk individuals. Dashed lines indicate uncertainty, only minimum ages and/or depths could be determined. Samples with vertical dashed lines in both directions represent basal cores, thus no determinations of root crown depth could be made.

Chapter 3

Comparative Shade Tolerances of Tamarisk and Box elder

Introduction

The distribution and abundance of a species across the landscape is a result of the interaction between site processes such as site history, stochastic events, and disturbance regime and species specific traits including dispersal ability, resistance to herbivory and predation, competitive ability, and stress tolerance. Superior competitive ability and tolerance to noncompetitive processes that restrict the abundance and survival of other species are two major mechanisms for species dominance (Grime 2001, MacDougall and Turkington 2005). Stress tolerance is important in both circumstances. Dispersal ability and chance determines which propagules reach a site, but stress tolerance often determines which species can survive, exclude competitors, and reproduce.

Competitive ability can be divided into competitive effect, the ability to suppress other plants through resource depletion, and competitive response, the ability to tolerate resource levels depleted by competition (Goldberg 1990). Superior response competitors withstand neighbor suppression and grow faster or live longer under low resource levels (Tilman 1982), while superior effect competitors reduce survival and growth of competitors and have large effects (per individual or per gram) on resource availability (Grime 1979).

In arid regions, water is often the limiting factor for plant growth and survival, but in riparian areas, phreatophytic species draw water from the capillary fringe above the water table. When the roots of potential competitors are in contact with the capillary fringe, competition for other resources, such as light may become more important. If two species have differing abilities to intercept light, the species with greater interception is the superior effect competitor. If two species differ in light use efficiency, the species that can survive and maintain growth at low light levels is the superior response competitor. A species that can drive understory light levels below that which competing species can survive, but at which seedlings of the same species can survive is the superior competitor for light.

A superior competitor for water can draw soil water levels below that which co-occurring species can acquire. Physiological evidence suggests that superior competitive ability for water is a key mechanism for the widespread success of tamarisk (*Tamarix ramosissima* Ledeb., *T. chinensis* Lour., *T. gallica* L., and their hybrids) in western riparian ecosystems (Busch and Smith 1995, Cleverly et al. 1997, Pockman and Sperry 2000, Horton et al. 2001a). Water in the capillary fringe is relatively abundant; however, episodic drought conditions are ubiquitous to arid region riparian zones. Competition for water is important among plants too young to reach the capillary fringe (Cooper et al. 1999) and when a seasonally variable water table depth does not allow plants to have continuous contact with the capillary fringe (Stromberg et al. 1996, Scott et al. 1999, Shafroth et al. 2000, Horton and Clark 2001). Tamarisk plants are capable of generating water potentials consistently lower than native woody riparian species through osmotic adjustment and superior resistance to xylem cavitation (Busch and Smith 1995, Cleverly et al. 1997, Pockman and Sperry 2000, Horton et al. 2001a). Thus, tamarisk may be able to reduce soil water levels to a level at which potential competitors are subject to desiccation, making tamarisk a superior effect and response competitor.

Competition can only determine species dominance if more than one potential competitor is able to inhabit a site. Stochastic fluctuations in river flow, water table depth, and precipitation events constrain plant growth and survival in arid region riparian ecosystems. The ability to maintain photosynthesis and stomatal conductance at low plant water potentials enables tamarisk to survive and maintain growth under conditions that are limiting for co-occurring native phreatophytes (Anderson 1982, Busch et al. 1992, Cleverly et al. 1997, Horton et al. 2001a).

Box elder and tamarisk are potential competitors in canyons of the upper Colorado River Basin. Box elder is a broad leaf native phreatophytic tree (Green 1934, Dawson and Ehleringer 1991). Tamarisk is a scale leaf phreatophytic shrub (Baum 1978). Due to its taller potential height and high leaf area, box elder may be a superior light competitor than tamarisk. There has been no previous research on the comparative shade tolerances of tamarisk and box elder. However, in separate studies, tamarisk photosynthesis is light saturated only at high levels of irradiance, 1100 μmol m^{-2} s^{-1}, (Anderson 1982 82), but box elder photosynthesis is saturated at much lower light levels, 300 μmol m^{-2} s^{-1} (Foster 1992). Tamarisk has superior drought tolerances compared with many other woody riparian species that occur on southwestern rivers, however the drought tolerances of tamarisk and box elder have not yet been studied. The species composition of sites with spatiotemporal limitations in light and water availability may be explained by the comparative tolerances of these two species to light and water availability.

The analysis in chapter 2 indicated that box elder could be competitively superior to tamarisk if sufficient box elder establishment occurred. In this chapter, I tested shade tolerance as a mechanism for box elder's competitive dominance over tamarisk. I also tested the theory that the effects of drought and shade may interact to influence the outcome of competition. Specifically, I addressed the following questions: (1) Can mature tamarisks be killed by limiting available light (PAR) to levels that commonly occur under box elder canopies? (2) How much shade is needed to diminish the growth of or kill tamarisk? (3) Is there a shade threshold below which box elders, but not tamarisk, can grow? (4) Do drought conditions tip the competitive balance towards tamarisk dominance?

Methods

Shade Tolerance of Mature Tamarisk

Light exclosures were built around mature tamarisk individuals along the Green River in Brown's Park National Wildlife Refuge, approximately ten kilometers upstream of Lodore Canyon (Figure 3.1). Three tamarisk individuals were chosen for analysis at each of five floodplain locations. The tamarisk were two to three meters tall, spatially isolated from adjacent tamarisk, and appeared healthy with > 75% live foliage. All treatments were assigned randomly at each location; (1) high shade (98%) with maximum PAR of 40 μmol m^{-2} s^{-1}, (2) low shade (30%, 1400 μmol m^{-2} s^{-}) and (3) control (2001 μmol m^{-2} s^{-1}). The light exclosures consisted of water and air permeable cloth draped over a PVC pipe and wire mesh frame. The exclosures completely surrounded the plants, with a one meter gap left between the exclosure and the ground surface to facilitate air circulation. Wind damage necessitated regular maintenance of the high shade treatment. The exclosures were maintained for two growing seasons; mid-day temperatures within the exclosures were measured during the summer to ensure that temperature was not elevated relative to the atmosphere. Percent live foliage was estimated in early spring after leaf expansion for each plant at the beginning of the treatment, and for the following two years. Percent live foliage was the amount of live vs. dead foliage on each individual. Twigs with foliage that abscised during the course of the experiment were included in the dead foliage category

Comparative Shade and Desiccation Tolerances of Tamarisk and Box elder

Comparative shade and desiccation tolerances of tamarisk and box elder were investigated with a 5 x 2 x 2 complete factorial greenhouse experiment conducted at Colorado State University. Cuttings were collected from box elder and tamarisk individuals from Lodore Canyon in early July 2004. They were rooted on a mist bench, grown under full light and moisture conditions through October 2004, and over wintered outdoors. In April 2005 the cuttings were brought indoors, potted in square 6.4 x 25.4 cm open ended pots filled with loamy river sediment and allowed to acclimatize for three weeks before implementing the treatments. Because many box elder cuttings failed to root, box elder seedlings were used for half of the box elder replicates. Seeds were collected from the study site in November 2004, cold stratified, sown in the greenhouse in early April 2005, and transplanted in early May.

On June 1, 2005, three box elder seedlings, three box elder cuttings, and six tamarisk cuttings were randomly assigned to each treatment. The treatments consisted of two levels of water stress and five levels of shade, for a total of ten treatments with six replicates (individual plants) per species per treatment combination. The potted plants were grouped together in trays by treatment, arranged alternately so that both species were equally represented in inside and outside rows, and placed in fiberglass hydroponics tanks, with the water table initially maintained at 15-cm depth for both treatments. The spatial arrangement of shade treatments in each tank was randomized. Due to the relatively small plant size, shading by adjacent plants was minimal.

Water stress treatments were assigned randomly to the two tanks. In the low water stress treatment, the initial 15 cm water table depth was maintained throughout the growing season. In the high water stress treatment, the tank was drained on July 6, and the plants were top watered to field capacity on July 17 and September 17. Each of the three droughts imposed on the high water stress treatment ended in watering or the final harvest. The three "drought" periods between watering lasted 11, 60 and 30 days. Shade treatments were assigned randomly to each group of plants for both water stress treatments. Water and air permeable shade cloth was draped over frames enclosing each treatment to control the maximum photosynthetically active radiation (PAR) reaching the plants. The greenhouse employed an automatic light control system which limited the maximum amount of light to 333 μmol m^{-2} s^{-1}, or 15% of full PAR for the area (85% shade). Treatments consisted of: (1) 85% shade (333 μmol m^{-2} s^{-1}), (2) 93% shade

(140μmol m^{-2} s^{-1}), (3) 97.5 % shade (50 μmol m^{-2} s^{-1}), (4) 98.6% shade (29 μmol m^{-2} s^{-1}), (5) 99.9% shade (2 μmol m^{-2} s^{-1}).

Ten individuals each of box elder seedlings, box elder cuttings and tamarisk cuttings were initially harvested, oven dried, and weighed to determine the mean initial plant weight. Commercially available water soluble fertilizer was applied to each plant at the onset of the experiment. Nutrient levels, soil texture, % organic material, and electrical conductivity for the soil and interstitial soil water were tested midway through the experiment and were comparable to levels found at the study site. Mortality counts were conducted biweekly. After 21 weeks, the plants were harvested, oven dried, and weighed. The mean initial weight for each species was subtracted from the final weight to determine the growth in grams per individual. Absolute growth rate is a function of initial plant size; therefore the mean relative growth rate for each individual was calculated. The mean relative growth rate (g of final biomass per g of initial biomass) for the growing season was calculated by subtracting the natural log of the final dry weight by the natural log of the mean initial dry weight (Hunt 1978) for all plants.

Treatment main effects (water stress, light stress, species) and interactions on survival were tested with likelihood ratio chi-square tests using a logistic regression model (Quinn and Keough 2002). The number of survivors for each light stress treatment per species was then compared by treating each water stress treatment as a replicate (see justification for pooling water stress treatments in results) and comparing the number of survivors using the F statistic from least square analysis for fixed effects, with significant differences determined by using differences of least square means ($\alpha = 0.05$). Treatment main effects and interactions on relative growth (proportional mass change g/g) were tested using the F statistic from least squares analysis for fixed effects. Pair-wise relative growth differences between tamarisk and box elder for each light stress treatment was analyzed using differences of least square means ($\alpha = 0.05$). SAS 9.1 was used for all statistical analysis (SAS 2002).

Results

Shade Tolerance of Mature Tamarisk

The low shade treatment had little effect on the size and percent live foliage of tamarisk plants (Fig. 3.1). However, the high shade treatment resulted in the death of two tamarisks and a 95-99% dieback of live foliage for the three surviving individuals after one year. After year two, one additional high shade tamarisk had died, and the remaining two high shade tamarisks survived only by producing basal shoots that escaped the shade treatment.

Comparative Shade and Desiccation Tolerances of Tamarisk and Box elder

Water Stress

Water stress was not a significant predictor of survival (df = 1, $\chi^2 = 0.16$, P = 0.69) for tamarisk or box elder in the factorial experiment. Water stress also had no significant effect on relative growth (df = 1, F = 0.87, P = 0.35), therefore data from the two water stress treatments were pooled for species comparisons by shade treatment. The high survival rates indicate that both species are highly drought tolerant and the imposed water stress was insufficient to cause mortality. The short term response of both species to the drought treatment was leaf abscission. After six weeks of drought, the tamarisks in shade treatments 1-3 experienced heavy defoliation. Only two box elders in treatment two were defoliated. After eight weeks of drought, the tamarisks in shade treatment one were completely defoliated, and 90% defoliated in treatments two and three. Box elders were 70% defoliated in treatment one and 30% defoliated in treatments two and three. The higher shade treatments apparently reduced evaporative loss, thus defoliation was not observed in treatment four.

Light Stress

Species identity was a significant predictor of plant survival (df = 1, $\chi^2 = 5.15$, P = 0.02), with the box elders having much lower mortality (Fig. 3.2). Light stress was not a significant predictor of survival when both species were pooled (df = 1, $\chi^2 = 0.50$, P = 0.48), however the interaction of light stress on species was a significant predictor of survival (df = 1, $\chi^2 = 3.93$, P = 0.05).

No tamarisk or box elder mortality occurred for shade treatment one (333 μmol m^{-2} s^{-1}) or two (140μmol m^{-2} s^{-1}), indicating that both species can survive a season of 93% shade. Tamarisk, but not box elder experienced mortality in shade treatment three (97.5% shade); (Fig 3.2-C). Differences in the number of survivors by species was statistically significant (P = 0.002). After nine weeks of shading four tamarisks had died, and when the treatments ended six of the original 12 tamarisks had died. Significant differences in mortality occurred between tamarisk and box elder (P = 0.005) for shade treatment four (98.6% shade); (Fig 3.2-B). All but one box elder survived, while three tamarisks died after nine weeks, and six had died by the treatments end.

Very high mortality occurred for both species under treatment five (99.9% shade); (Fig 3.2-A). Only one box elder and no tamarisk survived the full duration of the treatment. Ten tamarisks died during the first three weeks and all were dead by seven weeks, while seven box elders died after three weeks, ten after 13 weeks, and 11 by the treatments end

Light stress (df = 4, F = 25.70, $P < 0.0001$), species (df = 1, F = 99.79, $P < 0.0001$), and light stress * species (df = 4, F = 7.11, $P > 0.0001$) were all significant predictors of relative growth for both species. Box elder had significantly higher relative growth rates ($\alpha = 0.05$) compared to tamarisk across every light stress treatment except the highest light stress treatment, in which tamarisk suffered complete mortality and only one box elder survived.

Of particular interest is the transition point, the treatment level at which growth switches from positive to negative or zero. Box elder relative growth was positive for shade levels 1-4 (Fig. 3.3), and dropped below positive only in the highest shade treatment five. Tamarisk growth was lower than box elder growth for every treatment except shade treatment five, which was characterized by rapid and complete tamarisk mortality. Tamarisk relative growth was positive for treatments one and two, and negative in treatments three through five (Fig. 3.3). The growth data indicates that box elder is the superior light response competitor, and is able to maintain growth at PAR levels (29-50 μmol m^{-2} s^{-1}) too low for tamarisk growth.

Discussion

Shade Induced Mortality - Mature Tamarisk

A 98% reduction in photosynthetically active radiation (max PAR = 40 μmol m^{-2} s^{-1}) for two growing seasons resulted in mortality for 60% of the adult tamarisks analyzed. The two survivors suffered the loss of all live aboveground biomass but avoided mortality by producing basal shoots that exploited a gap in the base of the shade treatment canopies. The bottoms of the shade structures were kept open to allow air circulation, yet without these openings mortality likely would have been 100%. In Chapter 2 I documented heavy mortality of both mature and juvenile tamarisk in mixed box elder/tamarisk stands, with a box elder dominated overstory and low understory light levels (98.5 - 99.9% shade). Shade cloth does not perfectly mimic tree canopies because the light in forest understories has lower red:far red ratios than the light in the shade cloth treatments. However, higher red:far red ratios have been shown to affect morphology but not growth in low light (Schmidt and Wulff 1993). These results support the hypothesis that, excluding competition for water and nutrients, box elders can out-compete and cause the death of mature tamarisk through light interception alone. Light interception may prove to be an effective means of controlling tamarisk, which is highly tolerant of anoxia, fire, drought, burial, mechanical damage, and is resistant to herbivory (Everitt 1980, Brock 1994, Cleverly et al. 1997, Shafroth et al. 2005)

Comparative Drought Tolerance-Tamarisk and Box elder

The drought treatment had little effect on the growth and survival of either species across shade treatments, although both species dropped leaves. The drought treatment was not severe enough to cause mortality in either species and demonstrated that both species are highly tolerant of very low soil water availability.

Comparative Shade Tolerance-Tamarisk and Box elder

Both species had 100% survival and positive growth in shade treatments that range from 85-93%. However, at 97.5 - 98.6% (50-29 μmol m^{-2} s^{-1}) shade, differences in growth and survival were found. Box elder growth was positive, tamarisk growth was negative, and box elder mortality was 0-8%, while tamarisk suffered 50% mortality in both treatments. Light levels of 29-50 μmol m^{-2} s^{-1} were commonly found under box elder (Chapter 2) and tamarisk (Chapter 4) canopies, yet these light levels were insufficient to maintain tamarisk growth. Light levels below 2 μmol m^{-2} s^{-1} were insufficient for box elder growth, thus box elder is the superior response competitor, and is able to successfully exploit habitats with lower light levels then tamarisk.

Box elder was able to maintain growth at 98.6% shade, while tamarisk could not maintain growth at more than 85% shade. Box elder had higher growth than tamarisk for every shade level tested, indicating that box elder is the superior competitor for light. The ability to grow at very low light levels has also been observed in *Acer saccharum Marsh.* which had higher growth rates in 98% shade than co-occurring early successional *Betula* species (Walters and Reich 1996).

The differences in shade tolerances in box elder and tamarisk, and the higher growth rates for box elder provides a mechanism for the competitive superiority and the succesional replacement of tamarisk by box elder. However, box elder establishment is limited on regulated rivers, and controlled floods are required to produce suitable hydrologic conditions for seedling recruitment (DeWine 2005). Environmental management including controlled floods and box elder plantings could be used to promote box elder establishment which would lead to tamarisk control.

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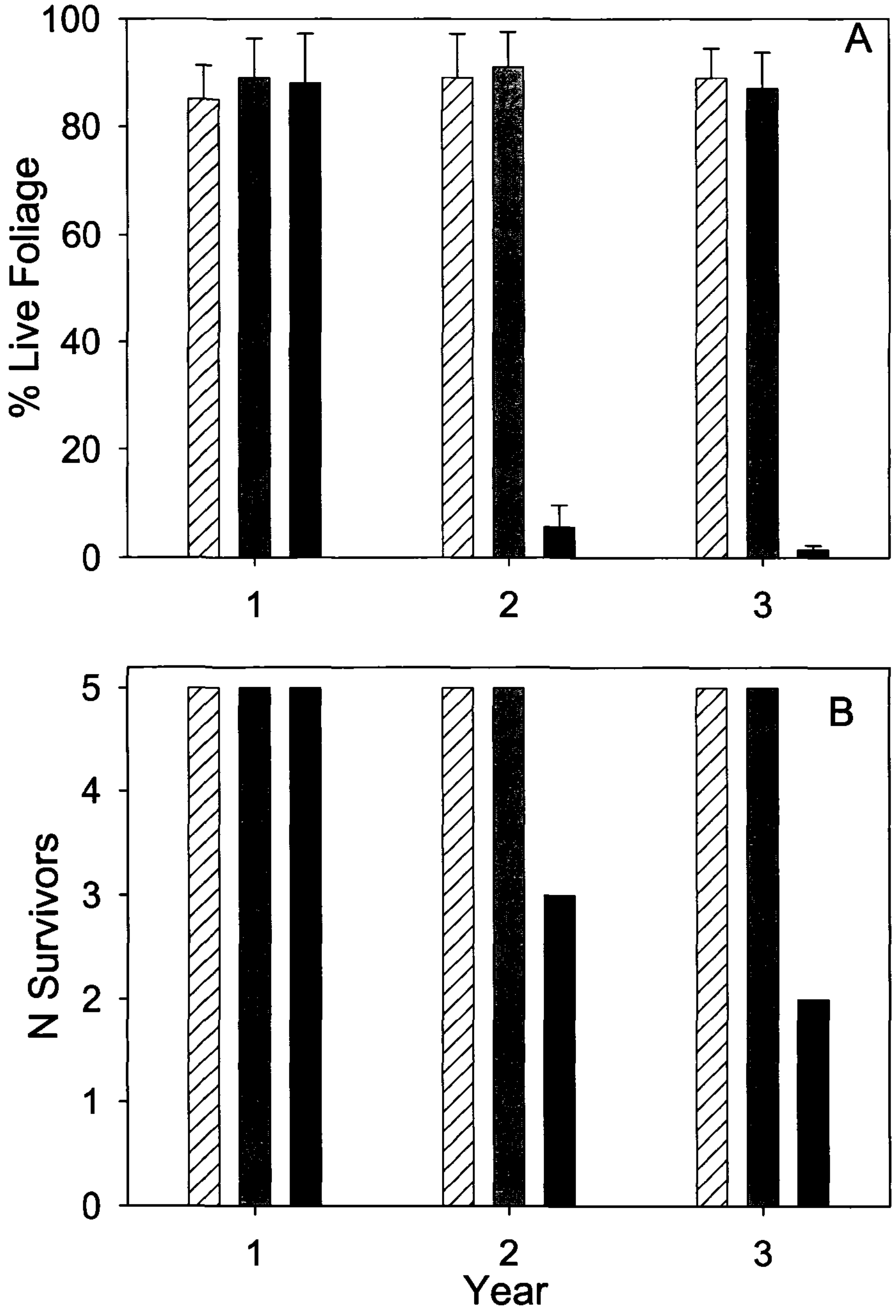

Figure 3.1 Percent live foliage (A), and # survivors (B) for tamarisk in control (hatched bars), moderate shade (gray bars), and high shade (solid bars) treatments for years 1-3. Mortality and live foliage assessments made at beginning of growing season. Error bars are +1 standard error.

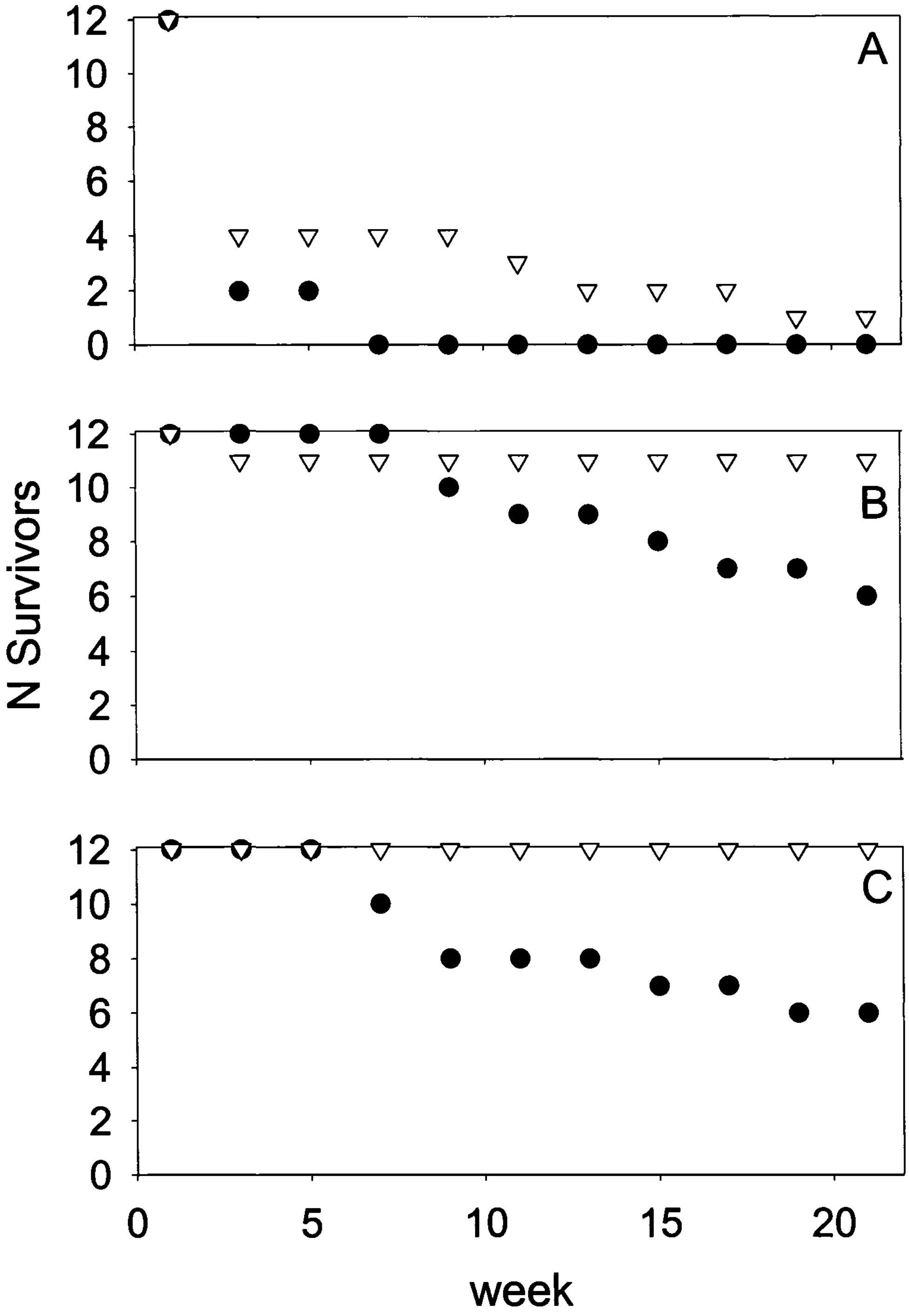

Figure 3.2 Biweekly tallies of survivors for 99.9% (A), 98.6% (B), and 97.5% (C) shade. Hollow triangles represent box elders and solid circles represent tamarisk.

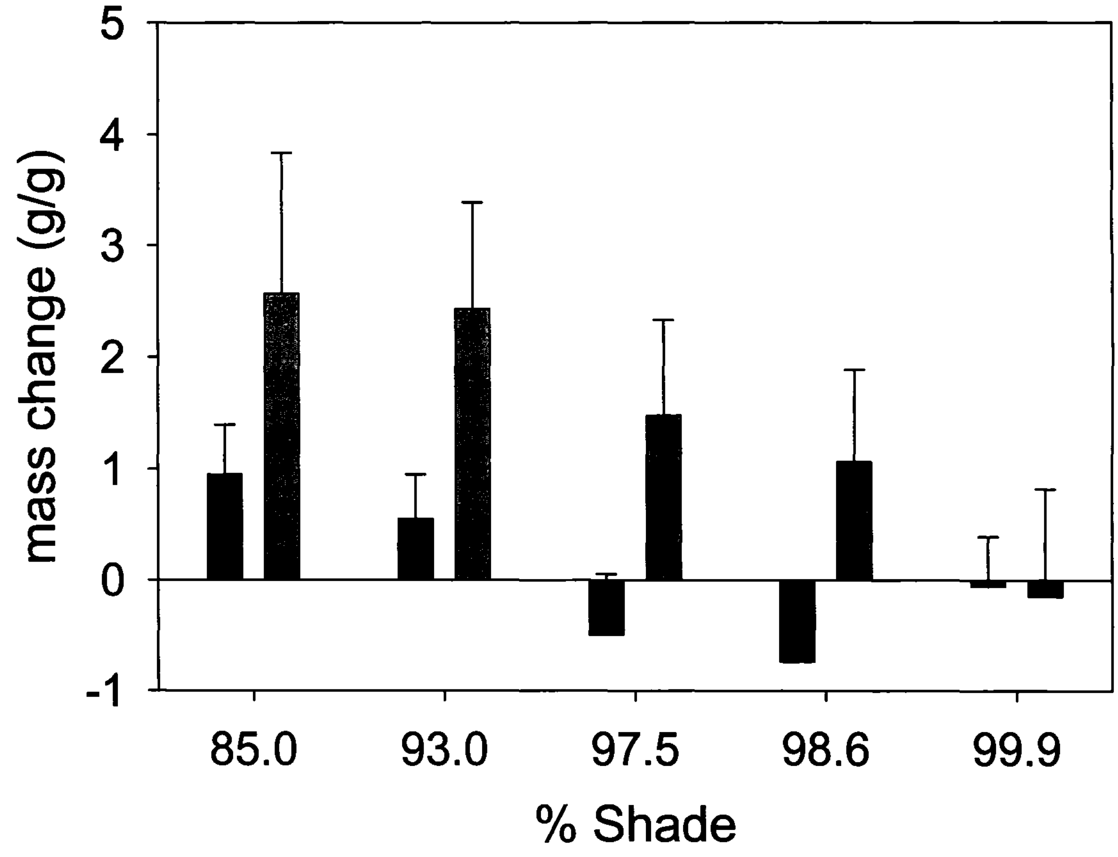

Figure 3.3 Relative growth, ln(weight $_{\text{final}}$) – ln (weight $_{\text{initial}}$), for tamarisk (solid black bars) and box elder (gray bars). Error bars are one standard error.

Chapter 4

Habitat Overlap and Facilitation in Tamarisk and Box elder Stands: Implications for Tamarisk Control Using Native Species

Introduction

Invasive plant management is typically approached using chemical and mechanical removal or traditional biological control. These "top-down" eradication techniques are focused solely on the removal of the target organism. Bottom-up control limits the resources available to the undesired species by manipulating disturbance, competition, and successional processes (McEvoy and Coombs 1999). In experimental settings, the addition of interspecific competition to the traditional top-down control methods of herbicide application, simulated grazing, and introduced insect herbivory, has led to increased non-native species control and has enhanced native plant establishment (McEvoy et al. 1993, Wilson and Partel 2003). Bottom-up control has the potential to prevent reinvasion by altering the conditions that allowed the initial invasion, yet bottom-up invasive species management is rarely implemented (Sheley 2003, D' Antonio et al. 2004).

The non-native invasive woody shrub, tamarisk (*Tamarix ramosissima* Ledeb., *T. chinensis* Lour., *T. gallica* L., and their hybrids), has invaded over a million hectares of riparian areas and other wetlands in arid and semiarid regions of western North America, transforming entire ecosystems in the process (Zavelta and Hobbes 2001). Millions of dollars are spent annually on top-down tamarisk removal projects (Shafroth et al. 2005). Current control techniques include herbicide application, mechanical removal, and the introduction of an insect herbivore. Aerial herbicide application is effective and relatively inexpensive, but the collateral destruction of desirable native species is difficult to avoid (Sprenger et al. 2002, McDaniel and Taylor 2003). Foliage and cut stem herbicide application is an effective but expensive control measure (Sprenger et al. 2002, 2004, Harms and Hiebert 2006). Mechanical control involves bulldozing the area and removing the root crowns, an effective but costly and disruptive procedure (Taylor and McDaniel 1998, Sprenger et al. 2002, McDaniel and Taylor 2003). An alternative mechanical method is removal of tamarisk root crowns by hand. This procedure is less disruptive but requires intensive labor (CDNR 2004). Traditional biological control, using the beetle, *Diorhabda elongata* Brullé *deserticola* Chen, is an inexpensive and potentially self sustaining technique. Preliminary results indicate that the beetles are capable of defoliating large patches of tamarisk, however it is unclear if the beetles will cause substantial tamarisk mortality (Deloach et al. 2004).

A major weakness of these techniques, with the possible exception of the traditional biological control, is a failure to correct the situation that led to the initial invasion and thus prevent reinvasion. Additionally, the loss of a canopy-shrub level after tamarisk removal has not been found to be offset by native woody species regeneration

(Harms and Hiebert 2006). The bottom-up approach of restoring flood flows to regulated rivers may aid native plant colonization and tamarisk suppression through competition by native species (Poff et al. 1997, Taylor and McDaniel 1998, Sher et al. 2002, Rood et al. 2003). However, managed flooding alone will not eliminate tamarisk or prevent reinvasion. Tamarisk is common in many unregulated rivers and it became well established on currently regulated rivers while they were free-flowing (Cooper et al. 2003, Birken and Cooper 2006). An additional bottom-up technique is needed to augment top-down control and flow restoration. The use of native trees such as box elder to suppress and potentially kill tamarisk is a technique with the potential to control tamarisk and prevent reinvasion while restoring native forest habitat.

Box elder is capable of out-competing, overtopping, and killing tamarisk (Chapter 2) through superior light interception and shade tolerance (Chapter 2-3). Observational evidence indicates that tamarisk may facilitate box elder establishment in canyons of the Green and Yampa Rivers in Dinosaur National Monument, Colorado. Facilitation generally increases in importance in stressful environments and gives way to competitive interactions in more benign environments (Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997, Brooker and Callaghan 1998). The semi-arid and environment of the study canyons may initially represent a stressful environment for box elder establishment. Tamarisk may initially facilitate box elder establishment by limiting evapotranspiration through light interception. As box elder continues to grow, the roots eventually reach the water table and a limiting resource, water, becomes abundant. The interaction between box elder and tamarisk may then switch to a competitive interaction.

The goals of this study were to: (1) Determine where the two species co-occur in Dinosaur National Monument by comparing the distribution of both species by fluvial landform and floodplain position, (2) determine if tamarisk facilitates box elder establishment, and (3) design bottom-up control recommendations by analyzing box elder seedling survival and growth across a range of litter type and depth, soil texture, shade intensity, and water table depths indicative of those found in Dinosaur National Monument.

Methods

Distribution: Fluvial Landforms

Images of Yampa and Lodore Canyons were generated using United States Geological Survey (USGS) digital orthophoto quarter quadrangles (30108 NW and 30108 SW) with one meter resolution. A polygon was drawn to delimit each discrete patch of tamarisk and box elder, and the percent canopy cover of each species within each polygon was visually estimated in the field. The fluvial landform for each stand was identified in the field and cross referenced with maps of the study area created for prior geomorphic studies on the Green (Grams and Schmidt 1999) and Yampa rivers (Larson 2004). The mapped fluvial landforms were channel margin deposits, debris fans, eddy bars, point bars and expansion gravel bars. Channel margin deposits were divided into: (1) pool margin and other fine grained alluvial deposits and (2) coarse grained talus. Pool deposits occur in canyon openings (parks) or areas of ponded flow upstream of flow constrictions such as debris fans, bedrock outcrops, and tight channel bends. Talus occurs along high gradient reaches lacking extensive fluvial deposits, subsequently fine grained sediments are sparsely distributed. Debris fan deposits occur at or near tributary junctions. The sediment texture is highly variable and poorly sorted, ranging from large boulders to fine silt. Eddy bars are composed of fine grained sediments deposited in areas of recirculating flows, downstream of debris fans or other constrictions. Expansion gravel bars occur downstream of the recirculation zone in regions of flow expansion. The deposits are dominated by gravel and cobbles, often with a sand cap. Point bar deposits occur on the inside of river bends. Sediments are typically gravel overlain with sand veneers.

Field drawn polygons were digitized using Arcview 3.0 (ESRI 1996). The area of each polygon was calculated, multiplied by the cover for each species, and summed to produce total areal cover (ha) for both tamarisk and box elder stands, on each river on each landform.

Distribution: Floodplain Position

Each tamarisk and box elder stand (see above methods for description of mapping protocol) was assigned a number. Forty stands of tamarisk and forty stands of box elder were randomly chosen for each river. Only stands containing box elders estimated to have established after the early 1960s were sampled because older box elders on the Green River are relicts of pre-regulation hydrological conditions and are located high above the current floodplain (DeWine 2005). A transect was established perpendicular to the river through the center of each stand, extending from the uppermost extent of riparian vegetation to the river. The minimum, maximum, and mean elevation above the river elevation at low flow was identified for each species within each patch. The relationship of species (tamarisk or box elder), river (Green and Yampa), and the interaction on maximum, minimum, and mean height above the river, was evaluated using the F statistic from least squares analysis for fixed effects. Pair wise differences between tamarisk and box elder stands on each river were analyzed using differences of least square means ($\alpha = 0.05$). SAS 9.1 was used for all statistical analysis (SAS 2002).

Box elder Seedling Survival under Tamarisk

Box elder seeds were collected in Lodore Canyon in the fall of 2003, dried and wet-stratified over the winter. Germinated seeds were transplanted into square 4 * 10 cm paper pots, filled with potting soil, and grown in the greenhouse for two months before being transplanted. The seedlings were transported by river raft to four sites systematically spaced throughout Lodore Canyon in June 2004. At each site a closed canopy tamarisk stand was divided in half and one treatment was randomly assigned to each half. All aboveground tamarisk biomass was mechanically removed for one treatment, while the tamarisk canopy was left intact for the other treatment. Twenty-five box elder seedlings were planted in each treatment at each site, for a total of 200 seedlings. Survivors were counted in the mid summer and fall of 2004. Volumetric water content (using time domain reflectometry) and temperature of the upper 10 cm soil horizon was measured in both treatments at each planting site at mid-day once in the summer and fall. Photosynthetically active radiation (PAR) was measured under the tamarisk canopy at all sites within two hours of solar noon on sunny days. Canopy PAR was divided by full sun PAR to calculate percent shade. The effect of the tamarisk removal treatment on seedling mortality was tested with likelihood ratio chi-square tests using a logistic regression model in SAS 9.1 (SAS 2002). Due to high mortality for the seedlings planted in 2004, the experiment was repeated with 320 seedlings at the same locations in 2005. To reduce desiccation induced mortality, 120 plants (60 in each treatment) were planted with one liter of Dri-Water™ irrigation gel. The gel consists of water and cellulose. As the cellulose breaks down water is released for plant use. Treatment main effects (supplemental water and tamarisk canopy) and interactions on mortality were tested with likelihood ratio chi-square tests using a logistic regression model in SAS 9.1 (SAS 2002).

Litter Effects on Box elder Emergence

The effect of tamarisk and box elder leaf litter on box elder seedling emergence was tested in a greenhouse experiment. Box elder seeds were collected from the study site in the fall, dried, and wet stratified over the winter. Leaf litter was collected from the understory of monospecific tamarisk and box elder stands. Trays were filled with soil and overlain with two or four cm of box elder or tamarisk litter, the mean and maximum litter depths found in the field (personal observation). Two hundred and fifty box elder seeds were placed on each litter treatment and a control without leaf litter. Trays were watered daily to field capacity and emerging seedlings were counted weekly for two months. Seedlings were counted when the first true (non cotyledon) leaves formed. The effects of litter type (tamarisk or box elder) and litter depth, and the interaction between litter depth and type on emergence were tested with likelihood ratio chi-square tests using a logistic regression model in SAS 9.1 (SAS 2002).

Soil Texture, Water Table Depth and Shade Effects on Box elder Seedlings

The influence of soil texture, water table depth, and shade intensity on box elder seedling survival and growth were investigated using a 3 x 3 complete factorial experiment conducted outdoors in Brown's Park Wildlife Refuge along the Green River. Box elder seeds were wet stratified over winter, sown in the greenhouse in early April, and potted in square 6 x 25 cm open ended pots with one of three sediment types collected from the Green and Yampa Rivers in mid-May. Ten randomly selected seedlings were harvested, dried, and weighed to determine the mean initial seedling weight. Seedlings were planted in the field on June 10th, immediately following the annual flow peak.

Three interacting treatments were used to represent the range of abiotic conditions found in the riparian zones of the study canyons. The water table treatments consisted of high (20 cm below soil surface), intermediate (45 cm depth), and low water tables (84 cm depth). The seedling roots were initially in contact with the water table in the high water table treatment, with the capillary fringe in the intermediate water table treatment, and well above the capillary fringe in the low water table treatment. The desired water table depth was achieved by planting the seedlings at different heights above the water table. Water table depth was estimated by surveying the ground surface relative to the river and assuming a relatively flat water table surface profile. Three shade treatments were implemented using cloth that blocked 98%, 92%, or 52% of PAR. The three soil treatments were coarse sand (D = 51% 0.5-2.0 mm, 46% 0.25-0.5mm, 2% 0.05-0.25 mm, 1% < 0.05mm), sand (D = 83% 0.25-0.5mm, 15% 0.05-0.25 mm, 2% < 0.05, or loamy sand (71% 0.25-0.5mm, 10% 0.05-0.25, 19% <0.05). Each water table * shade intensity * soil texture treatment combination had ten replicates.

All plants were harvested, dried, and weighed after 95 days at summer's end. Treatment main effects (water table depth, shade, and soil texture) and their interactions on seedling survival were tested with likelihood ratio chi-square tests using a logistic regression model. Treatment main effects and interactions on growth (final weight-mean initial weight) were tested using the F statistic from least squares analysis for fixed effects. Pair wise growth differences were analyzed using differences of least square means ($\alpha = 0.05$). SAS 9.1 was used for all statistical analysis (SAS 2002).

Results

Distribution: Fluvial Landform Type

Total box elder stand area was higher than tamarisk stand area on both the Yampa (33.5 vs. 16.3 ha) and Green rivers (29.9 vs. 18.7 ha). Yampa River box elder stand area was highest in pool margins (18.5 ha), and talus (10.7 ha). Debris fans (2.1 ha) and eddy margins (1.8 ha), had lower cover, and gravel bars (0.2 ha) and point bars (0.3 ha) had very low cover (Fig. 4.1-A). Green River box elder stand area was also highest in pool margins (17.0 ha), and lower on debris fans (4.8 ha), talus slopes (3.4 ha), eddy margins (3.3 ha), gravel bars (0.9 ha) and point bars (0.6 ha) (Fig. 4.1-B).

Tamarisk cover on the Yampa River was highest on gravel bars (9.0 ha), pool margins (4.8 ha) and eddy bars (1.7 ha), and lower on debris fans (0.6 ha), point bars (0.2 ha), and talus slopes (0.1 ha) (Fig. 4.1-A). Tamarisk cover on the Green River was highest on pool margins (6.6 ha), gravel bars (4.5 ha), and eddy bars (3.4 ha) with lower cover on debris fan deposits (2.0 ha), point bars (1.4 ha), and talus slopes (0.8 ha) (Fig 4.1-B).

Distribution: Floodplain Position

Box elders inhabited significantly higher elevation floodplain positions on the Yampa River compared to box elders on the Green River and tamarisk on both rivers at $\alpha = 0.05$ (Fig. 4.2). Box elders on the Green River occupied a similar maximum and mean floodplain position as tamarisks, but tamarisks on both rivers occupied a significantly lower minimum floodplain position than box elders on both rivers ($\alpha = 0.05$). Both species (df = 1, F = 29.68, $P < 0.0001$) and river (df = 1, F = 27.49, $P < 0.0001$) were significant predictors of mean height of plants above the river. Likewise, the interaction between species and river was also significantly related to mean height above the river (df = 1, F = 13.42, P = 0.0003).

Box elder Seedling Survival under Tamarisk

Box elder seedling mortality was very high by mid-summer in the 2003 tamarisk canopy removal treatment. By August, only 3% of the seedlings were alive in the tamarisk canopy removal treatment (- canopy). However, 23% of the seedlings survived in the intact tamarisk canopy treatment (+ canopy). At the end of the summer (October 6) only one seedling was alive in the + canopy treatment and there were no survivors in the – canopy treatment. Statistical analysis of the August survivor count indicated that treatment (+/- canopy) was a significant predictor of mid-summer survival (df = 1, χ^2 = 12.85, P = 0.0003), with higher seedling survival beneath the intact tamarisk canopy.

Mortality was lower in the 2005 experiment. Seedling survival was higher under intact tamarisks and with irrigation gel in both midsummer and fall (Fig 4.3). Only 2% of the seedlings survived the growing season in the - canopy - water treatment. However, 31% of the seedlings survived through the summer in the - canopy + water treatment. Seedling survival was highest under a tamarisk canopy, with 51% of the + canopy + water treatment seedlings alive and 14% of the seedlings in the + canopy -water treatment alive at summer's end. The canopy removal (df = 1, χ^2 = 12.46, P = 0.0004) and watering treatment (df = 1, χ^2 = 32.23, P < 0.0001) were significantly related to seedling survival, however the interaction was not significant (df = 1, χ^2 = 1.28, P = 0.26). PAR was reduced by 76-99% under tamarisk compared to the canopy removal treatments, resulting in lower soil temperatures (Fig. 4.4). However, soil moisture was also lower under the intact tamarisk canopies (Fig. 4.5).

Litter Effects on Box elder Emergence

Box elder seeds germinated and grew on tamarisk leaf litter 2-4 cm thick (Fig. 4.6). The number of emerging seedlings was lower than on the bare soil control, but much higher than on box elder leaf litter. Litter type (df = 1, χ^2 = 16.49, P < 0.0001), but not litter thickness (df = 1, χ^2 = 2.43, P = 0.12) was a significant predictor of seedling establishment. The litter type* litter thickness interaction was also a significant predictor of seedling establishment (df = 1, χ^2 = 13.11, P = 0.0003).

Soil Texture, Water Table Depth, and Shade Effects on Box elder Seedlings

Mortality was low across all treatments: 89% of the seedlings survived the duration of the experiment and no treatment main effects or interactions were statistically significant. Likewise growth was positive under all treatments indicating that box elder can grow and survive under the range of abiotic conditions imposed by this experiment. Shade (df = 2, F = 8.33, P = 0.0003), soil texture (df = 2, F = 89.95, $P < 0.0001$), water table depth (df = 2, F = 5.67, P = 0.004), the interaction of shade*soil texture (df = 4, F = 2.76, P = 0.03), and soil texture*water table depth (df = 4, F = 3.77, P = 0.006) were significantly related to box elder growth. Growth was significantly lower in the high (0.46 g) than the moderate (0.73 g) or low (0.80 g) shade treatments (α= 0.05). Growth in the loamy sand (1.32 g) was significantly higher than in the sand (0.36g) and coarse sand (0.31g) treatments (α= 0.05). Growth in the low water table treatment (0.49 g) was significantly lower than in the high (0.75 g), and medium (0.75 g) water table depth treatments at α= 0.05.

Discussion

Overlapping Distribution of Tamarisk and Box elder

The distribution of tamarisk and box elder overlaps on several landforms within the study canyons. Both species are common on pool margins and eddy bars, and to a lesser extent on point bars. These landforms are ideal locations for the implementation of bottom-up control measures which facilitate box elder establishment, growth and survival. Box elder, but not tamarisk, is common on talus dominated channel margins, therefore, extensive control measures are not necessary on talus deposits. Both species are common on debris fan deposits. However, debris fan deposits are characterized by large boulders with woody vegetation confined to inter-boulder patches of fine grained sediments. Bottom-up control would be difficult on debris fans where it would be infeasible to establish dense, closed box elder canopies. Tamarisk, but not box elder, is common on gravel bars. Gravel bars may be unsuitable for box elders because of these low lying landforms are frequently inundated. Therefore, gravel bars would not be a good choice for bottom-up control.

The two species also occupy overlapping floodplain elevations above the river. The mean, maximum, and minimum elevation of box elder in Yampa Canyon is significantly higher than the elevation of tamarisk, but box elder and tamarisk interact at many sites throughout the Yampa River. The mean and maximum elevations of box elders may be higher simply because tamarisk was not widespread in the area before the 1960s, and population members that established in the 1940s and 1950s are uncommon (Cooper et al. 2003). However, many box elders in the study area are at least 100 years old (DeWine 2005). Floods of sufficient magnitude to facilitate establishment at the highest elevations above the river are intrinsically rare. Thus, the box elder population may have been exposed to more high magnitude flows than the tamarisk population and consequently represented by a larger number of cohorts at high elevations. Mature box elders were not sampled on the Green River to avoid the confounding effects of river regulation, but in a previous study mature box elders on the Green and Yampa rivers were found to occupy similar elevations above the river (DeWine 2005). Box elders on the Green and Yampa do not inhabit the lowest floodplain positions occupied by tamarisk, perhaps because these environments are subjected to more frequent and longer duration flooding and scour. However, no comparative or equivalent studies have been conducted on the flood tolerance of box elder and tamarisk.

Facilitation

Tamarisk appears to facilitate box elder seedling survival by providing shade, which reduces air temperature and evapotranspiration in the sub-canopy. Similarly, shrubs have facilitated *Acer opalus* subsp. *granatense* seedling survival in the Mediterranean region of southern Europe (Gomez-Aparicio et al. 2004). However, the reduced water content observed under intact tamarisk stands in this study indicates that tamarisks also appear to compete with box elder seedlings for soil moisture. The combination of positive and negative interactions between plant species is widespread in plant communities, particularly in stressful environments (Callaway 1995, Callaway and Walker 1997). The higher survival rates for box elder seedlings under intact tamarisk canopies suggests that the net effect of tamarisk on box elder seedlings is positive. The addition of water significantly increased box elder seedling survival for both treatments. Therefore, desiccation appears to limit box elder seedling survival and irrigation can aid establishment.

Interactive effects involving the same species may alternately be facilitative or competitive depending on the life stages of the species involved (Walker and Vitousek 1991, Kellman and Kading 1992, Chapin et al. 1994). The benefactor can be negatively impacted, even killed by the beneficiary (McAuliffe 1984, 1986, Archer et al. 1988, Flores-Martinez et al. 1994). As demonstrated in chapters 2 and 3, the interaction does become competitive as the box elders grow, often resulting in tamarisk mortality.

Feasibility of Using Box elders as Bottom-up Control Agents

Unlike many woody floodplain plants, such as species of *Populus* and *Salix*, the large seeded box elder does not require bare mineral soil for establishment, as demonstrated by its germination on thick tamarisk litter. Seiwa and Kikuzawa (1996) found that leaf litter did not inhibit *Acer mono* Maxim. seedling establishment in a Japanese deciduous forest, but did prevent smaller seeded species from establishing. Box elder leaf litter did inhibit seedling emergence, contrasting with observational evidence of box elder seedlings establishing on 5cm thick deciduous tree leaf litter in eastern North America (Hosner and Minckler 1960).

The drought tolerance observed in box elder seedlings coupled with the adaptability to a range of PAR levels and soil textures indicates that box elder plantings can be successful throughout much of the study site. Box elder seedlings survived and grew in 2% of full sun irradiation, confirming the findings in chapter 3 that box elder seedlings are extremely shade tolerant. The seedlings survived and grew in all the soil textures tested, confirming observational evidence that box elders are able to grow on sediment textures ranging from clay to sand (Green 1934, Harlow et al. 1979). Box elder seedlings survived and grew with roots well above the water table, suggesting that they are highly drought tolerant. Box elder is widely regarded as drought tolerant, and planted on upland sites of the Great Plains as a windbreak (Plowman 1915, Green 1934). However, adult box elders in semiarid and arid region riparian areas are facultative phreatophytes, and are able to exploit groundwater moisture (Dawson and Ehleringer 1991, Kolb et al. 1997).

Management Implications

The management of succession to promote box elder seedling establishment in tamarisk stands is a potentially useful tool for tamarisk management where the two species ranges overlap. Box elder is found throughout North America, and is common in many narrow canyons in semiarid and arid regions of western North America, as is tamarisk, thus many potential regions of habitat overlap occur in tributaries and along the main stem of the Colorado River.

The facilitation of box elder seedling survival by tamarisk indicates that clearing tamarisk stands may be counterproductive in some areas. Tamarisk removal resets succession and the next colonizer is likely to be tamarisk due to its prodigious seed production and dispersal abilities (Neill 1985, Brotherson and Field 1987). Tamarisk is dependent on the availability of bare unshaded sediment for successful colonization (Shafroth et al. 1998). Leaving tamarisk stands intact and promoting box elder establishment through seeding or planting seedlings may require less labor and capital investment than tamarisk removal. Within a few decades dense box elder stands will overtop, kill and replace tamarisk, and the resulting shade would inhibit subsequent tamarisk establishment, and provide habitat for a wide range of bird and mammal species.

Box elder establishment could be facilitated by introducing cold stratified seeds following controlled or planned floods. Artificially wetting the floodplain has successfully resulted in the establishment of native woody riparian species, including species of *Salix* and *Populus* (Cooper and Van Havereren 1994, Friedman et al. 1995, Roelle et al. 2001, Sprenger et al. 2002). Seedling or larger tree plantings with irrigation or high river flows could also be an effective means of box elder establishment in tamarisk stands. It is not known if box elders can be established with pole plantings, although I successfully rooted small cut stems in moist sand. Pole plantings are effective methods of cottonwood (*Populus* sp.) and willow (*Salix* sp.) establishment (Anderson et al. 2004).

Other native trees capable of providing dense shade are also potential agents of bottom-up control. Candidate species include cottonwoods (*Populus* spp.), willows (*Salix* spp.), Arizona sycamore (*Platanus wrightii* S. Wats), and netleaf hackberry (*Celtis laevigata* var. *reticulate* (Torr.) L.Benson.). Cottonwood species may be the most promising because they can grow large with broad leaves and have a widespread distribution. However, cottonwood appears to be intolerant of shade particularly in combination with water stress (Cooper et al. 1999). Therefore, openings would need to be created in tamarisk patches for cottonwood establishment. Cottonwoods could be established via natural seedling recruitment following managed flooding, seedling plantings, or pole plantings.

The manipulation of succesional and competitive processes through the facilitation of native tree establishment may provide a valuable complement with top-down control methods and managed flows to tamarisk control. The key to integrating all potential tools is rigorous site assessments and prescriptions for management. Follow up monitoring and periodic adjustments to the system are critical to successful tamarisk control.

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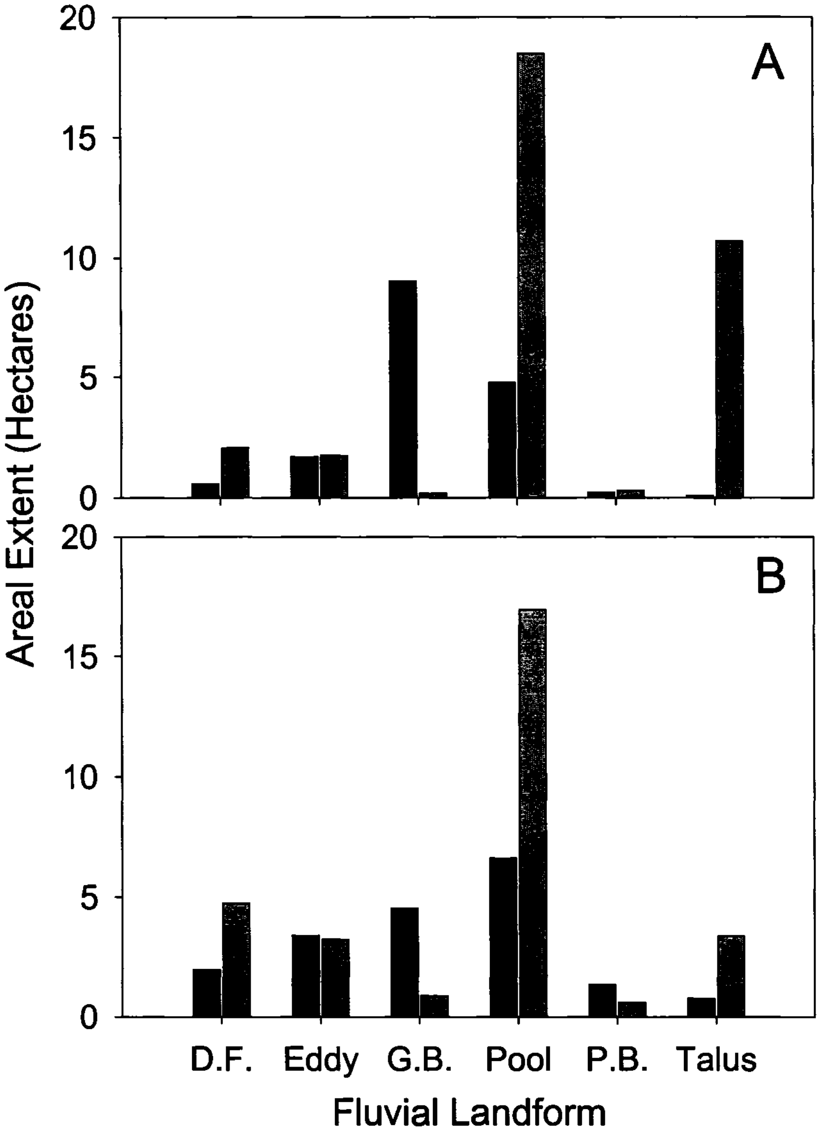

Figure 4.1 Areal extent (Hectares occupied* percent cover) for box elder (gray bars) and tamarisk (solid bars) by fluvial landform for (A) Yampa and (B) Green Rivers. Deposit types are: Debris fan deposits (D.F.), eddy bars (Eddy), gravel expansion bars (G. B.), pool margin and other fine grained channel margin deposits (Pool), point bars (P.B.), and colluvial talus (Talus).

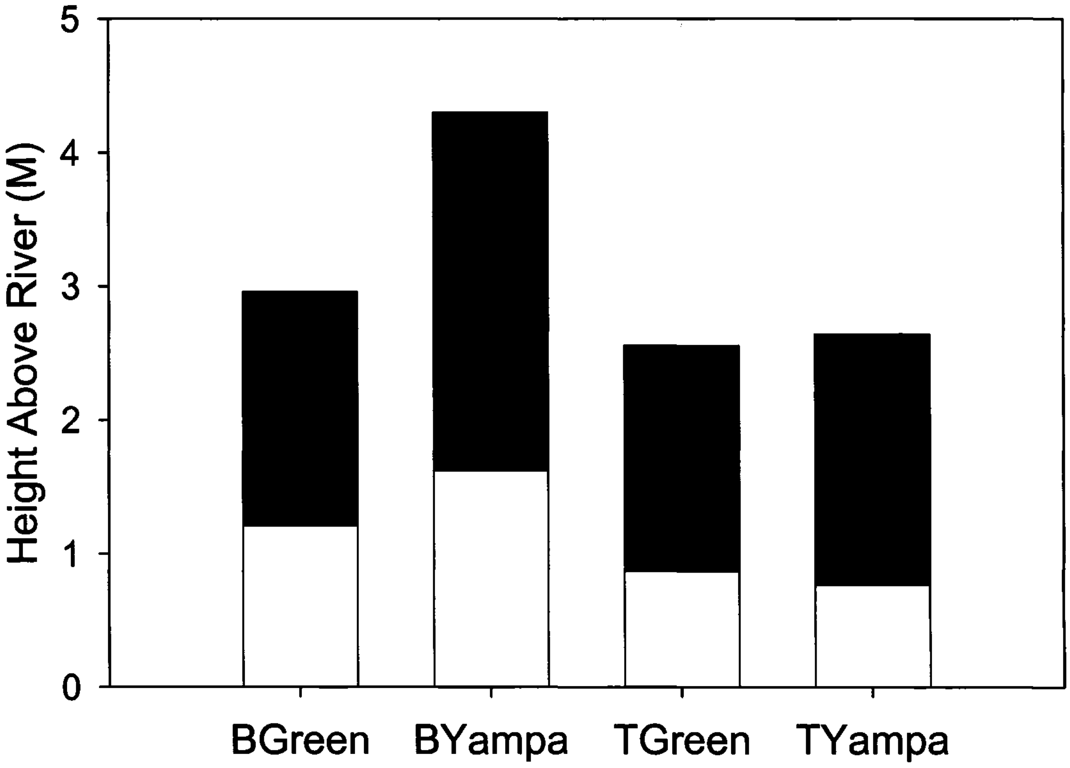

Figure 4.2 Average height above river for box elders on Green River (BGreen), box elders on Yampa River (BYampa), tamarisks on Green River (TGreen), tamarisks on Yampa River (TYampa). Lower limit of black bars indicate mean minimum height above river for sampled box elder or tamarisk patches, upper limit of black bars indicate maximum height above river for sampled box elder or tamarisk patches.

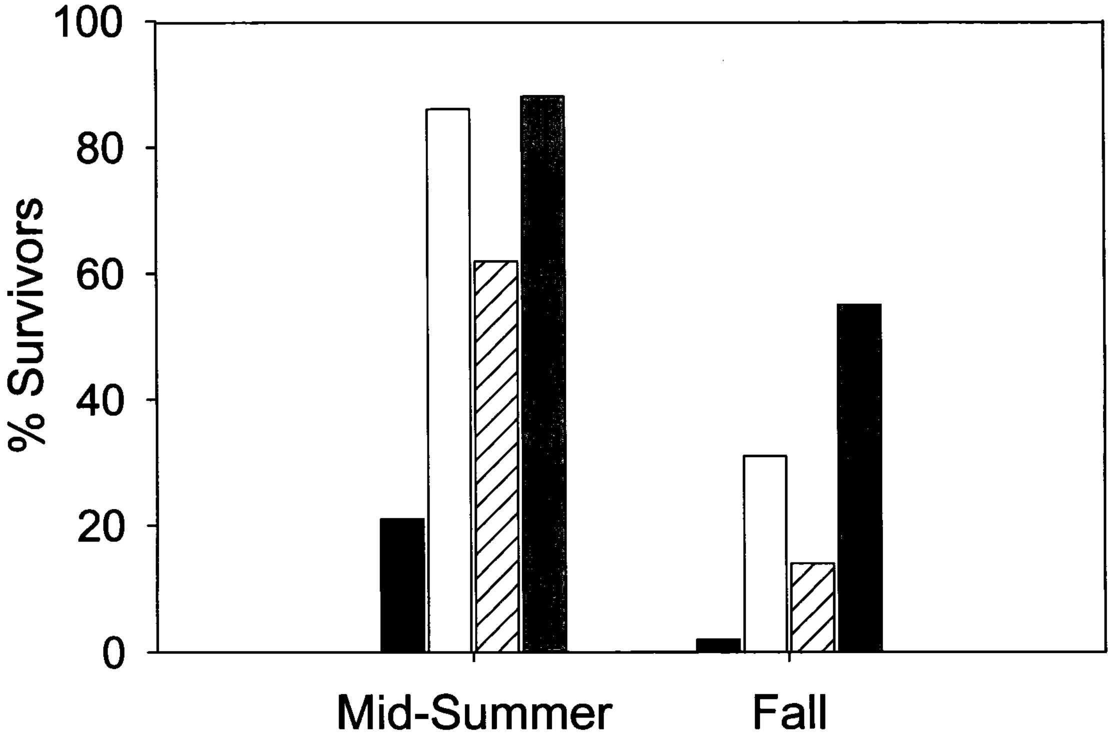

Figure 4.3 Number of seedling box elder survivors in mid summer and fall for 2005 planting experiment. Solid black bars indicate tamarisk canopy removal treatment, hollow bars indicate tamarisk canopy removal treatment with irrigation gel, hatched bars indicate intact tamarisk canopy treatment, and gray bars indicate intact tamarisk canopy treatment with irrigation gel.

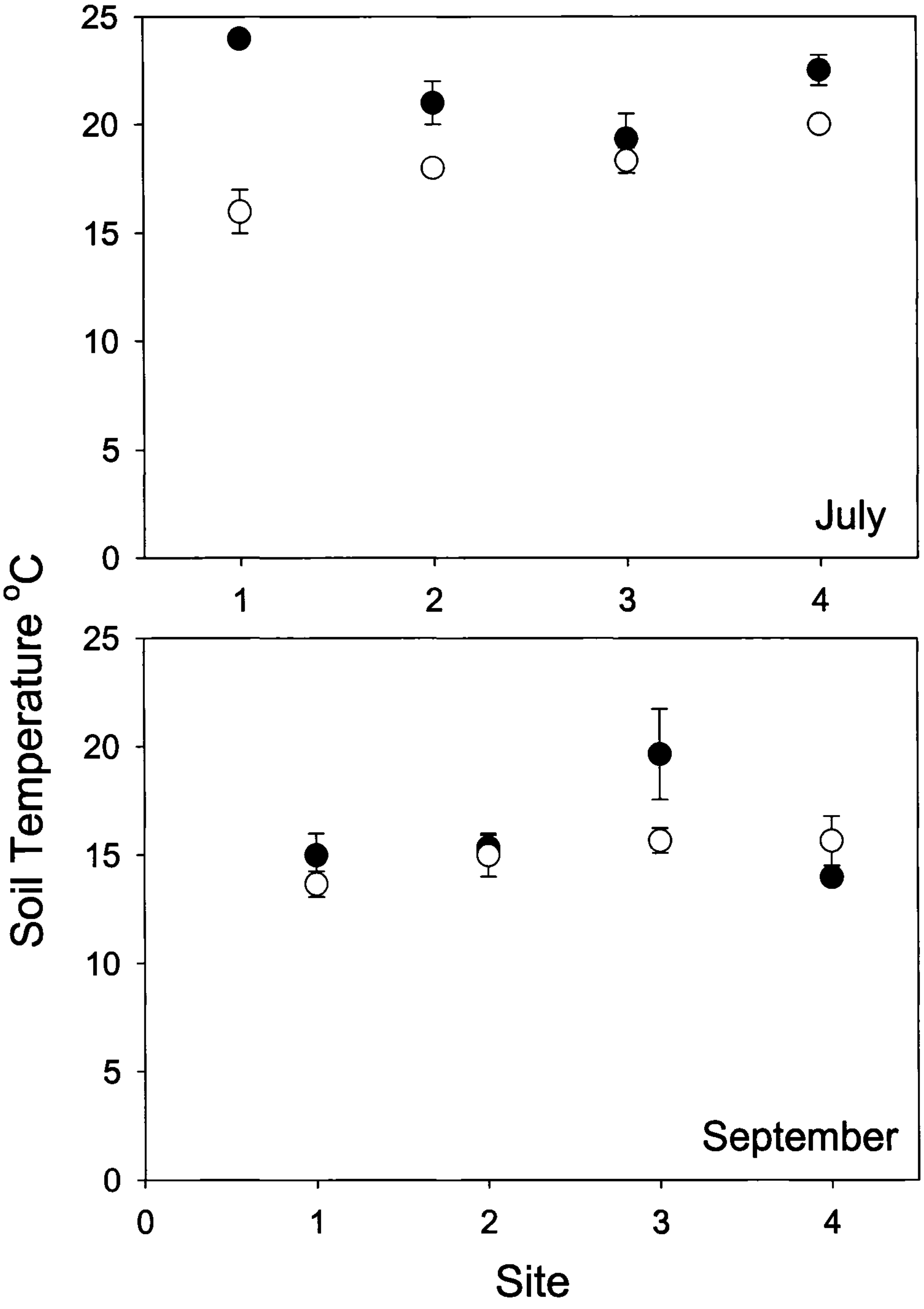

Figure 4.4 Soil temperature in top 10 cm of soil in July and September at each planting site. Solid circles indicate tamarisk canopy removal treatment; hollow circles indicate intact tamarisk canopy treatment.

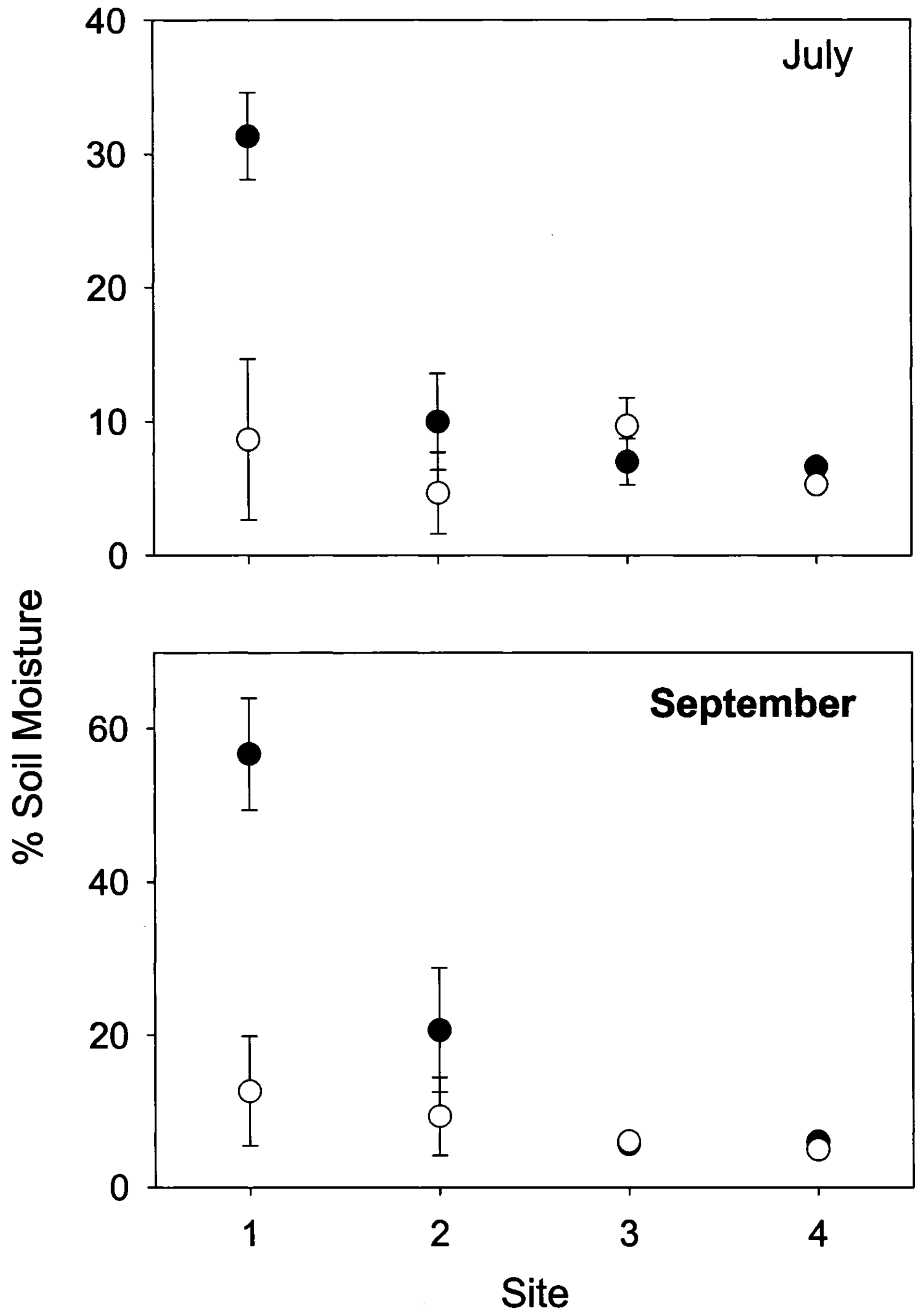

Figure 4.5 Soil moisture in top 10 cm of soil in July and September at each planting site. Solid circles indicate tamarisk canopy removal treatment; hollow circles indicate intact tamarisk canopy treatment.

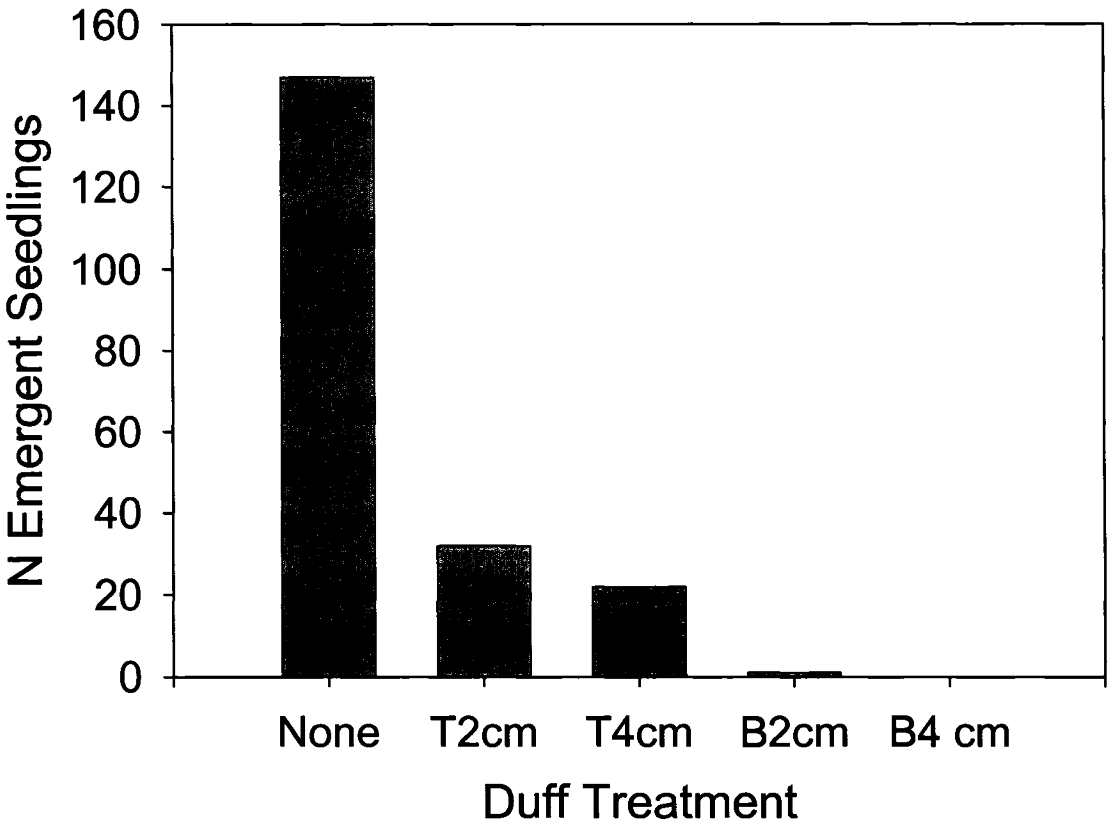

Figure 4.6 Number of emergent box elder seedlings for control (None), 2cm tamarisk litter (T2cm), 4cm tamarisk litter (T4cm), 2cm box elder litter (B2cm), and 4cm box elder litter (B4cm).

Chapter 5

Conclusion

Intra-specific competition and successional replacement by the native species, box elder, limits the growth and survival of tamarisk in the study area. Box elder was found to be the superior competitor to tamarisk in mixed stands, likely due to differences in light interception ability and shade tolerance. Dendrochronological evidence, mortality trends and understory composition analysis indicates that box elder seedlings have become established under tamarisk canopies and are capable of killing and replacing the tamarisk.

Field and greenhouse experiments confirmed these observations. Mature tamarisks were killed when subjected to shade levels equivalent to those found under box elder canopies. At shade levels of 97.5 - 98.6% (50-29 μmol m^{-2} s^{-1}), box elder growth was positive and tamarisk growth was negative. Box elder mortality was low (0% and 8%), but tamarisk suffered 50% mortality in both treatments. Therefore, box elder is the superior competitor for light and is able to successfully exploit lower light levels than tamarisk.

The manipulation of successional and competitive interactions in tamarisk stands by promoting box elder recruitment may provide a powerful bottom-up control to complement existing top-down tamarisk eradication efforts. Box elder is found throughout North America and is common in narrow canyons in semiarid and arid regions of western North America. Tamarisk is found in arid and semiarid areas throughout western North America, thus potential regions of habitat overlap are numerous. Tamarisk and box elder have overlapping distributions in the canyons of Dinosaur National Monument, Colorado. Both species inhabit similar floodplain positions above the river channel, and are common on fluvial landforms such as pool margins and eddy bars, and to a lesser extent on point bars. Control with box elder would be feasible throughout most of the range of tamarisk on both rivers, with the probable exception of the lowest floodplain positions.

Tamarisk canopies appear to facilitate the survival of shade tolerant box elder seedlings by providing protection from the desiccating influence of solar radiation. Box elder seedlings planted under tamarisk canopies had higher survival rates than box elder seedlings planted in adjacent cleared sites. The facilitation of box elder seedling survival by tamarisk indicates that the wholesale clearing of tamarisk stands may be counterproductive is some areas. Unlike box elder, tamarisk is dependent on the availability of bare unshaded mineral sediment for successful colonization (Shafroth et al. 1998). Clearing tamarisk stands effectively resets succession and the next colonizer is likely to be tamarisk due to its prodigious seed production and dispersal abilities (Neill 1985, Brotherson and Field 1987). However, if tamarisks are killed and left standing it is possible that the facilitative effect of the tamarisk canopy will be retained, and possibly enhanced due to the alleviation of root competition. Leaving the tamarisk alive and promoting box elder establishment may require less of a labor and capital investment, with dense box elder stands overtopping, killing and replacing the tamarisk. The resulting shade would inhibit subsequent tamarisk establishment.

Box elder establishment could be facilitated by sowing cold stratified seeds and implementing controlled or artificial flooding. Artificially wetting the floodplain has successfully resulted in the establishment of native woody riparian species (Friedman et al. 1995, Roelle et al. 2001, Sprenger et al. 2002). Naturally occurring box elder seedlings overtopped the tamarisk after approximately 15-20 years within the study area. Irrigation and fertilization may speed up this process. Seedling or larger tree plantings with supplemental irrigation could also be an effective means of box elder establishment in tamarisk stands. The water could be directly pumped out of the river along perennial streams.

The manipulation of successional and competitive processes through the facilitation of native tree establishment may provide a valuable complement to top-down control methods and managed flows for tamarisk control. Tamarisk control using co-occurring native plant species should be investigated throughout the range of tamarisk in western North America. The key to integrating all potential tamarisk control tools is rigorous site by site assessments followed by adaptive and creative management prescriptions. Follow up monitoring and periodic adjustments to the system are critical to successful tamarisk control.

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