DISSERTATION

CAUSES AND MANAGEMENT OF EXOTIC RIPARIAN PLANT INVASION IN

CANYON DE CHELLY NATIONAL MONUMENT, ARIZONA

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER

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ABSTRACT OF DISSERTATION

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CANYON DE CHELLY NATIONAL MONUMENT, ARIZONA

The ecological, economic and social impacts of invasive plant species on native plant communities have stimulated broad concern among researchers, land managers and the general public. Riparian areas are of particular concern because they are critical to regional biodiversity despite covering a small percentage of the landscape. Controlling harmful invasive plants is an important challenge for land managers and understanding how to effectively remove exotic species is essential to managing native ecosystems such as riparian areas. In the southwestern United States (U.S.), the most dominant riparian plant invaders are the woody species tamarisk (*Tamarix ramosissima* Ledebour, *T. chinensis* Loureiro, and their hybrids) and Russian olive (*Elaeagnus angustifolia* L.). Tamarisk and Russian olive have invaded riparian habitats throughout Canyon de Chelly National Monument in northeastern Arizona. The goals of my research were to: 1) describe the history and mechanisms of exotic plant invasion into Canyon de Chelly, 2) understand the niche space requirements of tamarisk, Russian olive and native cottonwood in terms of light and water and determine if tamarisk and cottonwood are facilitating the invasion of Russian olive, and 3) describe response of the riparian ecosystem to exotic plant removal and determine the effectiveness of two different removal strategies. My results from analyzing the history of invasion showed that although plantings and river regulation by dams probably played a role in tamarisk and Russian olive invasion into Canyon de Chelly, these species required hydroclimatic drivers and stream bed adjustments for wide-spread establishment. Controlled

experiments and field surveys in my second research study demonstrated that Russian

olive is exploiting empty niches along wide gradients of water and light availability in

southwestern riparian ecosystems. However, Russian olive invasion does appear to be

limited by seed dispersal. Finally, I found that both cut-stump and whole plant removals

similarly reduced exotic species cover and increased native species cover after two years.

Both removal methods also reduced aerial seed rain inputs of tamarisk seeds, cut-stump

removals increased available nitrogen near dead Russian olive boles within two years of

removal, and both treatments seem to have no effect on ground water levels. This

research helps guide the management of riparian plant communities in Canyon de Chelly,

across the southwestern U.S., and informs our understanding of exotic plant invasions.

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1   INTRODUCTION

The ecological, economic and social impacts of invasive plant species on native plant communities have stimulated broad concern among researchers, land managers and the general public (Zavaleta 2000). Exotic invasive species are organisms that expand or are introduced into new ranges and undergo dramatic population growth (Elton 1958). Understanding why exotic species are able to invade communities is a central question in ecology, with application to pressing environmental problems (Vitousek et al. 1997). Invasive species often compete with and exclude native species, threaten biodiversity, and alter physical and ecological processes (Simberloff 2005). They can modify landscapes in ways that enhance their survival or facilitate subsequent invasions (Cuddington and Hastings 2004, Niu et al. 2007). Studies of invasions can provide insights into fundamental ecological processes such as facilitation, competition, dispersal and establishment (Vitousek 1990, Shea and Chesson 2002).

Riparian areas are of particular concern because they are critical to regional biodiversity despite covering a small percentage of the landscape (Knopf et al. 1988, Sabo et al. 2005). Also, riparian areas have been invaded disproportionally more than other habitats world-wide, based on land-cover extent (Hood and Naiman 2000). Understanding the mechanisms of successful exotic species invasions is essential to managing critical native ecosystems such as riparian areas (Richardson et al. 2007). Controlling harmful invasive plants is an important challenge for land managers. Understanding how to best meet management goals by removing exotic species is essential to managing critical native ecosystems such as riparian areas (Harms and Hiebert 2006).

In the southwestern United States (U.S.), the most dominant riparian plant invaders are the woody deciduous trees tamarisk (*Tamarix ramosissima* Ledebour, *T. chinensis* Loureiro, and their hybrids) and Russian olive (*Elaeagnus angustifolia* L.) (Friedman et al. 2005a). Historically, southwestern floodplains were populated by stands of native cottonwood (*Populus deltoides* Marshall subsp. *wislizeni* (Watson) Eckenwalder; also referred to as *P. fremontii* S. Watson) and willows (*Salix* spp.). Tamarisk and Russian olive have different life history strategies than those of native riparian plants, which have allowed them to invade the southwestern U.S. Compared to the native riparian plants, tamarisk and Russian olive seeds are viable for longer, and have longer dispersal intervals than cottonwood and willow have (Cooper et al. 1999, Katz and Shafroth 2003). Also, mature tamarisk and Russian olive plants can tolerate long periods without available ground water whereas native cottonwood and willow cannot (Brotherson and Winkel 1986, Katz and Shafroth 2003).

Tamarisk and Russian olive have invaded riparian habitats throughout Canyon de Chelly National Monument in northeastern Arizona (Figure 1.1). During years 1934-1937, the U.S. Soil Conservation Service planted tamarisk and Russian olive in Canyon de Chelly to protect ancient Pueblo ruins and modern farms from river bank erosion (SCS 1934). Tamarisk and Russian olive now dominate the study area riparian vegetation. The historic stream beds in Canyon de Chelly, Canyon del Muerto and Chinle Wash were wide, shallow and braided, and Chinle Wash remains wide today. However, the tributary canyon streams have incised 1-5 m deep over the last 50 years (Rink 2003, Cadol 2007). Both the invasion and dominance of exotic riparian trees and the incision of the stream channel throughout Canyon de Chelly have caused concern among land managers and

local canyon residents in Canyon de Chelly. Historically, canyon residents have exploited annual flooding and shallow riparian water tables for residential and agricultural water use purposes. However, channel incision has caused the riparian water table to drop several meters below the floodplain surface, and the floodplain surface has been abandoned by the channel. Lowered water tables and lack of flooding presents a critical challenge to farming and living in the canyon. Land managers and residents of Canyon de Chelly wish to restore native vegetation and an active flood plain throughout the canyon system.

Land managers across the western US also seek to understand the best methods for controlling tamarisk and Russian olive and restoring native plant communities. This study aims to inform riparian management in Canyon de Chelly, across the western US, and also to advance understanding of mechanisms controlling ecological invasions. In my first chapter, I analyzed the processes that allowed exotic plants to invade Canyon de Chelly and determined the ecological response of plant communities to two removal methods of tamarisk and Russian olive. In my second chapter, I analyzed the history and timing of exotic plant invasion into Canyon de Chelly and attempted to determine mechanisms of tamarisk and Russian olive invasion into Canyon de Chelly. In the third chapter, I analyzed the seedling requirements of the native and exotic species to determine the niche space requirements of tamarisk, Russian olive and native cottonwood in terms of light and water. I also examined whether tamarisk and cottonwood are facilitating the invasion of Russian olive. Last, I studied the ecosystem response of the plant community following exotic plant removal to determine the effectiveness of two different removal strategies. This research will help guide the management of riparian

plant communities in Canyon de Chelly, across the southwestern U.S., and inform our

understanding of exotic plant invasions. From this work, managers can develop

approaches for restoring ecological and geomorphic processes along rivers throughout the

southwestern U.S.

Figure 1.1 Chinle Wash at White House Ruins overlook facing northeast, Canyon de

   Chelly National Monument, Arizona. Left photo was taken in 1942 by Ansel Adams©

   and the right photo was taken in 2005 by D. Cooper.

2   CONTROLS ON EXOTIC RIPARIAN TREE INVASION IN THE

CANYON DE CHELLY REGION

2.1   ABSTRACT

Understanding the mechanisms that allow exotic species to invade native communities is essential to managing landscapes throughout the world. In the southwestern United States (U.S.) the two prevailing invaders of riparian habitats are the exotic woody plant species tamarisk (*Tamarix ramosissima*, *T. chinensis*, and their hybrids) and Russian olive (*Elaeagnus angustifolia*). These plants were introduced throughout the southwest around 1900, and may be facilitated by land management activities such as river regulation. Tamarisk and Russian olive were planted during the 1930s in Canyon de Chelly National Monument, Arizona. In 1963, two dams were installed in the headwaters of the Canyon de Chelly watershed. I hypothesized that one of three factors triggered exotic plant invasion in Canyon de Chelly: the historic plantings, river regulation by dams, or twentieth century precipitation patterns. We aged 148 tamarisk and Russian olive samples from study site transects in Canyon de Chelly, and used tree ring analysis to determine the year of establishment, and the elevation of the germination point relative to the channel. I used Poisson regression and information theoretics to identify important precipitation variables driving annual tree establishment. The majority of tamarisk and Russian olive established in the late 1980s. Mixed-effect Poisson regression models including precipitation variables explained 12% of variation in Russian olive establishment but failed to explain variation in tamarisk establishment. Precipitation variables explained only a small part of the variation in exotic tree establishment; however, tamarisk and Russian olive establishment was coincident with

stream bed incision in Canyon de Chelly in the 1990s. My results suggest invasion of exotic plants in Canyon de Chelly was triggered by above-average precipitation years and stream channel change, rather than river regulation or purposeful plantings.

Key words: Russian olive; tamarisk, riparian; floodplains; exotic plant species; invasive species.

2.2 INTRODUCTION

The ecological, economic and social impacts of invasive plant species on native plant communities have stimulated broad concern among researchers, land managers and the general public (Zavaleta 2000). Invasive plants often exclude native plants and alter physical and ecological processes (Simberloff 2005). Riparian areas are of particular concern because they are critical to regional biodiversity despite covering a small percentage of the landscape (Knopf et al. 1988, Sabo et al. 2005). Also, riparian areas have been invaded to a greater extent than other habitats world-wide (Stohlgren et al. 1998, Stohlgren et al. 1999, Hood and Naiman 2000). Understanding the mechanisms of successful exotic species invasions is essential to managing critical native ecosystems such as riparian areas (Richardson et al. 2007).

In the southwestern United States (U.S.), the dominant riparian plant invaders are the woody species tamarisk (*Tamarix ramosissima* Ledebour, *T. chinensis* Loureiro, and their hybrids) and Russian olive (*Elaeagnus angustifolia* L.) (Friedman et al. 2005a). Historically, southwestern floodplains were populated by stands of native cottonwood (*Populus deltoides* Marshall subsp. *wislizeni* (Watson) Eckenwalder; also referred to as *P. fremontii* S. Watson) and willows (*Salix* spp.). The ability of tamarisk and Russian olive to invade the southwestern U.S. may be explained by differences in life history

strategies between these exotic plants and native ones. Seeds of cottonwood and willow disperse aerially in late spring and early summer and are viable for four to six weeks to coincide with spring peak river flows and germinate on moist substrate (Cooper et al. 2003, Rood et al. 2003). In contrast, tamarisk and Russian olive seeds have longer periods of seed dispersal and viability than cottonwood and willow (Cooper et al. 1999, Katz and Shafroth 2003). Mature tamarisk and Russian olive plants can tolerate long periods without available ground water whereas native cottonwood and willow cannot (Brotherson and Winkel 1986, Katz and Shafroth 2003).

Beginning in the late 1800s, government agencies and private landowners planted tamarisk and Russian olive for shelter belts and erosion control in the central U.S. (Di Tomaso 1998, Katz and Shafroth 2003). The U.S. Department of Agriculture planted tamarisk in Arizona, New Mexico and Nevada by 1910 (Carleton 1914), and Russian olive was introduced in western states by 1909 (Christensen 1963). In 1934 the U.S. Soil Conservation Service implemented a program to control stream erosion in the Colorado River basin by planting tamarisk and Russian olive throughout the Navajo Nation (SCS 1934). These plantings have been widely reported to be the main cause of tamarisk and Russian olive spread in the western U.S. (Robinson 1965, Katz and Shafroth 2003).

In addition to plantings, humans have dramatically altered the flow regime of rivers throughout the southwestern U.S. with dams and flow diversion structures (Graf 1999). Southwestern rivers were historically influenced by snowmelt- and rain-driven floods which reworked river beds, keeping them relatively free of vegetation (Webb and Leake 2006). River regulation has altered natural hydrologic processes, reducing snowmelt-driven flood peaks that occur during the period of native plant seed dispersal

(Stromberg 2001). Dams are reported to facilitate exotic plant establishment because tamarisk and Russian olive can exploit these altered flow regimes (Stromberg et al. 2007).

Annual precipitation is highly variable in the southwestern U.S. and directly influences river floods(Hereford and Webb 1992, Woodhouse et al. 2006). The pattern and timing of precipitation and flow influence riparian species distribution on southwestern floodplains (Levine and Stromberg 2001, Katz et al. 2005). Winter snow melt and high spring stream flows create habitat for native and invasive plants (Cooper et al. 2003). When late summer rain causes flooding, exotic plants can establish in greater numbers, whereas cottonwood and willow have no viable seeds available during that time. Precipitation amount and timing, in addition to plantings and dams, likely influenced the spread of exotic plants in the southwestern U.S. (Birken and Cooper 2006).

Tamarisk and Russian olive plantings, dam construction and precipitation variation all occurred in the recent history of Canyon de Chelly National Monument, Arizona (Canyon de Chelly) where the valley bottoms are currently dominated by dense and continuous stands of tamarisk and Russian olive (Figure 1.1). However, the events that triggered tamarisk and Russian olive invasion remain unknown. The goal of this study was to analyze the role of plantings, dams, and precipitation in facilitating exotic plant invasion into Canyon de Chelly. I hypothesized that if invasion was initiated by plantings, then the majority of tamarisk and Russian olives established in years with favorable precipitation soon after the plantings. Alternatively, if invasion was initiated by dam construction, then most tamarisk and Russian olives established in years with

favorable precipitation soon after dam construction. Finally, if precipitation conditions alone initiated invasion, then most tamarisk and Russian olives established in favorable precipitation years irrespective of plantings and dams (Figure 2.1). In particular, I predicted exotic plants would establish more in years with above-average monsoon precipitation than years with above-average winter precipitation, or total annual precipitation. For the purposes of my hypotheses, I define "favorable precipitation years" as those with above-average annual precipitation, leading to flooding that provides suitable substrate for germination, followed by at least two years of below-average annual precipitation without flooding which allows riparian seedlings to survive (Birken and Cooper 2006).

To test my hypotheses I aged tamarisk and Russian olive plants from Canyon de Chelly using dendrochronologic techniques to determine years when plants established. I evaluated the strength of evidence in these data for models representing my hypotheses.

2.3 METHODS

2.3.1 Study area

Canyon de Chelly National Monument is located in northeastern Arizona, within the Navajo Indian Reservation (Figure 2.2). The monument is formed by two canyons, Canyon de Chelly and Canyon del Muerto, which have incised through the Defiance Plateau and drain the western side of the Chuska Mountains. The canyons join 8.5 km east of Chinle, AZ forming Chinle Wash, a tributary of the San Juan River.

The Navajo Nation and the Bureau of Indian Affairs (US Department of the Interior) built two dams: Wheatfields dam near the head of Canyon de Chelly in 1963 and Tsaile dam near the head of Canyon del Muerto in 1964. Wheatfields is an off-channel

dam with capacity of 7,030,847 m^3. Wheatfields dam captures flow from Wheatfields

Creek and less than a half of the Canyon de Chelly drainage (Cadol 2007). Flow from

Wheatfields Creek is diverted into Wheatfields Lake behind the dam only during October

through March. Tsaile is an on-channel dam with a capacity of 9,991,203 m^3. Tsaile dam

captures all flow from Tsaile Creek that would otherwise drain to Canyon del Muerto,

which is more than half of all drainage area into Canyon del Muerto. Flow from Tsaile

Lake is released into Canyon del Muerto when the dam reaches capacity, typically during

years with average and above-average winter and monsoon precipitation. There are no

long-term records of stage height or dam release flow from Tsaile or Wheatfields dams

(Navajo Nation Safety of Dams, pers. comm. 2007).

Chinle receives an annual average of 23.3 cm of precipitation, with an average of

13.4 cm falling during the months June – October, and 9.9 cm falling between November

and May. The region is characterized by strong monsoon-driven precipitation events in

the late-summer when most of the annual precipitation occurs. An average of 30.5 cm of

snow falls each year. Chinle Wash is an ephemeral stream with a bimodal flow pattern.

Discharge peaks occur due to spring-time mountain snowmelt runoff and late-summer

monsoon rain events.

Tamarisk and Russian olive occur throughout the study area, and the riparian

vegetation composition and stream channel characteristics have changed markedly during

the last century (Figure 1.1). The historic Chinle Wash stream bed was wide, shallow and

braided. Today it is a single-threaded channel and deeply incised (one - five m deep)

along most of its length (Rink 2003, Cadol 2007).

2.3.2 Tree aging

We sampled tamarisk and Russian olive plants in four, four-hectare study sites, each encompassing the riparian zone width in Canyon de Chelly. Study sites included Lower White House, Upper White House, Sliding Rock, and Spider Rock (Figure 2.2). Transect were established perpendicular to the stream channel spaced systematically every 50 m. I selected one transect for plant-aging purposes in each removal area based on backhoe accessibility and the site having an abundance of woody plants. All exotic plants within 3 m of each transect were excavated using a backhoe and hand shovels. The elevation of each plant along each transect was determined by topographic surveying. Position of the ground surface on each plant stem was marked with a nail prior to excavation. Excavated plants were dried, cross-sectioned with a chainsaw and sanded. The germination point was identified as the point where the pith originates. The depth below ground surface (and elevation) of the germination point was determined by analysis of the plant cross sections and topographic survey data. Plant cross sections were analyzed using a precision binocular microscope to count annual growth rings. Methods for dating tamarisk and Russian olive and identifying germination points are based on Friedman et al. (2005b) and Birken and Cooper (2006). Plants within each species across all study sites were pooled for statistical analysis (N = 57 Russian olive, 72 tamarisk).

To produce a better understanding of the range of timing of woody plant invasion in Canyon de Chelly, I also subjectively sampled 13 large and seven small tamarisk, and five large and four small Russian olive and 118 cottonwood trees outside of my study sites, but within the study area (Figure 2.2). Cottonwood trees were sampled in 12 sites where large stands occur that appeared to have multiple size classes. I sampled three sites

in Canyon del Muerto, six in Canyon de Chelly and two in Chinle Wash. Five trees in each size class were sampled at each site, using an increment borer to extract cores as low to the ground surface as possible. Tree cores were mounted, dried, sanded and tree rings were analyzed as described above. All cottonwood ring counts represent minimum ages as they were extracted from the bole above the ground surface and most likely above the germination point (Scott et al. 1997). Subjectively chosen samples of tamarisk, Russian olive and cottonwood were not used in my statistical analyses.

2.3.3 Climate data

To understand the effect of climate on riparian tree establishment, river stage records are most useful because establishment on most rivers corresponds to floods (Scott et al. 1997, Birken and Cooper 2006). A US Geological Survey stream gage operated at the mouth of Canyon de Chelly from November 1999 through July 2006 and no long-term records of river stage exist for Chinle Wash at Canyon de Chelly. There is a weather station in Chinle, Arizona operated by the National Climate Data Center from 1936 to present, and I obtained daily precipitation data from the Western Regional Climate Center (http://www.wrcc.dri.edu/). For all discharge and precipitation data, I summed the daily totals to calculate cumulative water year (October through September) precipitation and discharge. I also calculated monsoon season and winter season precipitation and discharge by summing daily totals for July through October (monsoon) and November through March (winter). I used linear regression models to analyze the pair-wise relationships for water year and seasons between Chinle precipitation and stream discharge for years that they share (2000 - 2006, n = 7). There was a strong positive relationship between water year precipitation and discharge ($R^2 = 0.82$) and winter

precipitation and discharge ($R^2 = 0.73$). Therefore, I used the Chinle precipitation record as a proxy for stream flow in Chinle Wash.

For graphical analysis of regional precipitation dating from 1895 to present, I used divisional data for northeastern Arizona from the National Climate Data Center. The northeastern Arizona division (AZ, division 02) includes 114 stations for the period 1931 to 2007. Divisional data are compiled from all precipitation gauges in a division and extrapolated between gauges where data are missing (Guttman and Quayle 1996). All stations within the northeastern Arizona division were averaged for each month of the record (1895-2006). Prior to 1931, monthly averages were calculated from regression equations developed from Arizona state averages and station averages 1931-1986 (Guttman and Quayle 1996). I used a linear regression model to analyze the pair-wise relationship between Chinle and northeastern Arizona annual water year precipitation for years that they share (1936-2006, n = 70).

2.3.4 Statistical Analyses

To address my hypothesis that invasion was triggered by favorable precipitation years, I compared support in the data for a candidate set of linear models. Models included precipitation variables for monsoon season, winter season and total water year to test my prediction that exotic plant establishment would occur more frequently in years with above-average monsoon precipitation relative to years with above-average winter precipitation or total annual (water year) precipitation. I assumed a Poisson error structure because my data were counts including zeros (Crawley 2007). I employed mixed-effects models to include data across sites and incorporated "site" as a random effect, which allowed us to make inference to the landscape from which sites were

selected (Bolker et al. 2009). I tested 16 models each for tamarisk and Russian olive to estimate the relationship between plant establishment and water year precipitation, monsoon precipitation, winter precipitation, and individual precipitation events in the year of establishment and in the following two years (Table 2.1). Total annual water year precipitation was calculated as the sum of the months October of the previous year through September of the current year. Winter precipitation was calculated as the sum of the months November of the previous year through March of the current year. Monsoon precipitation was calculated as the sum of the months July through October of the current year.

All models included "site" as a random effect (four site levels) and climate variables as fixed-effects. Significance of the random effect 'site' was calculated from a likelihood ratio test. All models except the null model included a continuous predictor variable called "age" that accounts for the fact that I expect there to be more younger trees than older trees due to natural mortality: 'age' = n_{years}, n_{years} -one, ... one. Only years when establishment occurred were included in the models. Models for Russian olive establishment included 30 years (1966 – 1995) and models for tamarisk establishment included 25 years (1974-1998). I tested for over dispersion in the models using penalized, weighted residual sum of squares (pwrss) divided by the number of observations: pwrss/n (Pinheiro and Bates 2000). Values of pwrss/n = one indicated good fit, values <one indicate under dispersion and values >one indicate over dispersion (Pinheiro and Bates 2000).

Model fit was evaluated using Aikaike's Information Criterion for small sample size (AICc) and the random effect "site" was accounted for by adding 1 to the degrees of

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freedom. Because all models included the random effect "site," its effect on the complexity of the models was uniform across models. The best model for each species was inferred as the model with the minimum AICc and delta AICc (ΔAICc) was calculated for the remaining models as the difference from best model AICc. Models with ΔAICc greater than 10 were inferred to have little support from the data and thus eliminated (Burnham and Anderson 2002). I used the best model to simulate a model-estimated data set, and compared the estimated data to the raw observed data with a linear regression. All statistical analyses were conducted in the program R version 2.8.1 (R Development Core Team 2009).

2.4   RESULTS

The majority of tamarisk and Russian olive along my study transects established during the late 1980s (Figure 2.3). The oldest tamarisk established in 1974 and the oldest Russian olive in 1966. All mixed-effect Poisson regression models for tamarisk and Russian olive had pwrss/n values between 0.9 and 2.0, indicating that my data were not over dispersed and a Poisson error structure was an appropriate model (Pinheiro and Bates 2000).

The minimum AICc model, indicating the best fit model, for Russian olive establishment included the total number of monsoon events in the year of establishment (Table 2.2). Two other models had substantial support in the data (ΔAICc = 1.87 and 5.31, Table 2.2); one model included total water year precipitation in the year of establishment and the following year and the second model included total water year precipitation in the year of establishment, the following year, and the second year following (Table 2.2). Predictors from the best Russian olive model (lowest AICc)

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regressed against the observed data had an R^2 of 0.12 ($F_{1,28}$ = 3.78, P = 0.061, Figure 2.4).

The best model for estimating tamarisk establishment was the null model with an intercept, the random effect 'site' and no precipitation predictor variables. These results suggest that a model without precipitation variables more effectively predicted variation in tamarisk establishment than models with precipitation variables. Several other models had substantial support in the data, including most of the simplest models with one precipitation variable each (Table 2.2).

Within-site sediment thickness above the root crown averaged 7.7 ± 0.8 cm (mean ± SE) at Lower White House, 7.7 ± 0.6 cm at Upper White House, 6.4 ± 1.3 cm at Sliding Rock and 30.6 ± 3.7 cm at Spider Rock. These data suggest that little sediment accumulated on the floodplain after the majority of plants established. The cross sectional area of study transects was similar between sites with the oldest plants established along the abandoned flood plain margins and younger plants established closer to the narrow channel that had incised at least 2 m deep (Figure 2.5).

Most of the large plants sampled outside of my intensive study sites in Canyon de Chelly had rotten centers and I could only establish minimum ages. The oldest tamarisk established in approximately 1949 and Russian olive in 1964. The youngest plants had established adjacent to the stream channel in 1999 through 2002 (Figure 2.6).

The majority of cottonwoods from Canyon de Chelly had minimum establishment years from the 1940s and the 1980s-90s (Figure 2.3). Ring counts on cottonwood stems at the ground surface and age of the plant as determined by ring counts at the root crown have been shown to vary by 34 years, with a mean difference of seven years (Scott et al.

1997). Because my tree cores were collected near the ground surface, my age estimates of trees greater than 20 years old likely have true ages 7-10 years older than my increment core-based age estimate. Ring counts from cottonwoods with minimum establishment dates in the 1930s or 40s likely established between 1920 and 1930.

Average precipitation for Chinle during the period of record 1930 to 2006 was 23.3 cm and average precipitation for the northeastern Arizona region was 36.7 cm (Figure 2.3). A linear regression model between annual water year precipitation in Chinle and northeastern Arizona indicate a positive relationship between the two measures of precipitation (Estimate = 0.59, t = 6.85, P < 0.001 and R^2 = 0.40, $F_{1,\,69}$ = 46.92, P <0.001). Long-term precipitation records for northeastern Arizona indicate periods of consecutive years of above average (wet) and below average (dry) precipitation, which match patterns of precipitation in Chinle (Figure 2.3, R^2 = 0.40). Northeastern Arizona precipitation records indicate a dry period between 1895 and 1904, a wet period between 1905 and 1931, another dry period between 1932 and 1978 and another wet period between 1978 and 2000 (Figure 2.3).

2.5 DISCUSSION

The majority of tamarisk and Russian olive in my study sites established during the years 1985-1989. This invasion is very late compared to other southwestern U.S. rivers where tamarisk was widespread by the 1950s (Robinson 1965, Graf 1978, Birken and Cooper 2006). Because most plant establishment occurred long after plantings and dam construction, it appears that these events were not the primary triggers of invasion success. My analyses suggested that Russian olive establishment is related to

consecutive years of above-average precipitation in Chinle, Arizona, while tamarisk invasion was not associated with any precipitation variable I tested.

The oldest plant found in my study sites established in 1966 and the oldest outside of my study sites established in approximately 1949. These dates are surprisingly recent considering that thousands of tamarisk and Russian olive were planted in Canyon de Chelly during the 1930s (SCS 1934). Tamarisk are known to flower and produce seeds as young as two years old, and tamarisk populations established and expanded rapidly along other rivers at this time (Graf 1978, Di Tomaso 1998). An analysis of riparian vegetation cover change on aerial photographs of Canyon de Chelly from 1935 through 2004 indicated that riparian vegetation cover increased slowly between 1935 and 1981, and increased dramatically after 1981 (Cadol 2007).

There is no documentation of tamarisk and Russian olive in Canyon de Chelly before the 1934 plantings. However, it is likely that tamarisk arrived via seed from populations elsewhere in the region during or prior to the 1930s and could have already been present when the plantings occurred (Carleton 1914, Graf 1978). In contrast, Russian olive was not widespread on rivers in the region in 1930; it was introduced later than tamarisk and spread slowly across the western US due to its large seed size (Friedman et al. 2005a). The 1930s plantings in Canyon de Chelly could have been the first introduction of Russian olive to the area.

Several favorable precipitation years (years with above-average precipitation followed by two years of below-average precipitation) occurred between dam installation in 1964 and 1980 (Figure 2.1, Figure 2.3). However, I found no substantial establishment related to any of these years. If tamarisk and Russian olive invasion into my sites was

triggered by reduced peak stream flow caused by the installation of Wheatfields Dam near the top of Canyon de Chelly, I expected to find peak establishment during the 1960s and 70s soon after dam construction (Stromberg et al. 2007). Because Wheatfields dam is off-channel and it captures water draining less than half of the Canyon de Chelly watershed, and only during winter months, it likely has little impact on sediment yield, spring runoff or monsoon flows in Canyon de Chelly. I could find no direct link between dam installation in Canyon de Chelly and tamarisk and Russian olive establishment patterns.

Although Russian olive's presence may have been facilitated by plantings, my model results suggest that large scale Russian olive invasion throughout Canyon de Chelly was related to years with frequent summer monsoon rain events and high total water year precipitation. The best model for predicting Russian olive establishment included the number of monsoon storms in a year. The other two models with substantial support in the data included total water year precipitation in the year of establishment and the following year (Table 2.2, Table 2.3). Because annual precipitation in Chinle has a strong positive relationship with total annual discharge in Chinle wash, these results suggest that peak Russian olive establishment from 1985-87 corresponded to above-average monsoon storm precipitation, total precipitation, and high stream flow. However, when simulated data from the best model are regressed against the observed Russian olive establishment data, they only explained 12% of the variation (Figure 2.4), suggesting that other, unmeasured factors influenced Russian olive establishment, such as stream channel adjustments.

Tamarisk establishment was not related to the precipitation drivers tested in my models because the best model for tamarisk was the null model (Table 2.3). The null model did not include any precipitation variables, suggesting peak establishment years of tamarisk 1985-89 were not related to precipitation. On the Green River in Utah, Birken and Cooper (2006) found that tamarisk cohorts corresponded to years of high stream discharge followed by at least two years of below-average stream discharge. However, riparian tree establishment processes along braided, ephemeral streams such as Canyon de Chelly, function differently from establishment along a large, perennial river such as the Green River (Friedman and Lee 2002). Over-bank flooding on the Green River is rare compared to the historic Canyon de Chelly streams, where braided channel dynamics flooded large areas of the valley bottom, and floodplain sediments were reworked annually. Thus, prior to the late 1980's tamarisk establishment was uncommon.

Widespread tamarisk and Russian olive establishment from 1985-89 coincided with a period when Chinle Wash narrowed and incised in Canyon de Chelly. It is possible that channel bed incision facilitated tamarisk and Russian olive seedling and sapling survival, a process that my models could not account for because the exact timing of channel incision is unknown. Prior to channel incision, annual flooding and braided channel dynamics in Chinle Wash could have eroded most seedlings from the stream bed and limited establishment. However, a large series of floods causing widespread seed germination and survival could have constrained stream flow, triggered incision, and facilitated large scale exotic plant persistence.

Although the exact timing of incision is unknown, channel narrowing is evident on aerial photographs during and after 1981 (Cadol 2007). Stream channel cross section

data indicate that tamarisk and Russian olive established on an active flood plain that was subsequently abandoned due to stream incision (Figure 2.5, Jaeger, 2009). Abandonment is suggested by the thin layers of sediment deposited over plant root crowns, and the lack of subsequent establishment on this floodplain surface. By 2005 the stream channel was at least 2 m below the germination point of most plants, suggesting that incision occurred after plants established during 1985-1989. I suggest that years of high precipitation from 1983-1989 (Figure 2.3) created large spring and summer floods that provided suitable substrate for riparian plant germination. This occurred coincidentally with stream incision, allowing newly established plants to be safe from flood erosion as the stream cut 2-3 m deep into the floodplain, and the channel changed from a braided to meandering type. Also, riparian plants provided bank stability that could have exacerbated stream bed narrowing and incision (Jaeger 2009, Pollen-Bankhead et al. 2009). However, the causes of incision can be complex and varied including land-use, climate and river regulation and my data cannot suggest a cause of incision (Graf 1983, Graf et al. 1991, Friedman et al. 1998, Hereford 2002, Vincent et al. 2009).

Native cottonwood tree establishment in Canyon de Chelly appears to be related to wet and dry periods in northeastern Arizona (Figure 2.3). My minimum age estimates for cottonwood trees only allow us to make rough comparisons to annual precipitation patterns. Climate reconstructions based on dendrochonological analyses in the upper Colorado River basin demonstrated that the end of the 19th century was characterized by drought, with an abrupt transition to an extreme wet period between 1905 and the 1920s (McAuliffe et al. 2006, Woodhouse et al. 2006). Precipitation records for northeastern Arizona and flow reconstruction for the Escalante River in southeastern Utah corroborate

this pattern of consecutive years of above-average precipitation conditions between 1905 and 1933 (Figure 2.3, Webb et al. 1988). In northeastern Arizona, the period between 1932 and 1978 had consecutive below-average water year precipitation and the period between 1978 and 2000 had consecutive above-average water year precipitation (Figure 2.3). I expected more young than old cottonwood trees because of natural mortality. However, most cottonwoods in my sample population had minimum establishment years of 1930 to 1950, and 1980 to 2000 (Figure 2.3). Because my tree cores were collected near the ground surface, trees greater than 20 years old likely have true ages at least 7-10 years older than my increment cores indicate (Scott et al. 1997). The early pulse of cottonwood establishment appears to correspond with the regional wet period between 1905 and 1930. The later pulse of establishment between 1980 and 2006 corresponds with the wet period in the 1980s that may have also triggered Russian olive and tamarisk establishment.

Although plantings and river regulation by dams probably played a role in tamarisk and Russian olive invasion, my results suggest these species required natural precipitation drivers and stream bed adjustments for wide-spread establishment in the ephemeral Canyon de Chelly stream system. Exotic plant invasion depended upon a sequence of years with above-average precipitation in combination with stream incision that left them safe from erosion by subsequent floods.

2.6 ACKNOWLEDGEMENTS

2.7   LITERATURE CITED

Birken, A. S., and D. J. Cooper. 2006. Process of *Tamarix* invasion and floodplain development during the 20th Century along the Lower Green River, UT. Ecological Applications **16**:1103-1120.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends In Ecology & Evolution **24**:127-135.

Brotherson, J. D., and V. Winkel. 1986. Habitat Relationships of Saltcedar (Tamarix-Ramosissima) in Central Utah. Great Basin Naturalist **46**:535-541.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference:a practical information theoretic approach. Springer - Verlag, New York, USA.

Cadol, D. D. 2007. Aerial photographic analysis of channel change and riparian vegetation establishment in Canyon de Chelly National Monument, Arizona, 1935-2004. Master's. Colorado State University, Fort Collins.

Carleton, M. A. 1914. Adaptation of the tamarisk for dry lands. Science **39**:692-694.

Christensen, E. M. 1963. Naturalization of Russian Olive (Elaeagnus angustifolia L.) in Utah. American Midland Naturalist **70**:133-137.

Cooper, D. J., D. C. Andersen, and R. A. Chimner. 2003. Multiple pathways for woody plant establishment on floodplains at local to regional scales. Journal of Ecology **91**:182-196.

Cooper, D. J., D. M. Merritt, D. C. Andersen, and R. A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, USA. Regulated Rivers-Research & Management **15**:419-440.

Crawley, M. J. 2007. The R Book. Jon Wiley and Sons, West Sussex, England.

Di Tomaso, J. M. 1998. Impact, biology, and ecology of saltcedar (Tamarix spp.) in the southwestern United States. Weed Technology **12**:326-336.

Friedman, J. M., G. T. Auble, P. B. Shafroth, M. L. Scott, M. F. Merigliano, M. D. Preehling, and E. K. Griffin. 2005a. Dominance of non-native riparian trees in western USA. Biological Invasions **7**:747-751.

Friedman, J. M., and V. J. Lee. 2002. Extreme floods, channel change, and riparian forests along ephemeral streams. Ecological Monographs **72**:409-425.

Friedman, J. M., W. R. Osterkamp, M. L. Scott, and G. T. Auble. 1998. Downstream effects of dams on channel geometry and bottomland vegetation: Regional patterns in the Great Plains. Wetlands **18**:619-633.

Friedman, J. M., K. R. Vincent, and P. B. Shafroth. 2005b. Dating floodplain sediments using tree-ring response to burial. Earth Surface Processes and Landforms **30**:1077-1091.

Graf, J. B., R. H. Webb, and R. Hereford. 1991. Relation Of Sediment Load And Floodplain Formation To Climatic Variability, Paria River Drainage-Basin, Utah And Arizona. Geological Society of America Bulletin **103**:1405-1415.

Graf, W. L. 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. Geological Society of America Bulletin **89**:1491-1501.

Graf, W. L. 1983. The arroyo problem-paleohydrology and paleohydraulics in the short term. Pages 279-302 *in* K. J. Gregory, editor. Backgroun to paleohydrology: A perspective. John Wiley & Sons.

Graf, W. L. 1999. Dam nation: A geographic census of American dams and their large-scale hydrologic impacts. Water Resources Research **35**:1305-1311.

Guttman, N. B., and R. G. Quayle. 1996. A historical perspective of US climate divisions. Bulletin Of The American Meteorological Society **77**:293-303.

Hereford, R. 2002. Valley-fill alluviation during the Little Ice Age (ca. AD 1400-1880), Paria River basin and southern Colorado Plateau, United States. Geological Society of America Bulletin **114**:1550-1563.

Hereford, R., and R. H. Webb. 1992. Historic Variation Of Warm-Season Rainfall, Southern Colorado Plateau, Southwestern Usa. Climatic Change **22**:239-256.

Hood, W. G., and R. J. Naiman. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecology **148**:105-114.

Jaeger, K. 2009. Channel dynamics in Canyon de Chelly National Monument, AZ, with
emphasis on the effect of invasive plants. Dissertation. Colorado State University,
Fort Collins.

Katz, G. L., J. M. Friedman, and S. W. Beatty. 2005. Delayed effects of flood control on
a flood-dependent riparian forest. Ecological Applications **15**:1019-1035.

Katz, G. L., and P. B. Shafroth. 2003. Biology, ecology and management of Elaeagnus
angustifolia L. (Russian olive) in western North America. Wetlands **23**:763-777.

Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation
Of Riparian Ecosystems In The United-States. Wilson Bulletin **100**:272-284.

Levine, C. M., and J. C. Stromberg. 2001. Effects of flooding on native and exotic plant
seedlings: implications for restoring south-western riparian forests by
manipulating water and sediment flows. Journal of Arid Environments **49**:111-
131.

McAuliffe, J. R., L. A. Scuderi, and L. D. McFadden. 2006. Tree-ring record of hillslope
erosion and valley floor dynamics: Landscape responses to climate variation
during the last 400yr in the Colorado Plateau, northeastern Arizona. Global And
Planetary Change **50**:184-201.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed effects models in S and S-plus. Springer-
Verlag, New York.

Pollen-Bankhead, N., A. Simon, K. Jaeger, and E. Wohl. 2009. Destabilization of
streambanks by removal of invasive species in Canyon de Chelly National
Monument, Arizona. Geomorphology **103**:363-374.

R Development Core Team. 2009. R: A language and environment for statistical

    computing. *in*. R Foundation for Statistical Computing, Vienna, Austria.

Richardson, D. M., P. M. Holmes, K. J. Esler, S. M. Galatowitsch, J. C. Stromberg, S. P.

    Kirkman, P. Pysek, and R. J. Hobbs. 2007. Riparian vegetation: degradation, alien

    plant invasions, and restoration prospects. Diversity and Distributions **13**:126-

    139.

Rink, G. 2003. Vascular Flora of Canyon de Chelly National Monument, Apache County,

    Arizona. Master's Thesis. Northern Arizona University, Flagstaff, AZ.

Robinson, T. W. 1965. Introduction, spread and areal extent of saltcedar (*Tamarix*) in the

    western states. *in*. United States Geological Survey Professional Paper, 491-A.

Rood, S. B., J. H. Braatne, and F. M. R. Hughes. 2003. Ecophysiology of riparian

    cottonwoods: stream flow dependency, water relations and restoration. Tree

    Physiology **23**:1113-1124.

Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz,

    C. Soykan, J. Watts, and A. Welter. 2005. Riparian zones increase regional

    species richness by harboring different, not more, species. Ecology **86**:56-62.

Scott, M. L., G. T. Auble, and J. M. Friedman. 1997. Flood dependency of cottonwood

    establishment along the Missouri River, Montana, USA. Ecological Applications

    7:677-690.

SCS, U. S. 1934. United States Soil Conservation Service Region Eight Records. *in* U. o.

    N. Mexico, editor. Center for Southwest Research.

Simberloff, D. 2005. Non-native species do threaten the natural environment! Journal Of

    Agricultural & Environmental Ethics **18**:595-607.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs **69**:25-46.

Stohlgren, T. J., K. A. Bull, Y. Otsuki, C. A. Villa, and M. Lee. 1998. Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecology **138**:113-125.

Stromberg, J. C. 2001. Restoration of riparian vegetation in the south-western United States: importance of flow regimes and fluvial dynamism. Journal of Arid Environments **49**:17-34.

Stromberg, J. C., S. J. Lite, R. Marler, C. Paradzick, P. B. Shafroth, D. Shorrock, J. M. White, and M. S. White. 2007. Altered stream-flow regimes and invasive plant species: the Tamarix case. Global Ecology And Biogeography **16**:381-393.

Vincent, K. R., J. M. Friedman, and E. R. Griffin. 2009. Erosional Consequence of Saltcedar Control. Environmental Management **44**:218-227.

Webb, R. H., and S. A. Leake. 2006. Ground-water surface-water interactions and long-term change in riverine riparian vegetation in the southwestern United States. Journal of Hydrology **320**:302-323.

Webb, R. H., J. E. O'Connor, and V. R. Baker. 1988. Paleohydrology reconstruction of flood frequency ont he Escalante River, south-central Utah. Pages 403-418 *in* V. R. Baker, R. C. Kochel, and P. C. Patton, editors. Flood Geomorphology. John Wiley and Sons.

Woodhouse, C. A., S. T. Gray, and D. M. Meko. 2006. Updated streamflow

    reconstructions for the Upper Colorado River Basin. Water Resources Research

    42.

Zavaleta, E. 2000. The economic value of controlling an invasive shrub. Ambio **29**:462-

    467.

2.8 TABLES

Table 2.1 Candidate model set for tamarisk and Russian olive tree establishment. Variables included: intercept (a), Site as a random effect (4 sites levels), Age as a continuous variable, Total water year precipitation (WY), Largest winter event, Largest monsoon event, Total number of monsoonal events, Total monsoon precipitation(July-October), Total winter precipitation (November – March). Variables for water year, winter and monsoon precipitation appeared for the current year of establishment, the following year (+1) and the second year following (+2).

Number	Model
1 (null)	$a + Site_{random}$
2	$a + Age + Site_{random}$
3	$a + WY + Age + Site_{random}$
4	$a + WY + WY_{+1} + Age + Site_{random}$
5	$a + WY + WY_{+1} + WY_{+2} + Age + Site_{random}$
6	$a + Largest\ winter\ event + Age + Site_{random}$
7	$a + Largest\ monsoon\ event + Age + Site_{random}$
8	$a + Total\ number\ of\ monsoonal\ events + Age + Site_{random}$
9	$a + Monsoon + Age + Site_{random}$
10	$a + Monsoon + Winter_{+1} + Age + Site_{random}$
11	$a + Monsoon + Winter_{+1} + Monsoon_{+1} + Age + Site_{random}$
12	$a+Monsoon+Winter_{+1}+Monsoon_{+1}+Winter_{+2}+Monsoon_{+2}+Age+Site_{random}$
13	$a + Winter + Age + Site_{random}$
14	$a + Winter + Monsoon + Age + Site_{random}$

15        $a + \text{Winter} + \text{Monsoon} + \text{Winter}_{+1} + \text{Age} + \text{Site}_{\text{random}}$

16        $a + \text{Winter} + \text{Monsoon} + \text{Winter}_{+1} + \text{Monsoon}_{+1} + \text{Winter}_{+2} + \text{Age} + \text{Site}_{\text{random}}$

Table 2.2. Results of mixed model Poisson regressions relating tamarisk and Russian olive establishment in Canyon de Chelly study sites to precipitation variables in Chinle, AZ. For explanation of variables, see Table 2.1. Aikaike's information criterion for small samples (AICc) are given for measures of model fit and ΔAICc indicates the rank of a model compared to the model with the minimum AICc. The best model has the minimum AICc, indicating the most support in the data and has a ΔAICc of zero.

<u>Russian olive</u>

Number	Model	AICc	ΔAICc
8	a +Total number of monsoonal events + Age +$Site_{random}$	125.3	0
4	a + WY + WY_{+1} + Age + $Site_{random}$	127.2	1.87
5	a + WY + WY_{+1} + WY_{+2} + Age + $Site_{random}$	130.7	5.31

<u>Tamarisk</u>

Number	Model	AICc	ΔAICc
1 (null)	a + $Site_{random}$	193.1	0
2	a + Age + $Site_{random}$	195.9	2.86
3	a + WY + Age + $Site_{random}$	197.2	4.10
6	a + Largest winter event + Age + $Site_{random}$	197.3	4.24
7	a + Largest monsoon event + Age + $Site_{random}$	197.7	4.60
13	a + Winter + Age + $Site_{random}$	198.1	5.04
9	a + Monsoon + Age + $Site_{random}$	198.9	5.90
4	a + WY + WY_{+1} + Age + $Site_{random}$	199.7	6.60
5	a + WY + WY_{+1} + WY_{+2} + Age + $Site_{random}$	201.2	8.19
14	a + Winter + Monsoon + Age + $Site_{random}$	201.4	8.34

Table 2.3. Parameter estimates for the best models (lowest AICc, Table 2.2) for estimating annual Russian olive establishment. The random effect 'site' was included in all models and its P-value calculated from a likelihood ratio test.

Model	Parameter	Estimate	Variance	SE	P
8	Intercept	-1.751		0.655	0.008
	Total number of monsoon events, 0.0799			0.018	<0.001
	Age	-0.1216		0.025	<0.001
	Site (random)		0.9247	0.088	<0.001
4	Intercept	-1.997		0.668	0.003
	Water Year	0.0223		0.012	0.0723
	Water Year $_{+1}$	0.0491		0.01	<0.001
	Age	-0.0849		0.022	<0.001
	Site (random)		0.9247	0.088	<0.001
5	Intercept	-2.021		0.724	0.005
	Water Year	0.0222		0.012	0.075
	Water Year $_{+1}$	0.0494		0.010	<0.001
	Water Year $_{+2}$	0.001		0.013	0.9302
	Age	-0.0853		0.022	<0.001
	Site (random)		0.9247	0.0878	<0.001

2.9 FIGURES
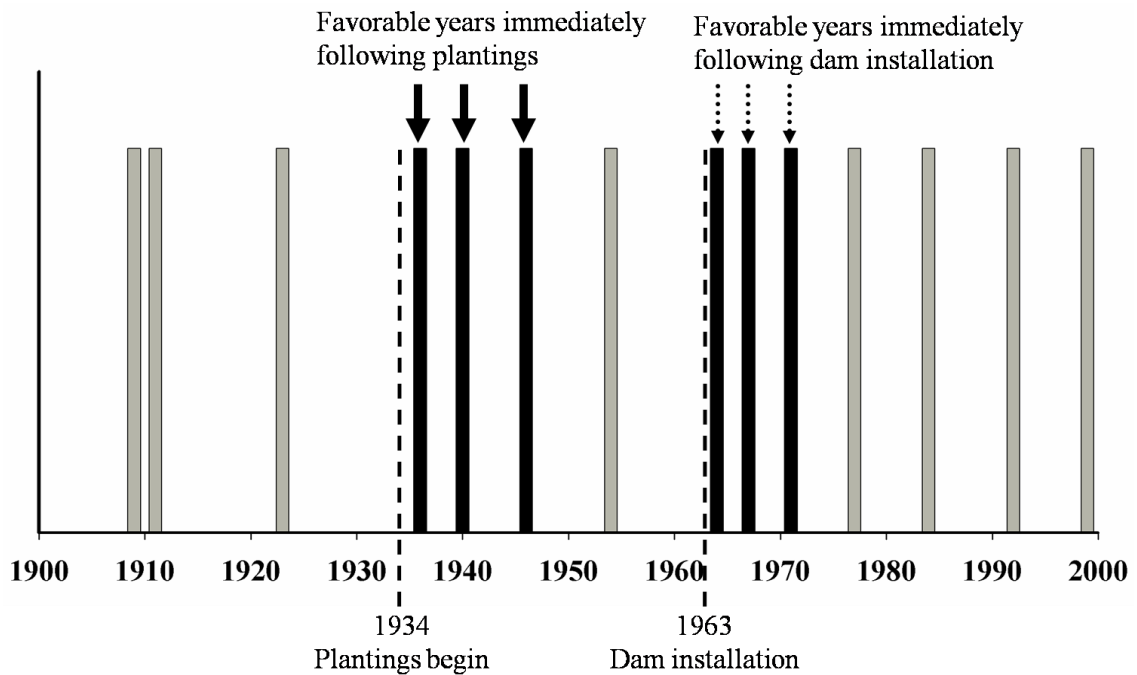
Figure 2.1 Hypotheses of expected tamarisk and Russian olive establishment based on the timing of plantings, dam installation and favorable climate periods. Bars represent favorable years for tamarisk and Russian olive establishment. Favorable years consist of years with above-average rainfall followed by at least two years of below-average rainfall totals. Hypothesis 1: Establishment events correspond with favorable years immediately following plantings, which occurred during the 1930s-1950s (solid arrows). Hypothesis 2: Establishment events correspond with favorable years immediately following dam installation, which occurred in 1963/64 (dotted arrows). Hypothesis 3: Establishment events correspond with any favorable precipitation years indicated by the gray bars, independent of plantings and dam installation.
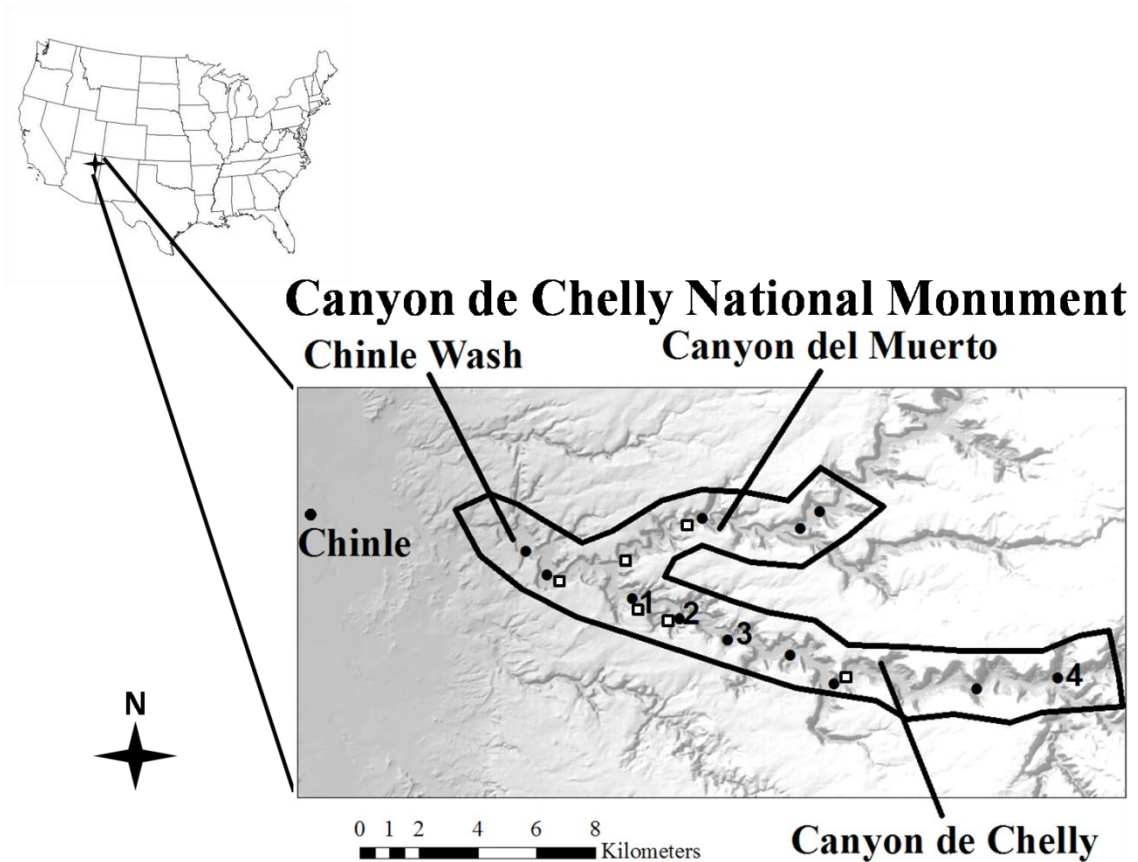
Figure 2.2 Map of Canyon de Chelly National Monument, Arizona, United States. The cross on the map of the United States indicates the location of Canyon de Chelly and the enlarged area. Study sites are indicated by numbers: 1 - Lower White House, 2 – Upper White house, 3 – Sliding Rock, 4 – Spider Rock. Squares indicate locations where large and young tamarisk and Russian olive plants were subjectively sampled. Circles indicate cottonwood tree coring sites.
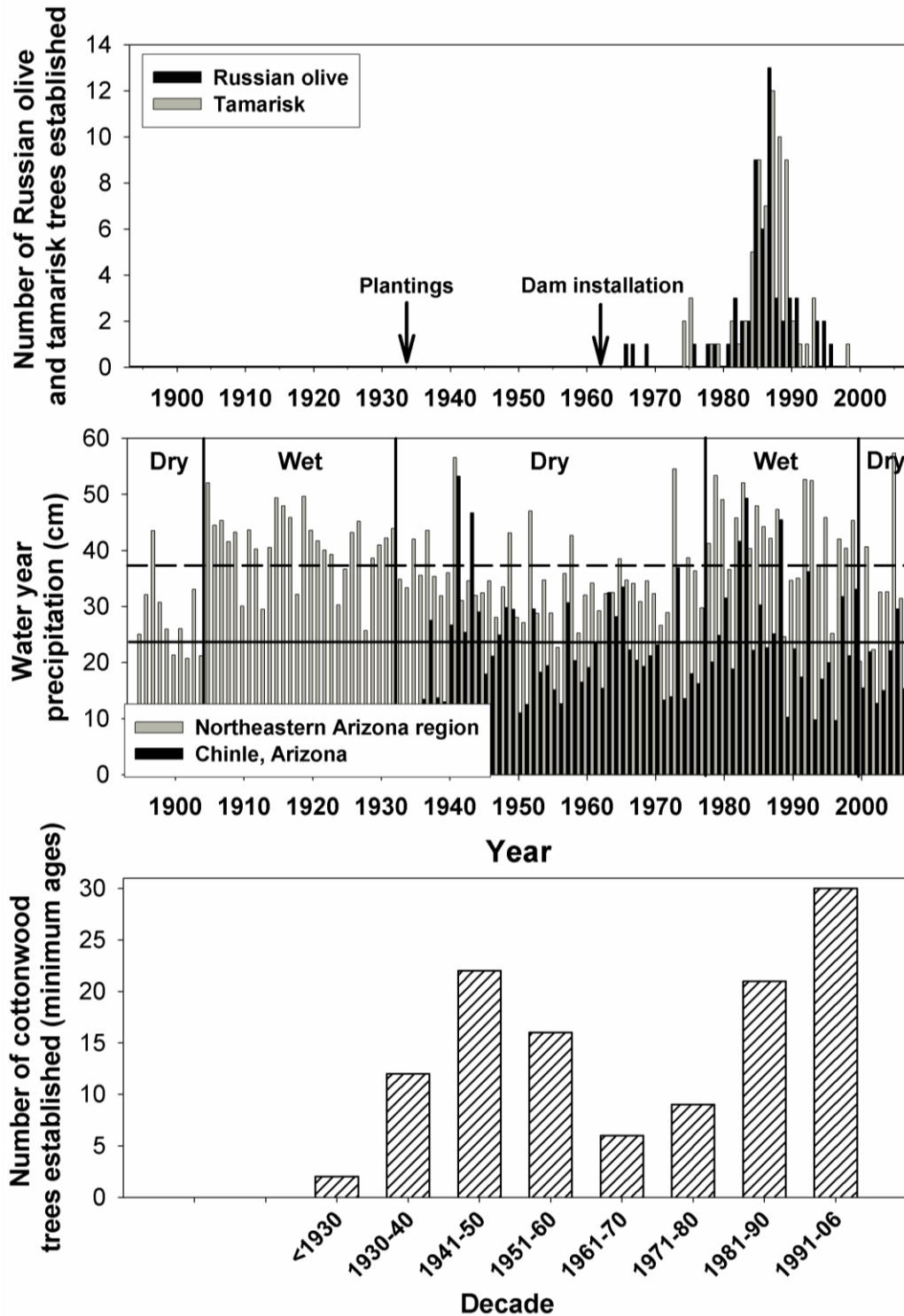
Figure 2.3 Top panel: the number of Russian olive trees (black bars) and tamarisk trees (gray bars) that established each year in Canyon de Chelly. Plantings in 1934 and dam installation in 1963/64 are indicated with arrows. Middle panel: Northeastern Arizona

regional water year precipitation (cm) for years 1895 – 2006 (gray bars) with long-term

average noted with a dashed line (36.7cm) and total water year precipitation for Chinle

for years 1936 - 2006 (black bars) with long-term average indicated by a solid line (23.3

cm). Wet and dry periods are noted in the middle panel as consecutive years with

multiple above-average or below-average precipitation. Bottom panel: The number of

cottonwoods establishing in Canyon de Chelly in 10-year time periods from 1930 - 2000.
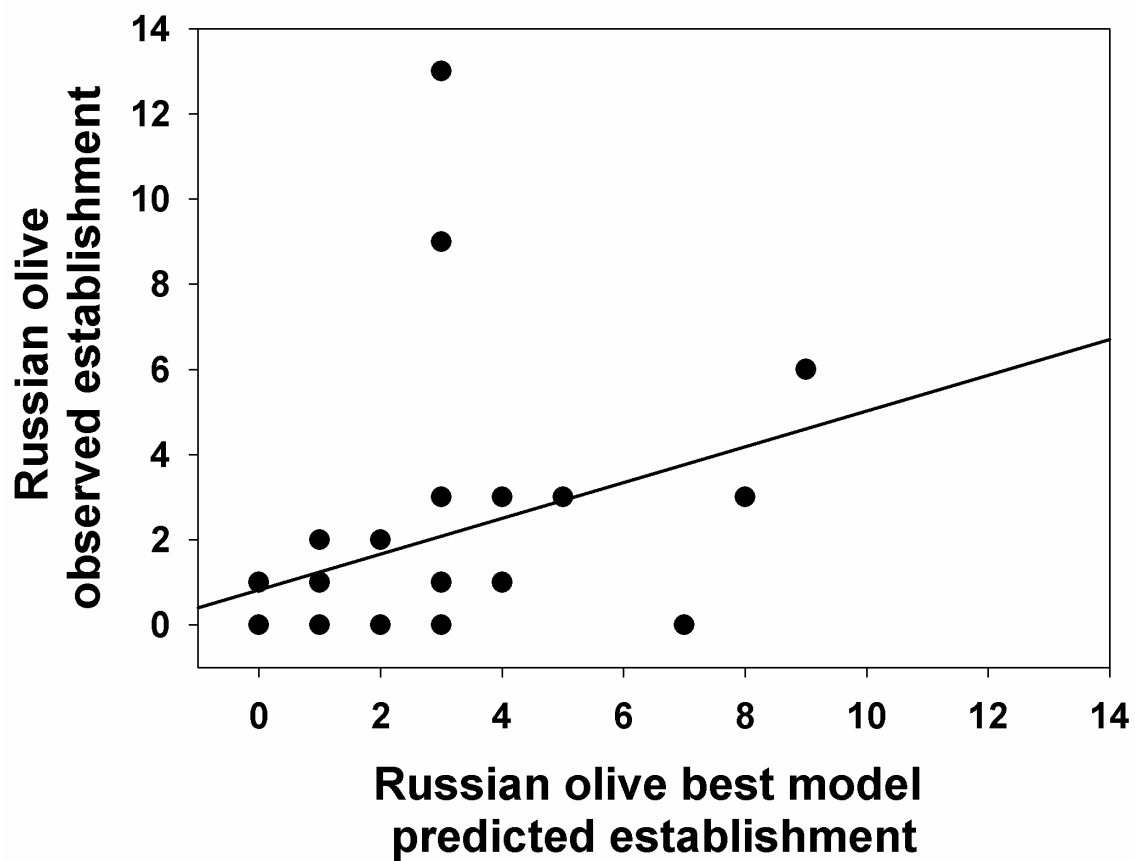
Figure 2.4 Observed Russian olive establishment (number of trees per year) regressed against the best (minimum AICc) model predictions of Russian olive establishment (number of trees per year). Linear regression line is shown, $R^2 = 0.12$.
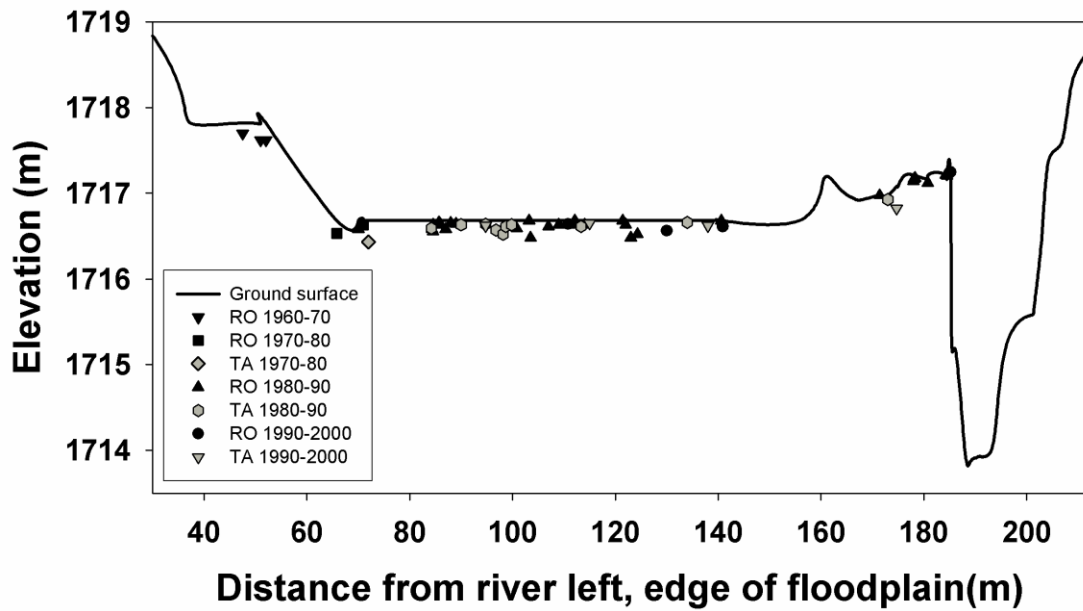
Figure 2.5 Cross sectional elevation of the main wash at Lower White House Site facing downstream. The solid line indicates ground surface and symbols indicate plant species, ages and locations: gray shapes indicate tamarisk (TA) and black shapes indicate Russian olive (RO).
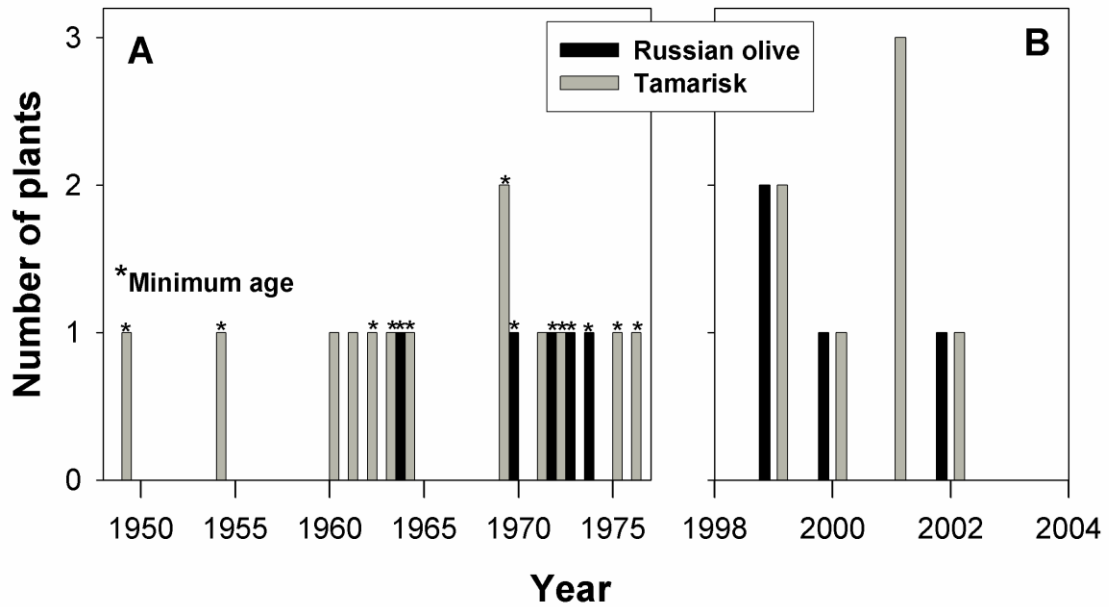
Figure 2.6 The number of subjectively sampled large tamarisk and Russian olive (A, left panel) and young plants (B, right panel) established in each year from 1949-2002. Tamarisk plants are gray bars and Russian olive black bars. Stars indicate plants with rotten or missing centers and therefore represent minimum age estimates.

3   CAN ONE INVASION LEAD TO ANOTHER? NICHE SPACE AND THE FUTURE OF SOUTHWESTERN U.S. RIPARIAN ZONES

3.1   ABSTRACT

Understanding the processes that allow new species to invade established communities offers a fundamental challenge in ecology. Exotic plant invasion may be aided by facilitation and empty niche exploitation, yet these ecological processes are poorly understood in species-rich ecosystems such as riparian areas. In the southwestern United States (U.S.) two exotic woody plant species have invaded riparian habitats: tamarisk (*Tamarix ramosissima*, *T. chinensis*, and their hybrids) and Russian olive (*Elaeagnus angustifolia*). I worked in sites within Canyon de Chelly National Monument, Arizona and on other streams in the region to address the following questions: (1) does Russian olive have a broader establishment niche than cottonwood and tamarisk, allowing it to exploit empty niches? And (2) can tamarisk and cottonwood facilitate Russian olive invasion? I analyzed riparian tree seedling requirements in a controlled experiment, performed empirical field studies, and analyzed stable oxygen isotopes in plant, soil and ground water to determine the water sources used by Russian olive. My experiment revealed that Russian olive survival was significantly higher in dense shade, and low moisture conditions than tamarisk and cottonwood. Field observations indicated that Russian olive established up to eight meters above the stream channel and water table in sites where flooding cannot occur, and under dense canopies of tamarisk, cottonwood and Russian olive. Tamarisk and native riparian plant species seedlings could not establish in these dry, shaded habitats. Russian olive plants can rely on water from shallow soil layers until they are approximately 15 years old before utilizing ground

water sources. Russian olive did not show a preference for shaded habitat and its establishment is not limited to sites where it can be facilitated by cottonwood and tamarisk. However, my results demonstrate that it has a broader establishment niche than cottonwood and tamarisk. There is great potential for continued Russian olive invasion because large amounts of suitable habitat exist across the southwestern US. Russian olive will likely increase in abundance, creating shaded habitat unsuitable for tamarisk and cottonwoods. Generalist invaders with broad niches have the potential to exclude native species and create novel ecosystems dominated by exotic species.

Key words: invasion; Russian olive; riparian; floodplains; exotic plant species; invasive species.

3.2   INTRODUCTION

Exotic invasive species are organisms that expand or are introduced into new ranges and undergo dramatic population growth (Elton 1958). Understanding why exotic species are able to invade communities is a central question in ecology with application to pressing environmental problems (Vitousek et al. 1997). Invasive species often compete with and exclude native species, threaten biodiversity, and alter physical and ecological processes (Simberloff 2005). They can modify landscapes in ways that enhance their survival or facilitate subsequent invasions (Cuddington and Hastings 2004, Niu et al. 2007). Studies of invasions can provide insights into fundamental ecological processes such as facilitation, competition, dispersal and establishment (Vitousek 1990, Shea and Chesson 2002).

Invasion facilitation, in which one species enhances the survival and reproduction of an invader, has been demonstrated in several ecosystems (Simberloff 2006, Brooker et

al. 2008). For example, animals can facilitate the reproduction of invasive plant species by dispersing their seeds, and native plants can enhance the establishment of invaders by creating sheltered microsites or enhancing soil nutrients (Tecco et al. 2006, Cavieres et al. 2008, Rowles and O'Dowd 2009).

Invasions may also occur when species exploit empty niches with unused resources, such as shaded habitat in an ecosystem where few species are shade-tolerant (Davis et al. 2000, Fridley et al. 2007). Generalist species with broad niche requirements are well-suited to exploit unused resources in highly productive ecosystems (Tilman 2004, Davies et al. 2007). Decreased levels of light (shade) as forests develop can provide opportunities for shade-tolerant invasive species, but little is known about the potential for shade-producing species to facilitate invasions (Martin et al. 2009).

Riparian areas, characterized by periodic flooding, support diverse habitat types and contribute significantly to regional biodiversity (Naiman et al. 1993, Naiman and Decamps 1997, Sabo et al. 2005). In the western United States (U.S.), riparian areas cover less than 1% of the land area but support up to 80% of breeding bird species (Knopf et al. 1988). However, frequent disturbance creates opportunities for exotic plant invasions into riparian zones, which have experienced unusually high levels of invasion relative to other habitats world-wide (Stohlgren et al. 1998, Hood and Naiman 2000).

The two dominant riparian invaders in the southwestern U.S. are the woody species tamarisk (*Tamarix ramosissima* Ledebour, *T. chinensis* Loureiro, and their hybrids) and Russian olive (*Elaeagnus angustifolia* L.) (Friedman et al. 2005a). Tamarisk was introduced into the region in the mid-1800s and spread along rivers (Graf 1978). Russian olive was introduced in the early 20th century, but has increased notably only in

the last 30 years (Friedman et al. 2005a). Historically, southwestern riparian areas were populated by stands of native cottonwood trees (*Populus deltoides* Marshall subsp. *wislizeni* (Watson) Eckenwalder; also referred to as *P. fremontii* S. Wats.) and willows (*Salix* species) (Turner 1974, Webb and Leake 2006). Tamarisk and Russian olive seeds are viable for longer, and have longer dispersal time periods than cottonwood and willow (Cooper et al. 1999, Katz and Shafroth 2003). Also, mature tamarisk and Russian olive plants can tolerate long periods without available ground water while cottonwood trees cannot (Brotherson and Winkel 1986, Katz and Shafroth 2003).

The establishment requirements of Russian olive seedlings remain poorly understood, yet are essential to its invasion success. I have observed Russian olive seedlings germinating in densely shaded areas high above the limits of flooding and the riparian water table, in habitats where tamarisk and cottonwood seeds cannot germinate. Little is known about obligate riparian tree establishment in areas that do not flood (Shafroth et al. 1995). Shaded and unflooded riparian habitats may represent empty niches because few native species can exploit these harsh conditions (DeWine and Cooper 2009).

We tested mechanisms that could drive exotic plant invasion in southwestern riparian ecosystems by addressing two questions: (1) does Russian olive have a broader establishment niche than cottonwood and tamarisk, allowing it to exploit empty niches? (2) Can cottonwood and tamarisk facilitate Russian olive invasion by providing shaded habitat? I determined the light and water requirements for tamarisk, cottonwood and Russian olive seedlings in a controlled experiment and field studies to identify the habitats where each species can establish. Tamarisk invasion in the southwestern US may

be slowing because it has filled most suitable floodplain niche space (Friedman et al. 2005a). In contrast to tamarisk, an abundance of suitable habitat for Russian olive may exist in these mature riparian forests.

3.3   METHODS

3.3.1   Study site

Studies were conducted at two scales. Regional scale investigations were conducted along rivers throughout the Colorado River Basin, including the Upper and Lower Colorado River Basin as defined by the U.S. National Hydrologic Unit System (http://nationalatlas.gov/articles/water/a_hydrologic.html, Figure 3.1). Fine scale investigations were conducted in Canyon de Chelly National Monument, within the Navajo Indian Reservation near Chinle, AZ. Two main canyons, Canyon de Chelly and Canyon del Muerto (Figure 3.1), have incised through the Defiance Plateau and drain the western side of the Chuska Mountains. Where the two canyons meet, Chinle Wash is formed. My study area included the lower 25 km of Canyon de Chelly, the lower 17 km of Canyon del Muerto, and the first 10 km of Chinle Wash.

Chinle receives an average of 23 cm of precipitation per year, largely from late summer monsoon storms. Chinle Wash is ephemeral with a bimodal flow pattern. Stream discharge peaks occur in the spring driven by mountain snowmelt and in late-summer driven by monsoon rain storms.

During years 1934-1937, the U.S. Soil Conservation Service planted tamarisk and Russian olive in Canyon de Chelly to protect ancient Pueblo ruins and modern farms from river bank erosion (SCS 1934). Tamarisk and Russian olive now dominate the study area riparian vegetation. The historic stream beds in Canyon de Chelly, Canyon del

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Muerto and Chinle Wash were wide, shallow and braided, and Chinle Wash remains wide today. However, the two tributary canyon streams have incised 1-8 m over the last 50 years (Rink 2003, Cadol 2007).

3.3.2   Seedling survival experiment

I compared tamarisk, Russian olive and cottonwood seedling survival using a split-split plot design experiment. Seeds were collected in May and June 2007. Tamarisk and cottonwood seeds were collected as they dispersed in early summer. Russian olive seeds ripen in the late summer and require stratification during freezing winter temperatures, so I collected seeds from the 2006 crop that over-wintered on parent trees. Seeds were germinated under saturated soil conditions, seedlings grown for four weeks and then transplanted individually into five cm x five cm x 25 cm tall pots filled with soil collected from Chinle Wash. The soil had a particle size distribution of 94% sand, 2% silt, 1.6% clay and 1.5% gravel by weight. All treatments were located in a fenced exclosure outside in full sun in Chinle, AZ.

I used four water treatments (shallow water table without rain additions, and low, average and high monsoon rain additions without a shallow water table), and three shade treatments (99%, 90% and 0% shade produced using fabric) in my experiment. Shade levels were chosen based on previous research showing that tamarisk and cottonwood can survive *in situ* under 0-90% shade (DeWine and Cooper 2009). Each water/shade treatment consisted of one plot with 12 replicates of each species (cottonwood, tamarisk, and Russian olive) randomly distributed within the plot for a total of 36 pots per plot. Shade levels were determined by measuring photosynthetically active radiation (PAR, μmol) under dense tamarisk and cottonwood stands, as well as full sun. Shallow water

table plots were in water-filled basins that maintained a water table 10 cm below the soil surface. In the rain treatments, seedlings were top-watered. I simulated daily rainfall totals of monsoon rainfall events based on Chinle, AZ precipitation (1951-present). Most monsoon rain storms occur from July through September and precipitation typically falls within a few hours (Gochis et al. 2006). I applied rain quantities based on average rainfall in Chinle during the monsoon seasons of 1980 through 2006. I simulated low, average and high monsoon rain years based on the frequency and duration of rain events. Low monsoon rain years of <50% of average monsoon rainfall, received 5 mm of rain twice each week. Average rain years of 100% to 125% of average monsoon rainfall, received 5 mm of rain three times per week and 20 mm of rain once each week. High rain years of >200% of average monsoon rainfall, received 5 mm four times per week and 20 mm twice per week. Water was applied using a drip irrigation system, and quantity and uniformity were checked using gauges spaced evenly among the plots. Permanent wilting point of sandy soils is reported between three and five percent volumetric water content (VWC) (Kramer and Boyer 1995). My treatments produced average VWC of 4.53% ± 0.19 (low rain, ±1 SE), 4.93% ± 0.07 (average rain), 5.53% ± 0.13 (high rain) and 42.67% ± 0.71 (shallow water table). When ambient rain occurred, rain treatments were adjusted to maintain appropriate soil moisture. Seedling survival and each plant's height (mm) was measured weekly for 10 weeks from July – September, 2007.

I used logistic regression to analyze the effects of shade and water table / rain treatment (water) on seedling survival. Few tamarisk and cottonwood plants survived the low water and low light treatments, and my ability to detect a three-way interaction was hindered by excessive zeros. Therefore, I analyzed each species separately using two-way

logistic regression models to test the effects of shade and water on seedling survival. Only one cottonwood and no tamarisk seedlings survived in 99% shade treatments and no tamarisk survived in low water treatments, so these treatments were omitted from the models for the respective species.

I tested the difference in growth rates (mm/week) between species across treatments using an analysis of variance on log-transformed growth rates of surviving plants. The Cox proportional hazards model was used to test for differences between treatments and species on seedling time-to-death (weeks). Analyses were conducted in SAS version 9.2 (SAS Institute, Cary, NC, USA).

3.3.3 Seedling transects in Canyon de Chelly

I compared natural tamarisk, Russian olive, and cottonwood seedling establishment in the field along 12 transects, four randomly located in Chinle Wash, Canyon del Muerto and Canyon de Chelly (Figure 3.1). Each transect was oriented perpendicular to the stream and extended from one canyon wall to the opposite canyon wall. Along each transect, seedlings within two m of the transect line were counted in the fall of 2006 and again in 2007. Elevation along each transect was measured relative to the channel thalweg using a laser level. Distance from the nearest seed source and photosynthetically active radiation (PAR) in μmol using a Li-Cor 189 was measured for points where height was measured.

A random coefficients regression model with Poisson errors was used to test the relationship between number of Russian olive seedlings and (1) height above the thalweg; (2) PAR; and (3) distance from seed source; among each transect-year combination where Russian olive seedlings were found. This model considered transects as drawn

randomly from a larger population, but data along each transect as non-independent. The

model adjusted for count data by using a Poisson error structure that excluded the

possibility of negative counts, and accounts for non-normal errors and a large number of

zeroes in the population (Crawley 2007). I fit random coefficients models with Poisson

errors for transect-year combinations of cottonwood and tamarisk, excluding transect-

years where no seedlings were found. Analyses were conducted in the R program version

2.8.1(SAS Institute Inc. 2008, R Development Core Team 2009).

3.3.4   Regional sampling

To analyze tamarisk, Russian olive, and cottonwood seedling establishment

requirements at a regional scale, I sampled rivers in the region surrounding Canyon de

Chelly. I used the US National Hydrologic Unit System to identify 42 subbasins in the

Upper and Lower Colorado River Basins in the Canyon de Chelly region and randomly

selected 11 sample subbasins; subbasins at higher elevations and other climates were

excluded (http://nationalatlas.gov/articles/water/a_hydrologic.html , Figure 3.1).

Randomly selected subbasins included: Chaco Wash and Upper San Juan River in NM,

Dinnebito Wash, Jadito Wash, Silver Creek, Puerco River and Leroux Wash in AZ,

Montezuma Wash and Lower San Juan River in UT, and the Middle Dolores and Lower

Dolores River in CO (Figure 3.1). I did not sample the Colorado River due to limited

access.

One plot, 100 m long oriented parallel with the stream and as wide as the riparian

vegetation zone, was established 500 m upstream of a bridge crossing the largest stream

in each subbasin. I mapped the major riparian plant community types (monotypic or

mixed stands of tamarisk, cottonwood, Russian olive and grassland species) on the

floodplain and terraces within each plot and tallied Russian olive seedlings and saplings (one to five years old) in one randomly established one m^2 subplot within each vegetation type. A total of 30 subplots were established across sites. I estimated percent canopy cover of over-story in each subplot. I surveyed ground surface elevation along a transect perpendicular to the channel in the center of the plot to establish elevation of surfaces relative to the channel thalweg.

3.3.5   Russian olive water use

To determine if Russian olive can establish and persist on terraces with deep riparian water tables, I analyzed Russian olive water sources using stable oxygen isotope ratios of xylem water, soil water and ground water. In fall 2007, sections of suberized stem tissue from 17 Russian olive plants of various ages were collected from a mixed-age stand of Russian olive and cottonwood approximately eight m above the incised Canyon de Chelly wash. Samples were sealed in glass jars and frozen until laboratory analysis. Plant age was determined by counting growth rings from an increment core or main-stem cross-section of each sampled plant. I collected three one-two kg soil samples from 10-30 cm deep (upper soil) and four samples from 40-70 cm deep (lower soil) to represent soil water within 1 m of the surface. Water samples were collected from ground water monitoring wells near the sample site by bailing the well dry at least three times, and collecting fresh inflowing ground water. Ground water at the site is >eight m below the soil surface. Soil and water samples were frozen until analyzed. Water for analysis was extracted from plant tissue and soil using a cryogenic vacuum distillation line. Oxygen isotope ratios of the extracted xylem, soil and ground water samples were determined by CO_2 equilibration using a VG Microgas Injector (packed column GC) coupled to a VG

Optima Stable Isotope Ratio Mass Spectrometer (Isoprime Inc, Machester, UK). Oxygen isotope ratios of the samples were calculated relative to a standard:

$$\delta^{18}O\ (‰) = [(^{18}O/^{16}O)_{Sample}/(^{18}O/^{16}O)_{Standard} - 1] \times 1000$$

using Standard Mean Ocean Water (SMOW) as the standard (Ehleringer 1989).

Plant samples were divided into two groups: plants 15 years and older (n = nine) and plants less than 15 years old (n = eight). I conducted an analysis of covariance on the oxygen isotope ratios of all plants with respect to age and group ($\geq$15 years or <15 year). Within group, there was no evident age trend; therefore, I conducted t-tests for unequal variance on the oxygen isotope ratios between the two soil layers, ground water, and the two age groups of plants. I used a Bonferroni adjustment for multiple comparisons (k = 10) to determine significance of the t-test p-values. Analyses were conducted in the R program version 2.8.1 (SAS Institute Inc. 2008, R Development Core Team 2009).

3.4   RESULTS

3.4.1   Seedling survival experiment

Seedlings of Russian olive grew faster than those of tamarisk and cottonwood in nearly all treatments (F = 163.56 and F = 59.96, P< 0.0001), and cottonwood grew more rapidly than tamarisk (F = 25.46, P < 0.0001) (Figure 3.2). Survival of Russian olive seedlings exceeded that of tamarisk and cottonwood in all treatment combinations except the shallow water table-90% shade treatment, where 100% of Russian olive and cottonwood seedlings survived. The cottonwood seedling survival rate exceeded that of tamarisk in all treatments. Tamarisk seedling survival was >50% only in the shallow water table-90% shade treatment (Figure 3.3).

The three-way interaction between water (water table and rain treatments), shade and species identity on seedling survival was not significant in a logistic regression model (P = 0.45). However, because very few tamarisk and cottonwood plants survived in low water and low light treatments, my ability to detect a three-way interaction was hindered by excessive zeros. Shade and water treatments significantly affected Russian olive survival ($\chi^2 = 34.71_2$, P < 0.001 and $\chi^2 = 39.02_3$, P < 0.001) and there was evidence that the effect of water depended on the effect of shade ($\chi^2 = 12.75_6$, P = 0.057). Russian olive survival was similar across water treatments but decreased significantly under low water conditions and in 99% shade (Figure 3.3). Shade and water significantly affected cottonwood survival ($\chi^2 = 12.56_1$, P < 0.001 and $\chi^2 = 20.71_3$, P < 0.001) and the effect of water depended on the effect of shade ($\chi^2 = 8.83_3$, P = 0.0316). Cottonwood survival was higher in 90% than 0% shade and decreased in reduced water treatments, but response to the water treatment varied by shade treatment (Figure 3.3). Shade and water significantly influenced tamarisk survival ($\chi^2 = 11.54_1$, P < 0.001and $\chi^2 = 24.4_2$, P < 0.001) and there was no interaction between water and shade ($\chi^2 = 0.84_2$, P = 0.658). Tamarisk survival was higher in 90% than 0% shade and lower in treatments with reduced water availability (Figure 3.3).

Time-to-death survival analysis generally matched the results of the logistic regression analysis. Within species, time-to-death increased in treatments receiving more water, and increased from 99% shade, to 0% shade, to 90% shade. Tamarisk died 1.77 times faster than cottonwood (z = 4.2, P < 0.001) and 3.96 times faster than Russian olive (z = 8.54, P < 0.001).

3.4.2   Seedling transects in Canyon de Chelly

Russian olive seedlings occurred along eight of 12 transects in 2006 and 11 transects in 2007. Tamarisk seedlings were found on two transects in 2006 and one in 2007. Cottonwood seedlings were found on four transects in 2006 and two in 2007. Russian olive seedlings occurred at elevations from the channel to eight m above the thalweg and along a PAR gradient from 10 - 2200 μmols (Figure 3.4). Russian olive seedling presence was negatively related to distance from seed source (Table 3.1). These patterns are supported by the random coefficients model where height above thalweg and light availability were not significant (Z = -1.107, P = 0.2682 and Z = -0.629, P = 0.5295, Table 3.1) and distance from seed source was nearly significant (Z = -1.833, P = 0.0598, Table 3.1). Russian olive seedlings survived from 2006 to 2007 on two transects: 39 seedlings at 0.5 m above the thalweg and one seedling five m above the thalweg, yielding a 2.4% seedling survival rate across transects. No cottonwood or tamarisk seedlings survived from 2006 to 2007.

Cottonwood and tamarisk established only where seasonal flooding and the capillary fringe wetted soils, which was within one m elevation above the channel thalweg and under high light conditions of 1200-2200 μmols (Figure 3.4). Height above thalweg was a significant factor in the cottonwood random coefficients model (Z = -2.99, P = 0.003, Table 3.1), and light availability and distance to seed source were not significant (Z = 1.58 P = 0.114 and Z = -1.645, P = 0.100, Table 3.1). One cottonwood seedling was found in deep shade but did not survive, and a model without this seedling indicated that light availability is a significant factor (Z = 2.14, P = 0.0324). Because

tamarisk was found on only three transect-years, I could not develop a random coefficients model.

3.4.3 Regional sampling

Tamarisk occurred along all 12 rivers sampled, cottonwood and Russian olive on five rivers and sand bar willow (*Salix exigua* Nutt.) on four rivers. Adults of each species occurred in monospecific and mixed species stands. Russian olive seedlings were found on three river reaches, but only where Russian olive adults were present and only under canopies of Russian olive, willow, tamarisk, or cottonwood. Russian olive was the only woody plant found in the understory of other species. Russian olive saplings occurred where the mean canopy coverage was 55.6 ± 18.4 (± 1 SE, Figure 3.4).

3.4.4 Russian olive water use

Analysis of covariance on $\delta^{18}O$ of all Russian olive plants indicated no overall age trend, or age trend within group (t = -0.003, P = 0.997 and t = 0.316, P = 0.757). When the analysis was run with main effects only of age and group, no trend with age was evident (t = 0.313, P = 0.7592) but there was a significant effect of group on $\delta^{18}O$ (t = 4.064, P = 0.0012). All p-values for t-tests between plants, soil and ground water were multiplied by ten for a Bonferroni multiple comparisons adjustment (k = 10). The $\delta^{18}O$ of plants <15 and ≥15 years were significantly different (t = 8.673, P < 0.0001.). The $\delta^{18}O$ of plants ≥15 was different from upper soil (10 - 30cm depth) and lower soil (40 - 70cm depth) (t = -9.9, P = 0.001 and t = -5.95, P = 0.001). The $\delta^{18}O$ of ground water was different than plants <15, plants ≥15, upper soil and lower soil (t = -18.76, -8.497, -18.55, -14.61, and P-values ≤ 0.001). The $\delta^{18}O$ of plants <15 years old was not different from

that of upper or lower soil water (t = 2.31, P = 0.70 and t = 2.06, P = 0.67). The δ^{18}O of upper soil was not different than lower soil (t = 3.99, P = 0.10, Figure 3.5).

3.5   DISCUSSION

Our controlled experiments and field surveys demonstrated that Russian olive has a broader establishment niche than cottonwood and tamarisk. I found Russian olive establishing and surviving in moderate to high shade environments, provided mostly by tamarisk and cottonwood, suggesting some degree of facilitation. However, facilitation, if it is occurring, is not the sole means of invasion because Russian olive did not show a preference for shaded habitat under tamarisk, cottonwood or in my shade experiments. My results clearly demonstrate the potential for empty niche exploitation by Russian olive to promote long-term changes in vegetation composition.

We found Russian olive establishing up to eight m above the stream channel in riparian environments where flooding cannot occur and soils are wetted only by precipitation. This confirms that Russian olive establishment is not solely flood dependent. My oxygen isotope analysis showed that Russian olive can persist on soil water for up to 15 years before their roots reach the riparian water table and utilize ground water. Although my isotope sampling occurred at one site and one time it represents typical summer conditions and suggests the potential for Russian olive in my study area to establish and survive on soil water. In contrast, tamarisk and cottonwood seedlings established only in environments wetted by floodwaters and areas lacking dense shade (Shafroth et al. 1995, Sher et al. 2002). Russian olive was the only species to survive in my experiments in all 99% shade treatments and it was found established under dense canopies of tamarisk, cottonwood and Russian olive in the field. Tamarisk

and cottonwood canopies provide suitable shaded habitat for Russian olive establishment, but this shade excludes their own seedlings.

Russian olive can establish in shade or full sun, where the water table is shallow or deep, and in flooded or rain-wetted sites, suggesting that its potential habitat in the western US is vast. Cottonwood, tamarisk and Russian olive are the second, third and fourth most frequently occurring woody plant species along rivers in the western US, with sand bar willow being most common (Friedman et al. 2005a). Although Russian olive occurs almost as frequently as cottonwood and tamarisk, it does not yet cover as much area (Friedman et al. 2005a). Mature tamarisk and cottonwood stands are not self-replacing because establishment rarely occurs under closed-canopy forests (DeWine and Cooper 2009). However, Russian olive can create self-replacing stands that exclude tamarisk and cottonwood seedling establishment.

Although neither cottonwood nor tamarisk seedlings survived the 99% shade treatment in my controlled experiment, these high light-loving species both had higher survival in 90% than 0% shade. These unexpected results suggest two things: 1) shade reduces water stress, thereby increasing seedling survival, and 2) the shade tolerance of tamarisk and cottonwood is exceeded in most field settings where closed tamarisk and cottonwood canopies typically have greater than 90% shade (DeWine and Cooper 2009).

Under simulated monsoon rain treatments in my experiment, cottonwood seedlings were able to survive under the relatively low water conditions of two-four rain events per week. However, it is unlikely that cottonwood seeds could germinate or seedlings could survive to maturity under such low water conditions (Mahoney and Rood 1998, Cooper et al. 1999). Cottonwood seedlings had higher survival and growth rates

than tamarisk under a variety of light and water conditions, not just the flooded, high-light conditions where cottonwood is known to outperform tamarisk (Cooper et al. 1999, Sher and Marshall 2003).

Although Russian olive invasion is not limited by light availability or the presence of a shallow riparian water table, it appears to be limited by seed dispersal. In Canyon de Chelly, Russian olive seedling establishment was negatively related to distance from a seed source. Because Russian olive seeds are relatively large (1-1.5 cm long) and are spread mainly by birds and mammals, its dispersal lags behind cottonwood and tamarisk's wind-born seeds. Large seeds provide the advantage of increased resources during germination and the early stages of seedling establishment, whereas tamarisk or cottonwood seeds have little endosperm (Katz and Shafroth 2003). Large seed size may allow seedlings to withstand low water conditions and maintain high growth rates.

Russian olive appears to be exploiting empty establishment niches among woody riparian vegetation in southwestern ecosystems. It can persist along wide gradients of water and light availability, and its broad habitat tolerances will likely lead to its population increase. As the Russian olive population expands across the western US, it may create shaded habitat where tamarisk and cottonwood cannot establish, potentially leading to their population decline. Species with broad niches tend to be successful invaders in ecosystems where they can exploit open niche space (Goodwin et al. 1999, Marvier et al. 2004). In addition, species with slow colonization rates may be over-looked as invaders even though they may threaten native ecosystems and outcompete native species (Martin et al. 2009). Invaders with broad niches have the potential to exclude native species and create novel ecosystem states where community composition is

dominated by exotic species (Lovei 1997, Vitousek et al. 1997). Thus, understanding

what constitutes open niche space for each species is critical to understanding its

potential to be a successful invader.

3.6 ACKNOWLEDGEMENTS

3.7 LITERATURE CITED

Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler,
P. Liancourt, K. Tielborger, J. M. J. Travis, F. Anthelme, C. Armas, L. Coll, E.
Corcket, S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. Pugnaire, C. L. Quiroz,
P. Saccone, K. Schiffers, M. Seifan, B. Touzard, and R. Michalet. 2008.
Facilitation in plant communities: the past, the present, and the future. Journal of
Ecology **96**:18-34.

Brotherson, J. D., and V. Winkel. 1986. Habitat Relationships of Saltcedar (Tamarix-
Ramosissima) in Central Utah. Great Basin Naturalist **46**:535-541.

Cadol, D. D. 2007. Aerial photographic analysis of channel change and riparian vegetation establishment in Canyon de Chelly National Monument, Arizona, 1935-2004. Master's. Colorado State University, Fort Collins.

Cavieres, L. A., C. L. Quiroz, and M. A. Molina-Montenegro. 2008. Facilitation of the non-native Taraxacum officinale by native nurse cushion species in the high Andes of central Chile: are there differences between nurses? Functional Ecology **22**:148-156.

Cooper, D. J., D. M. Merritt, D. C. Andersen, and R. A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, USA. Regulated Rivers-Research & Management **15**:419-440.

Crawley, M. J. 2007. The R Book. Jon Wiley and Sons, West Sussex, England.

Cuddington, K., and A. Hastings. 2004. Invasive engineers. Ecological Modelling **178**:335-347.

Davies, K. F., S. Harrison, H. D. Safford, and J. H. Viers. 2007. Productivity alters the scale dependence of the diversity-invasibility relationship. Ecology **88**:1940-1947.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.

DeWine, J. M., and D. J. Cooper. 2009. Habitat overlap and facilitation in tamarisk and box elder stands: implications for tamarisk control using native plants. Restoration Ecology **17**.

Ehleringer, J. R., C. B. Osmond. 1989. Stable isotopes. Pages 281-300 *in* R. W. Pearcy, J. R. Ehleringer, H. A. Mooney, P. W. Rundel, editor. Plant Phisiological Ecology Field Methods and Instrumentation. Chapman and Hall, New York.

Elton, C. S. 1958. The Ecology of invasions by animals and plants. The University of Chicago Press, Chicago.

Fridley, J. D., J. J. Stachowicz, S. Naeem, D. F. Sax, E. W. Seabloom, M. D. Smith, T. J. Stohlgren, D. Tilman, and B. Von Holle. 2007. The invasion paradox: Reconciling pattern and process in species invasions. Ecology **88**:3-17.

Friedman, J. M., G. T. Auble, P. B. Shafroth, M. L. Scott, M. F. Merigliano, M. D. Preehling, and E. K. Griffin. 2005. Dominance of non-native riparian trees in western USA. Biological Invasions **7**:747-751.

Gochis, D. J., L. Brito-Castillo, and W. J. Shuttleworth. 2006. Hydroclimatology of the North American Monsoon region in northwest Mexico. Journal of Hydrology **316**:53-70.

Goodwin, B. J., A. J. McAllister, and L. Fahrig. 1999. Predicting invasiveness of plant species based on biological information. Conservation Biology **13**:422-426.

Graf, W. L. 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. Geological Society of America Bulletin **89**:1491-1501.

Hood, W. G., and R. J. Naiman. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecology **148**:105-114.

Katz, G. L., and P. B. Shafroth. 2003. Biology, ecology and management of Elaeagnus angustifolia L. (Russian olive) in western North America. Wetlands **23**:763-777.

Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation Of Riparian Ecosystems In The United-States. Wilson Bulletin **100**:272-284.

Kramer, P. J., and J. S. Boyer. 1995. Water relations of plants and soils. Academic Press, London.

Lovei, G. L. 1997. Biodiversity - Global change through invasion. Nature **388**:627-628.

Mahoney, J. M., and S. B. Rood. 1998. Streamflow, requirements for cottonwood seedling recruitment - An interactive model. Wetlands **18**:634-645.

Martin, P. H., C. D. Canham, and P. L. Marks. 2009. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Frontiers in Ecology and the Environment **7**:142-149.

Marvier, M., P. Kareiva, and M. G. Neubert. 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Analysis **24**:869-878.

Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: Riparian zones. Annual Review Of Ecology And Systematics **28**:621-658.

Naiman, R. J., H. Decamps, and M. Pollock. 1993. The Role of Riparian Corridors in Maintaining Regional Biodiversity. Ecological Applications **3**:209-212.

Niu, H. B., W. X. Liu, F. H. Wan, and B. Liu. 2007. An invasive aster (Ageratina adenophora) invades and dominates forest understories in China: altered soil microbial communities facilitate the invader and inhibit natives. Plant and Soil **294**:73-85.

R Development Core Team. 2009. R: A language and environment for statistical computing. *in*. R Foundation for Statistical Computing, Vienna, Austria.

Rink, G. 2003. Vascular Flora of Canyon de Chelly National Monument, Apache County, Arizona. Master's Thesis. Northern Arizona University, Flagstaff, AZ.

Rowles, A. D., and D. J. O'Dowd. 2009. New mutualism for old: indirect disruption and direct facilitation of seed dispersal following Argentine ant invasion. Oecologia **158**:709-716.

Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, and A. Welter. 2005. Riparian zones increase regional species richness by harboring different, not more, species. Ecology **86**:56-62.

SAS Institute Inc. 2008. SAS. *in*, Cary, North Carolina, USA.

SCS, U. S. 1934. United States Soil Conservation Service Region Eight Records. *in* U. o. N. Mexico, editor. Center for Southwest Research.

Shafroth, P. B., G. T. Auble, and M. L. Scott. 1995. Germination and Establishment of the Native Plains Cottonwood (Populus-Deltoides Marshall Subsp Monilifera) and the Exotic Russian-Olive (Elaeagnus-Angustifolia L). Conservation Biology **9**:1169-1175.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends In Ecology & Evolution **17**:170-176.

Sher, A. A., and D. L. Marshall. 2003. Seedling competition between native Populus deltoides (Salicaceae) and exotic Tamarix ramosissima (Tamaricaceae) across water regimes and substrate types. American Journal of Botany **90**:413-422.

Sher, A. A., D. L. Marshall, and J. P. Taylor. 2002. Establishment patterns of native Populus and Salix in the presence of invasive nonnative Tamarix. Ecological Applications **12**:760-772.

Simberloff, D. 2005. Non-native species do threaten the natural environment! Journal Of Agricultural & Environmental Ethics **18**:595-607.

Simberloff, D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecology Letters **9**:912-919.

Stohlgren, T. J., K. A. Bull, Y. Otsuki, C. A. Villa, and M. Lee. 1998. Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecology **138**:113-125.

Tecco, P. A., D. E. Gurvich, S. Diaz, N. P. Perez-Harguindeguy, and M. Cabido. 2006. Positive interaction between invasive plants: The influence of Pyracantha angustifolia on the recruitment of native and exotic woody species. Austral Ecology **31**:293-300.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences of the United States of America **101**:10854-10861.

Turner, R. M. 1974. Quantitative and historical evidence of vegetation changes along the upper Gila River, Arizona. U.S. Geological Survey Professional Paper **655-H**.

Vitousek, P. M. 1990. Biological Invasions and Ecosystem Processes - Towards an Integration of Population Biology and Ecosystem Studies. Oikos **57**:7-13.

Vitousek, P. M., C. M. Dantonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: A significant component of human-caused global change. New Zealand Journal Of Ecology **21**:1-16.

Webb, R. H., and S. A. Leake. 2006. Ground-water surface-water interactions and long-term change in riverine riparian vegetation in the southwestern United States. Journal of Hydrology **320**:302-323.

3.8   TABLE

Table 3.1 Results of a random coefficients model analysis where number of seedlings was the dependent variable and height away from the thalweg (meters, Height), distance from seed source (meters, Seed source), and amount of light (μmol, Light) were the independent variables, within the random groups "transect-year" for Russian olive and cottonwood seedlings. Significant factors are indicated by bold text p-values.

	Russian olive				Cottonwood			
	Estimate	SE	z value	P (>|t|)	Estimate	SE	z value	P (>|t|)
(Intercept)	2.1935	0.3584	6.121	**<0.001**	-3.985	1.5709	-2.537	**0.0142**
Height	-0.1845	0.1667	-1.107	0.2682	-3.311	1.3854	-2.992	**0.0028**
Light	-0.0744	0.1184	-0.629	0.5295	0.0016	0.0008	1.581	0.1139
Seed source	-0.0577	0.0307	-1.883	**0.0598**	-0.01517	0.0103	-1.645	0.1000

3.9 FIGURES
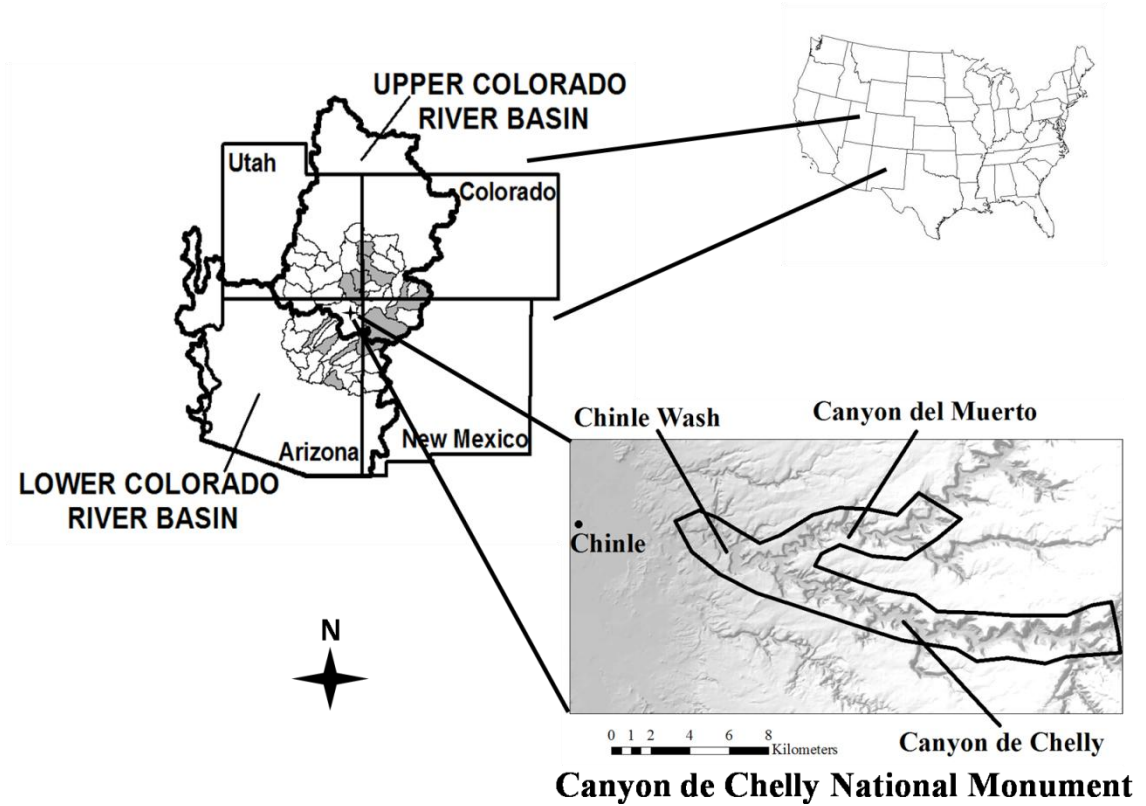
Figure 3.1. Maps of Canyon de Chelly National Monument (lower right panel) and regional sampling area (upper left panel). The bold line notes Canyon de Chelly study area, and its location on the regional map identified with a cross. My regional sampling area included 42 Colorado River subbasin units depicted by small basin outlines. I randomly selected 11 subbasins (gray-filled) from the total 42 subbasins for regional study sites.
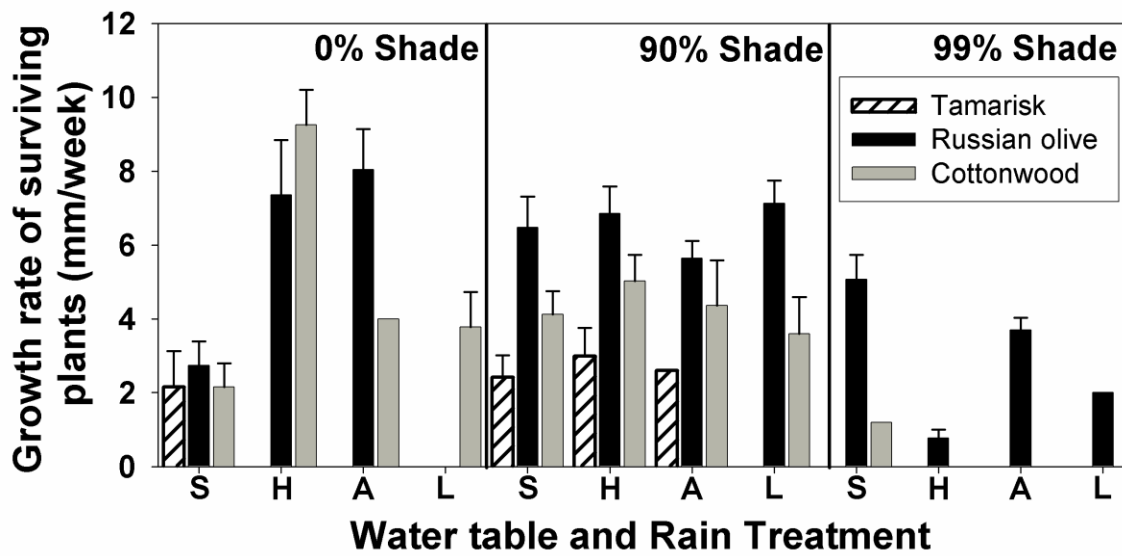
Figure 3.2. Growth rate of surviving plants after 10 weeks of shade and water treatment

(mm/week ±SE). Bars without SE indicate treatments are where only one plant survived.

Shade treatments are the large boxes: 0% shade, 90% shade, and 99% shade treatment.

Water treatments are indicated along the x-axis: S = shallow water table, H = high rain, A

= average rain and L = low rain. Species are indicated by shaded bars.
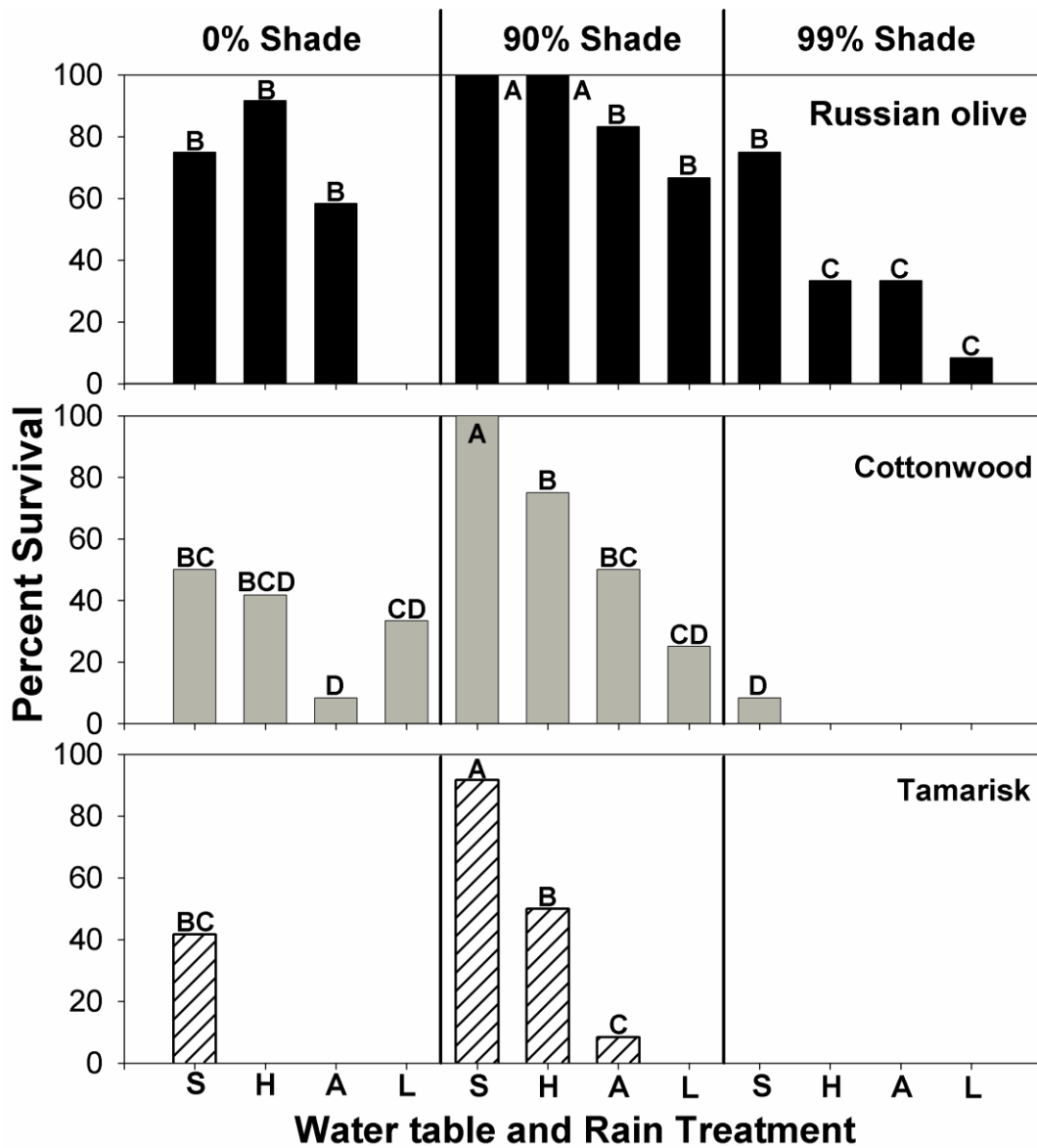
Figure 3.3. Percent survival of Russian olive (top), cottonwood (middle) and tamarisk (bottom) for each shade and water treatment. Shade treatments are the large boxes: 0% shade, 90% shade, and 99% shade treatment. Water treatments are indicated along the x-axis: S = shallow water table, H = high rain, A = average rain and L = low rain. Different letters indicate significantly different survival rates, pooling variance with alpha level 0.05.

67
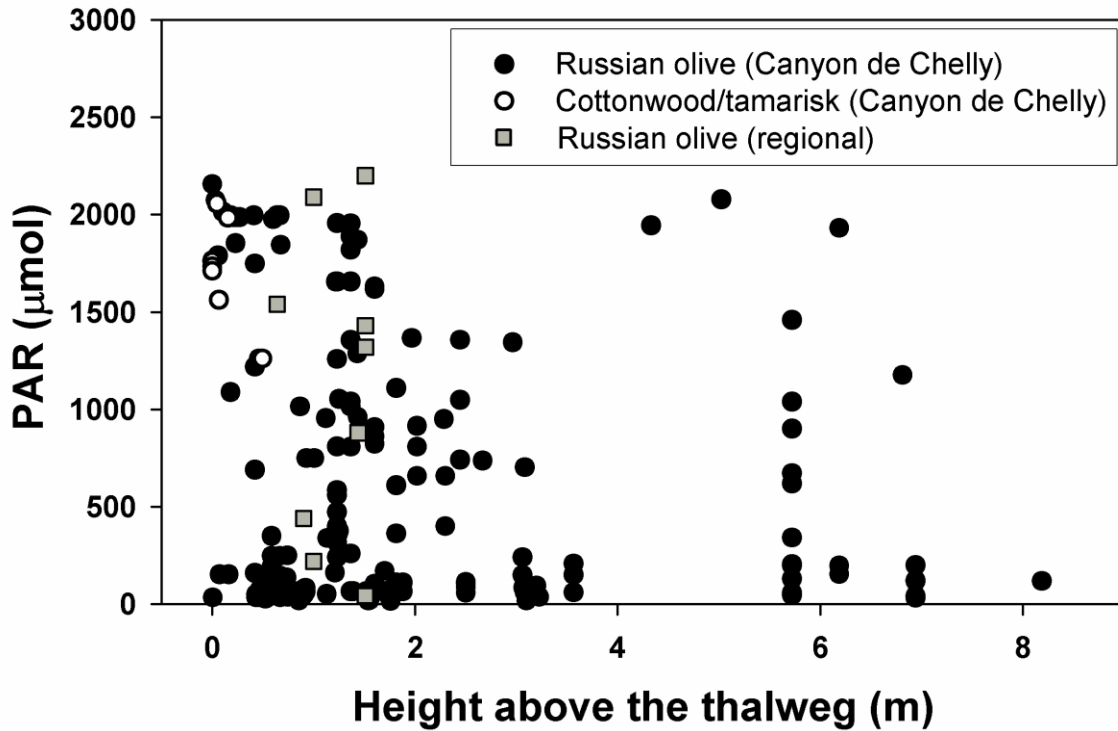
Figure 3.4. Presence of seedlings along a height above thalweg (m, x-axis) and PAR (μmol, y-axis) gradients. Zero μmol is 100% shade and 2200 μmol is full sun. Seedlings of Russian olive (black or gray) and tamarisk and cottonwood (white) were sampled in Canyon de Chelly (circles) and regionally (squares).
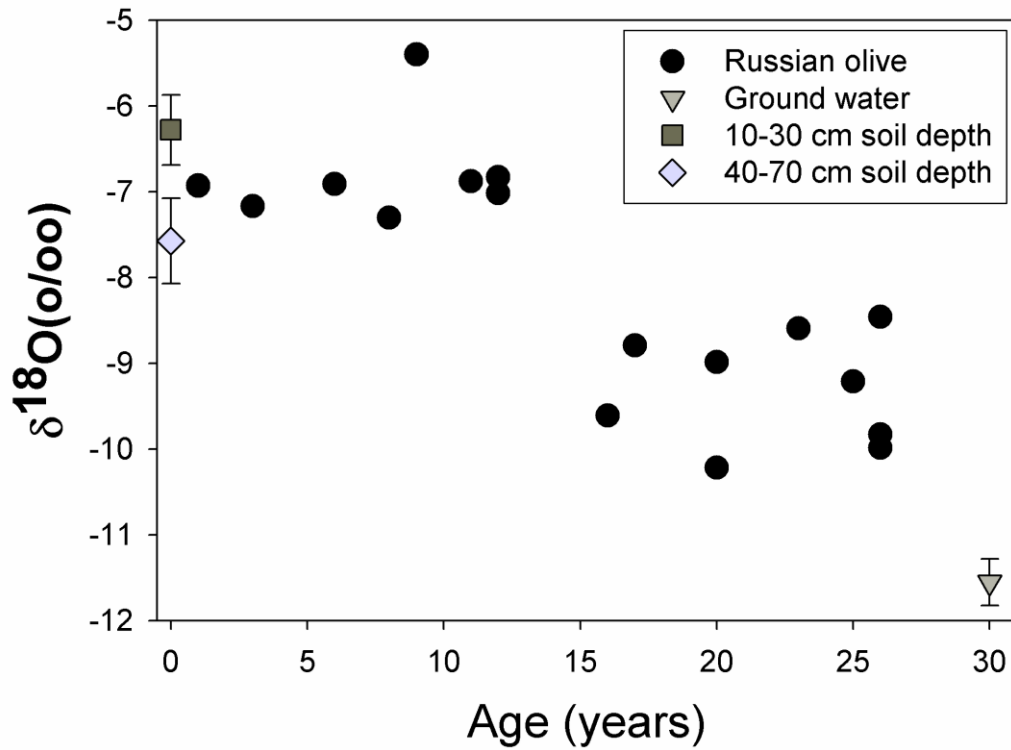
Figure 3.5. Average $\delta^{18}O$ (‰) for Russian olive of different ages (black circles), ground water (gray inverted triangle), soil of 10-30 cm depth (gray square) and soil of 40-70 cm depth (gray diamond). Error bars indicate ±1 SE.

4   ECOSYSTEM RESPONSE TO EXOTIC PLANT REMOVAL

4.1   INTRODUCTION

Mitigating the effects of harmful invasive plants is an important challenge for scientists and land managers. Invasive plants often exclude native plants and alter physical and ecological processes (Simberloff 2005). Riparian areas are of particular concern because they are critical to regional biodiversity despite covering a small percentage of the landscape (Knopf et al. 1988, Sabo et al. 2005). Also, riparian areas have been invaded disproportionately more than other habitats world-wide (Hood and Naiman 2000). Understanding how to effectively meet management goals by removing exotic species, preventing future invasions and restoring native vegetation is essential to managing critical native ecosystems such as riparian areas (Harms and Hiebert 2006).

In the southwestern United States (U.S.), the most dominant exotic riparian plant invaders are the woody deciduous trees tamarisk (*Tamarix ramosissima* Ledebour, *T. chinensis* Loureiro, and their hybrids) and Russian olive (*Elaeagnus angustifolia* L.) (Friedman et al. 2005a). Historically, southwestern floodplains were populated by stands of native cottonwood (*Populus deltoides* Marshall subsp. *wislizeni* (Watson) Eckenwalder; also referred to as *P. fremontii* S. Watson) and willows (*Salix* spp.). Tamarisk and Russian olive have different life history strategies than these native riparian plants, which may have allowed them to invade floodplains in the U.S. Cottonwood and willow seeds disperse aerially in late spring and early summer, are viable for four to six weeks to coincide with spring peak river flows and germinate on moist substrate (Cooper et al. 2003, Rood et al. 2003). Tamarisk and Russian olive seeds have longer viability and dispersal periods than cottonwood and willow (Cooper et al. 1999, Katz and Shafroth

2003). Also, mature tamarisk and Russian olive plants can tolerate long periods without available ground water whereas native cottonwood and willow cannot (Brotherson and Winkel 1986, Katz and Shafroth 2003).

Efforts to control exotic riparian plants have been implemented in many areas of the southwestern U.S. (Bay and Sher 2008). Most efforts have targeted tamarisk infestations and there have been fewer Russian olive control efforts. Common goals of tamarisk control programs include restoring native vegetation, increasing water yield in rivers, and improving wildlife habitat (Shafroth et al. 2005). There is disagreement among scientists and managers on the success of different control strategies for meeting restoration goals (Harms and Hiebert 2006, Sher et al. 2008). A key problem is the lack of research to understand vegetation history prior to exotic plant invasion and the lack of post-treatment monitoring which limits our understanding of vegetation response to the treatments (Shafroth et al. 2008).

Seeds may play a critical role in determining vegetation composition following disturbances (Gurevitch et al. 2002). Aerial seed rain inputs and soil seed banks are important propagule sources that influence plant colonization after exotic plant removal (Vosse et al. 2008). Analyses of the seed bank can aid in understanding which plant species formerly grew in an area and which species could potentially germinate on each site in the future (Olano et al. 2005). Riparian soil seed banks are influenced by river flow regimes past and present. Seeds are deposited locally by resident plants and by floods that transport seeds from upstream sources. Within any riparian area, the seed bank reflects the past and present plant communities, as well as upstream and distant plant communities whose seeds arrived in river-deposited sediment, and by wind and animal

dispersal (Goodson et al. 2001). Seed banks represent vegetation variation across space and time and thus are useful restoration tools (Richter and Stromberg 2005).

Nutrient availability may also influence vegetation establishment after exotic plant removal. In arid region ecosystems, shrubs and other large plants have been shown to concentrate nutrients and moisture around them, becoming "islands of fertility" (Schlesinger et al. 1996, Schade and Hobbie 2005). Soil beneath the canopy of shrubs can have higher available nitrogen than soil in the inter-shrub spaces (Schlesinger and Pilmanis 1998). Tamarisk and Russian olive, as large shrubs, may create spatial heterogeneity in soils and leave a soil signature after they have been removed. Russian olive in particular may have a lasting impact on floodplain soils since it forms a symbiosis with bacteria that fix nitrogen (Bertrand and Lalonde 1985, DeCant 2008). Nitrogen-fixing exotic plants in other habitats have been shown to alter vegetation by increasing available soil nitrogen (Hughes and Denslow 2005). In addition, Russian olive leaf litter is higher in nitrogen than native cottonwood (Simons and Seastedt 1999). Thus, Russian olive locations may form patches of local nitrogen richness.

Tamarisk dominance along western rivers concerns water managers because tamarisk water use may be depleting already scarce water supplies in the southwestern US (Van Hylckama 1970, Stromberg et al. 2009). Although early studies of tamarisk water use showed alarming rates of evapotranspiration within tamarisk stands, more recent research has shown tamarisk water use to be equivalent or less than native riparian tree water use (Cleverly et al. 2006, Nagler et al. 2009). However, water salvage continues to be one of the leading reasons that land managers want to eliminate tamarisk along southwestern streams (Shafroth et al. 2005, Nagler et al. 2009).

There is strong motivation to remove exotic plants along southwestern rivers, but there remains a need to guide management decisions regarding the most cost-effective removal strategies and native plant restoration following removal treatments (Harms and Hiebert 2006, Shafroth et al. 2008). In this study, I compare cut-stump and whole-plant removal treatments of tamarisk and Russian olive with untreated controls in Canyon de Chelly National Monument (Canyon de Chelly), where tamarisk and Russian olive have invaded riparian habitats along the canyon streams (Figure 1.1). In the majority of the study area, exotic plant infestation is located on a terrace that represents the historic braided channel and floodplain in Canyon de Chelly (Cadol 2007, Jaeger 2009). Due to channel incision over the last 20 years, the current stream channel bed is $2 - 4$ m below terraces that now support dense and mature tamarisk and Russian olive stands. This topographic situation is distinct from previous riparian restoration efforts that have focused on active floodplains (Bay and Sher 2008). This study examines the establishment of dryland vegetation after tamarisk and Russian olive removal (Friedman et al. 1995, Taylor and McDaniel 1998).

I focused on the role of seeds, nutrients, ground water dynamics and plant removal method on the floristic composition of the post-treatment plant community. I addressed three questions related to exotic plant removal: (1) How do the two removal methods affect post treatment riparian vegetation composition, aerial seed rain inputs, and ground water dynamics? (2) How does soil seed bank composition influence post-treatment vegetation? And, (3) Is available soil nitrogen increased near dead Russian olive plants following removal? I analyzed differences in plant community composition, ground water levels, and aerial seed rain between the cut-stump removal and the whole-

plant removal areas. I also analyzed differences in seed bank composition across the study area to understand historic and potential vegetation composition. Finally, I compared available soil nitrogen adjacent to dead Russian olive plants in removal areas to available soil nitrogen in areas lacking Russian olive.

4.2   METHODS

4.2.1   Study area

My study was conducted in Canyon de Chelly National Monument, within the Navajo Nation near Chinle, AZ. Two main canyons, Canyon de Chelly and Canyon del Muerto (Figure 4.1), have incised through the Defiance Plateau and drain the western side of the Chuska Mountains. Where the two canyons meet, Chinle Wash is formed. Our study area included the lower 25 km of Canyon de Chelly, the lower 17 km of Canyon del Muerto, and the first 10 km of Chinle Wash.

Chinle receives an annual average of 23.3 cm of precipitation, with an average of 13.4 cm falling during the months June – October, and 9.9 cm falling between November and May. The region is characterized by strong monsoon-driven precipitation events in the late summer when most of the annual precipitation occurs. An average of 30.5 cm of snow falls each year. Chinle Wash is an ephemeral stream with a bimodal flow pattern. Discharge peaks occur due to spring-time mountain snowmelt runoff and late-summer monsoon rain events.

During years 1934-1937, the U.S. Soil Conservation Service planted tamarisk and Russian olive in Canyon de Chelly in an effort to protect ancient Pueblo ruins and modern farms from river bank erosion (SCS 1934). Tamarisk and Russian olive now dominate the study area riparian vegetation. The historic stream beds in Canyon de

Chelly, Canyon del Muerto and Chinle Wash were wide, shallow and braided, and Chinle Wash remains wide today. However, the tributary canyon streams have incised 1-5 m deep over the last 50 years (Rink 2003, Cadol 2007).

4.2.2 Study design

Plant removals occurred in six 1.1-km-long study reaches which were the width of the riparian plant community. The upstream 300 m of each reach was the untreated control, and directly downstream was a 300 m long cut-stump treatment, where plants were cut by chainsaw and stumps treated with Garlon® 4 herbicide by Canyon de Chelly staff. This configuration was required to limit the downstream effects of each study reach treatment on the controls. Downstream of the cut-stump treatment was a 200 m buffer zone, and then a 300-m-long whole-plant removal treatment where all tamarisk and Russian olive were removed by Canyon de Chelly staff using a backhoe to extract the largest roots under the bole (Figure 4.2). Exotic plant removals were started the winter of 2005 and continued through fall of 2006. Wood produced by the treatments was piled and burned on site.

4.2.3 Vegetation

I sampled the vegetation within study plots along regularly-spaced transects in the six study areas. Transects were aligned perpendicular to the canyon and the wash. There were three transects in each treatment (control, cut-stump and whole-plant removal) spaced 100 m apart, for a total of nine transects in each of the six sites, for a total of 54 transects. Transects were as long as the riparian plant community was wide. Along each transect, circular plots five m in radius were placed adjacent to each other along the transect length. For example, 10 plots were sampled in a 100-m-wide riparian plant

community. One three m radius and one 0.5 m radius subplot were nested in each five m radius plot and subplots shared the same center as the five m radius plot. I counted and measured all shrub and tree stems within each five m radius plot. Within each three m radius plot, percent woody species (canopy) cover was visually estimated. Within each 0.5 m radius plot, percent cover of herbaceous plants was visually estimated. Species were identified and characterized as native or exotic according to the USDA PLANTS database classifications (USDA 2009). For statistical analysis, all cover estimates within plots were summed within each transect because plots within transect were not independent. Transects were treated as the sampling unit. I analyzed the effect of treatments (control, cut-stump and whole plant) and years (pretreatment: 2005, and post-treatment years: 2007 and 2008) on composition of herbaceous and woody vegetation (percent native species cover and percent exotic species cover) using a random effects model where "treatment nested within site" is treated as a random effect, allowing us to make inference to the landscape from which sites were selected (Bolker et al. 2009).

4.2.4 Seed rain

Density of wind-dispersed seeds was monitored using seed sticky traps. Seed traps were built from a 30 cm x 30 cm slab of plywood oriented horizontal to the ground and 1 m above the ground and attached to a fence post. These were treated with Tanglefoot©, a sticky substance that traps seeds. Nine seed traps were established in each of the six study sites for a total of 54 traps. Each study site had three transects perpendicular to the channel, one transect in each treatment (control, cut-stump and whole-plant removal) along which three seed traps were evenly spaced. Seed traps were established in May of 2005 and monitored weekly each summer through 2007. Trapped

seeds were counted weekly, and removed from the traps, from late-May through mid-August.

Data were log-transformed to correct for over-dispersion and mixed-effects Poisson regression was used to analyze the effect of treatment and week (time in the summer) on tamarisk aerial seed rain. We assumed a Poisson error structure because our data were counts including zeros (Crawley 2007). We employed mixed-effects models to include data across sites and incorporated "site" as a random effect, which allowed us to make inference to the landscape from which sites were selected (Bolker et al. 2009). I analyzed one pre-treatment (2005) and one post-treatment year (2007). For models of both 2005 and 2007, the random effects "Site", "Trap within Site", "Site and Treatment interaction", and "Site and week interaction" were incorporated into the mixed effects model. The fixed effects treatment, week (time during the summer) and tamarisk canopy cover over each trap were tested for significance in predicting variation in tamarisk seed rain.

4.2.5 Ground water

Depth to the water table was measured using fully slotted ground water monitoring wells that were installed using hand augers. Six to 12 monitoring wells were installed in each of the six study sites; the number of wells depended on how deep the water table was, with more wells in sites with shallow water table. Each study site had three ground water well transects perpendicular to the channel, one transect in each treatment and control plot. Each transect contained two to four wells spaced evenly along the transect and at least one well on each channel bank. Ground water wells were installed in May of 2005 and monitored weekly each summer through 2007. I employed a

mixed-effects model to include data across sites and incorporated "site" as a random effect, which allowed us to make inference to the landscape from which sites were selected (Bolker et al. 2009). Ground water variation among years is non-linear, therefore to test pre- and post-treatment years, 2005 and 2007 were modeled separately. In 2007, only pre-monsoon season data were analyzed (May – July 15) to assess dry season ground water decline. Models for years 2005 and 2007 included the random effects "site", "treatment within site", and "week by site." The fixed effects treatment, week (time during the summer), and distance (distance from the stream channel) were tested for significance in predicting variation in ground water depth. In the linear mixed effects regression model, P-values were not calculated because there is some debate among prominent statisticians regarding the appropriate way to calculate degrees of freedom for general linear mixed models with crossed random effects (Ben Bolker, Douglas Bates, comments on https://stat.ethz.ch/pipermail/r-sig-mixed-models/). Therefore, the importance of a predictor was judged based on whether its estimate ± SE overlaps zero.

4.2.6   Soil seed bank

The riparian soil seed bank was analyzed using samples collected in June 2007 from 12 randomly selected points in Canyon de Chelly. The riparian zone was stratified by plant patch type (Russian olive, tamarisk, cottonwood/willow, and meadow) and floodplain terrace (active channel, young terrace, and old terrace). Floodplain terraces were determined from aerial photographs taken of Canyon de Chelly during 1935, 1965, 1974, 1981 and 2004. Little vegetation established along the wash between 1935 and 1981, thus old terraces were those terraces that were stabilized prior to the 1981 aerial photographs and low terraces were those terraces stabilized by vegetation prior to the

2004 aerial photographs (Cadol 2007). Soil samples were collected at one random location within each patch type and terrace age combination in each site. A 30 cm x 30 cm x five cm square of top soil was extracted at each sample location, placed in a plastic bag, and immediately transported back to the greenhouse in Chinle. Soil seed bank samples were spread in individual trays in a greenhouse and watered twice daily with one cm of water through the summer and fall. Germinating seedlings were identified upon flowering and removed. Some plants were brought to Colorado State University in the fall of 2007 and placed in a heated greenhouse until they flowered. An analysis of variance model was used to analyze the effect of plant patch type and floodplain terrace on relative abundance of exotic species, native species and obligate wetland species in the soil seed bank.

4.2.7   Soil nitrogen

Soil nitrogen (N) availability was analyzed using resin bags (Binkley and Matson 1983). Resin bags absorb available nitrate and ammonium from the soil and provide an estimate of available soil N for plants (Binkley and Matson 1983). Pre-treatment soil nitrogen was analyzed by randomly placing five resin bags within each of four plant patch types within each site: meadows (areas lacking woody canopy cover), native (native riparian woody plant species), tamarisk and Russian olive. Resin bags were placed approximately 10 cm below the ground surface. They were installed in July of 2005 and removed in November 2005.

Following our cut stump treatments, soil N was analyzed near cut Russian olives and in adjacent areas without Russian olives in 2006 and 2007. Three plant community sampling plots were randomly chosen in each cut-stump treatment (Sites 3-6, Figure 4.1).

Five resin bags were placed 40 cm deep around the cut Russian olive bole closest to each randomly chosen plot, in each of four study sites. Resin bags were installed in September of 2006 and collected in March of 2007 to exploit high soil moistures during the winter and capture the spring pulse of nutrient availability for plants following the winter season. Another set of resin bags was installed in September of 2007 and collected in March of 2008. As a reference, five resin bags were placed 10 m north of the closest cut Russian olive bole. Control resin bags were placed in an X pattern, 75 cm from each other. Mixed effects models were used to determine the effect of plant patch type in 2005 and the effect of Russian olive cut-stump presence in 2006 and 2007. Site was incorporated as a random effect in 2005 and site as well as plot within site were incorporated as random effects in 2006 and 2007. All soil nitrogen data were log-transformed to meet normality assumptions. All statistical analyses were conducted in either SAS version 9.2 or the R program version 2.8.1 (SAS Institute Inc. 2008, R Development Core Team 2009).

4.3 RESULTS

4.3.1 Vegetation

Herbaceous species cover

A total of 105 herbaceous species were identified in the vegetation plots (Appendix A.). Species with the most cover across all sites included exotic and native species (Table 4.1). Both the cut stump and the whole plant removal treatments reduced exotic herbaceous species and increased native herbaceous species cover (Figure 4.3). A random effects model on percent exotic herbaceous species cover that included predictors treatment, year (2005, 2007, and 2008), the interaction between treatment and year, and

"treatments within site" as a random effect, indicated that the effect of treatment depended on year. Both the cut-stump and whole plant treatments decreased the percent of exotic herbaceous species compared to the control, from 2005 through 2008 (estimate = -7.43, t = -2.86, P = 0.0005, and estimate = -10.54, t = -3.95, P < 0.001). The cut-stump treatment increased the percent of native herbaceous species compared to the control, from 2005 through 2008 (Estimate = 7.55, t = 2.92, P = 0.004) and the whole plant removal treatment increased the percent of native herbaceous species compared to the control, across years (Estimate = 10.64, t =4.01, P < 0.001). For species richness, there was no effect of cut-stump or whole plant removal treatment compared to the control across years (t = 0.37, P = 0.72 and t = -0.24, P = 0.81) but there was a significant effect of year on species richness across treatments (Estimate = 1.26, t = 4.88, P < 0.001).

Woody plant species cover

A total of 14 woody plant species were found in plots (Appendix A.). Species with the highest cover across all sites included tamarisk, cottonwood, and Russian olive (Table 4.2). The cut stump and whole plant removal treatments reduced exotic woody plant canopy cover (predominantly tamarisk and Russian olive) to zero in 2007 and 2008, whereas native canopy cover remained constant across treatments and years (Figure 4.4). A random effects model on percent exotic woody species cover that included the predictors treatment, year (2005, 2007, and 2008), the interaction between treatment and year, and "treatments within site" as a random effect, indicated that the effect of treatment depended on year. The cut-stump treatment decreased the percent of exotic woody species compared to the control, from 2005 through 2008 (Estimate = -16.67, t = -5.02, P < 0.001) and the whole plant removal treatment decreased the percent of exotic

woody species compared to the control, across years as well (Estimate = -24.26, t = -7.05, P < 0.001). Neither cut-stump nor whole plant treatment had an effect on the percent of native woody species compared to the control, from 2005 through 2008 (Estimate = -1.12, t = -0.45, P = 0.66 and estimate = -2.22, t =-0.85, P = 0.40).

4.3.2   Seed rain

Native cottonwood and willow aerial seed rain peaked earlier than tamarisk seed rain across sites between years, and occurred during May and June. Tamarisk seed rain peaked during May through July, and occurred for longer duration than cottonwood and willow every year, and continued until late August in all years (Figure 4.5 and Figure 4.6). A mixed-effects Poisson regression model for 2005 tamarisk seed rain indicated that, prior to removal, seed rain density (number of seeds/m^2/day) was not different between treatment sites (Z = -0.14, P = 0.89 and Z = 1.08, P = 0.28) but week (time during the summer) and percent tamarisk cover around each trap were significant predictors of seed rain density (Z = 5.75, P < 0.001 and Z = 2.95, P = 0.003). A mixed-effects Poisson regression model for 2007 tamarisk seed rain indicated that treatment had a significant effect on seed rain, with both the cut-stump and the whole plant treatments significantly reducing seed rain when compared to the control (Z = -5.90, P < 0.001 and Z = -4.56, P < 0.001). Week (time during the summer) was also a significant factor in estimating variance in 2007 tamarisk seed rain (Z = 3.79, P < 0.001), but tamarisk cover at the traps was not a significant factor (Z = -0.37, P = 0.71).

4.3.3   Ground water

All monitored reaches within Canyon de Chelly had losing streams, with the elevation of ground water levels relative to stream elevation decreasing with distance

away from the channel (Figure 4.7). In general, depth to ground water was most shallow during the winter and spring, decreased during the summer dry season, and increased starting at summer's end during the monsoon rainy season (Figure 4.8).

A mixed effect regression model for ground water depth in 2005 (pre-treatment) showed that neither treatment accounted for any variation in ground water depth compared to controls (-20.26 ± 32.53 (estimate $\pm$ SE), t = -0.62 and 30.45 ± 48.34, t = 0.63). However, the predictors week (time during the summer) and distance (distance from the streambed) did account for variation in ground water depth (8.01 ± 3.34, t = 2.40 and 3.76 ± 1.98, t = 1.90).

A mixed-effects model for ground water depth in 2007, prior to the monsoon season, showed no effect of either treatment (17.38 ± 48.59, t = 0.36 and -20.49 ± 51.51, t = -0.40), but the effect of the treatment depended on distance from the streambed (-0.66 ± 0.66, t = -1.00 and -1.51 ± 0.56, t = -2.71). As in 2005, the predictors week and distance did account for variation in ground water depth (8.69 ± 1.44, t = 6.04 and 2.59 ± 0.42, t = 6.15).

4.3.4   Soil seed bank

In general, the soil seed bank had fewer exotic species and more native species than the vegetation that was found in the field treatment plots in 2008 (Figure 4.9). There were many more wetland species found in the soil seed bank across sites than in the treatment plots (Appendix A.). Patch type did not affect species composition in the soil seed bank, but floodplain terrace age did affect species composition (Figure 4.10).

The average percent of germinating exotic species did not vary across patch types ($F = 1.63$, $P = 0.16$), or between floodplain terraces of different ages ($F = 2.00$, $P = 0.14$)

and the percent of exotic species in a given patch type did not depend on terrace age (F = 0.47, P = 0.75, Figure 4.10).

The average percent of germinating native species varied across patch types and across floodplain ages (F = 2.50, P = 0.04 and F = 6.61, P = 0.01) and the percent of native species in a given patch type did not depend on floodplain age (F = 0.81, P = 0.52).

The average percent of germinating wetland species did not vary across patch types and varied slightly across floodplain terrace ages (F = 1.15, P = 0.34 and F = 3.75, P = 0.06) and the percent of wetland species in a given patch type did not depend on floodplain age (F = 0.23, P = 0.92).

4.3.5   Soil nitrogen

In 2005 vegetation patch type: meadow, native riparian trees, tamarisk and Russian olive did not affect available soil nitrate, but did affect available soil ammonium (Figure 4.11). The importance of predictors was based on whether its estimate ± SE overlapped zero. A mixed-effects regression model showed that the groups were weak predictors of variation in soil nitrates: meadow (-0.07 ± 0.83, (estimate ± SE) t = -0.08), native (-0.09 ± 0.81 t = -0.11), tamarisk (-1.04 ± 0.82 t = -1.27), and Russian olive (0.015 ± 0.82, t = 0.02). However, for ammonium, all groups were strong predictors of available soil ammonium: meadow (0.30 ± 0.17, t = 1.766), native (1.38 ± 0.16 t = 8.70), tamarisk (0.97 ± 0.16 t = 5.98), and Russian olive (0.99 ± 0.17, t = 5.83). Native riparian tree patches had the highest concentration of soil nitrates and ammonium, whereas meadows, tamarisk and Russian olive all had comparatively lower levels of these substances (Figure 4.11).

In 2006, available soil nitrate and ammonium levels were elevated within a 2 m radius of removed Russian olive boles compared to reference areas that lacked Russian olive (Figure 4.12). A mixed effects regression model showed that reference areas (0.84 ± 0.35 t = 2.44) and Russian olive individuals (1.84 ± 0.35 t = 5.25) were strong predictors of variation in available soil nitrate. A mixed effects regression model showed that reference areas (0.28 ± 0.18 t = 1.51) and Russian olive boles (1.03 ± 0.19 t = 5.53) were strong predictors of variation in available soil ammonium. However, in 2007 only available soil nitrate levels were elevated within a 2 m radius of dead Russian olive boles compared to reference areas and levels of soil ammonium were not elevated (Figure 4.12). A mixed effects regression model showed that reference areas (0.56 ± 0.37 t = -1.50) and dead Russian olive boles (0.96 ± 0.36 t = 2.62) were strong predictors of variation in available soil nitrate. A mixed effects regression model showed that that reference areas (-0.30 ± 0.20 t = -1.51) and dead Russian olive boles (0.10 ± 0.19 t = 0.51) were weak predictors of variation in available soil ammonium.

4.4 DISCUSSION

In all removal treatment sites, tamarisk and Russian olive removal efforts successfully reduced tamarisk and Russian olive presence to zero (Figure 4.4). At the same time, native woody species cover remained constant across all sites and treatments throughout the study period (Figure 4.4). Both treatments were effective in removing tamarisk and Russian olive and maintaining the existing native woody plant vegetation. Herbaceous vegetation composition changed substantially in the removal treatments. Exotic herbaceous species cover decreased and native species cover increased significantly in the cut stump and whole plant treatments from 2005 to 2008 compared to

the control, which remained relatively constant. I found no differences in herbaceous vegetation composition between whole plant and cut-stump treatments even though the whole-plant removal created more soil disturbance (Figure 4.3). Other studies also showed that mechanical disturbance in tamarisk removal sites did not result in an increase in exotic grass cover (Sher et al. 2008). However, herbaceous species richness remained similar among treatments between years (Figure 4.3), which has been shown by others who found that species richness did not change in sites where tamarisk was removed compared to untreated controls (Harms and Hiebert 2006). In general, few studies have followed vegetation composition after removal of riparian exotic plants, yet these results can be critical to informing future management decisions regarding the type of exotic plant removal treatments that could be used (Shafroth et al. 2008).

In all years, tamarisk had a later seed dispersal peak and longer seed dispersal period, compared to native riparian seed dispersal, which peaked earlier and ended earlier than tamarisk (Figure 4.5 and Figure 4.6). Both removal treatments significantly reduced the density of tamarisk seed rain received in the treatment plots, indicating that removal plots would have lower likelihood of reinvasion by tamarisk (Figure 4.6). Interestingly, peak seed rain varied substantially between years with 2006 having an earlier peak than 2005 and 2007. This may be due to 2006 having a drier winter and spring compared to 2005 and 2007; water availability has been shown to affect riparian tree productivity (Figure 4.13, (Rood et al. 2003).

Ground water in my sites varied widely between seasons and with distance from the stream channel, reaching its peak during the late winter and early spring after monsoon season flooding followed by consistent base flow in the stream channel during

the winter and spring (Figure 4.8, Figure 4.7). Ground water levels then declined from early to late summer during the driest part of the year in June and increased in response to monsoon season rain and floods during the wettest part of the year in August and September (Figure 4.8, Figure 4.13). Following removal of tamarisk and Russian olive in my treatment plots, the ground water did not show evidence of increasing due to phreatophytic vegetation removal. It is possible that my removal sites were too small to affect the riparian water table, but our results indicate it is unlikely that removal of exotic riparian vegetation will lead to increases in the water table. Recent studies have shown that tamarisk stand evapotranspiration is relatively low and that removal of tamarisk is unlikely to lead to increases in stream or ground water availability (Nagler et al. 2008).

I found higher native species abundance and lower exotic species abundance in the soil seed bank than in the vegetation in treatment plots in 2008 (Figure 4.9). This indicates that a viable native seed bank persists for many decades under favorable conditions. Also, I found only six obligate wetland plant species in the vegetation in our treatment plots and they occurred in very low abundances (Appendix A., Figure 4.9). However, I found 13 obligate wetland species in the soil seed bank and most occurred in high abundances (Appendix A., Figure 4.9). Soil seed bank species distributions varied little across vegetation patch type except in samples from the active channel bed, which had lower native and wetland species abundance and higher exotic species abundance than floodplain patch types (Figure 4.10). Interestingly, species distributions did vary across floodplain terrace ages. High floodplain terraces that were stabilized before 1981, and likely have not been flooded since they were stabilized, had more native and wetland species than the younger floodplain terraces. These results indicate that the higher the

flood disturbance frequency, the younger the age of the seed bank which supported fewer native species and wetland species and slightly more exotic species.

Live Russian olive roots did not provide more available nitrogen to the soil, but when Russian olive trees are killed with cut-stump plus herbicide methods, the decomposing roots provide a brief increase (within two years) in soil nitrogen, especially nitrate concentration. Although influxes of soil nitrogen provided by exotic species have been shown to encourage the invasion of other plant species, it is unlikely that Russian olive will facilitate future invasions because available soil nitrogen dropped within two years of Russian olive plant removal in our cut-stump sites (Hughes and Denslow 2005). Our results contrast with Decant (2008), who showed increased available nitrogen under live Russian olive trees; however, southwestern riparian systems do not appear to be nitrogen-limited, leading to a minimal impact of Russian olive on soil nutrients dynamics.

4.4.1 Management implications

Although whole-plant removal of exotic woody species provides thorough removal, it is costly in terms of time and money and our results indicate that it does not provide more benefit to riparian vegetation than cut-stump with herbicide removal methods. Both methods decrease exotic herbaceous species cover and increase native species cover after two years. Both methods decrease tamarisk aerial seed rain inputs and neither method increases ground water levels compared to controls. There is great potential for native species and wetland species colonization of these sites from the seed bank. However, most of these sites, although they are riparian, are rarely flooded because the stream channel in Canyon de Chelly has incised two to four meters from the adjacent floodplain. There was an incision event in the late 1980s (Chapter 2) that left the former

floodplains in my study sites abandoned. With the removal of tamarisk and Russian olive, these sites are transitioning to xeric grasslands, as indicated by common species in our survey plots (Table 4.1). These conditions are in contrast with other successful removal sites in the western US where greater native species cover is correlated with great water availability, rain input, and flooding frequency (Bay and Sher 2008). Further study in our xeric sites should include active revegetation, where native seeds are added to removal sites, with possible water additions to increase native species cover.

Local soil seed banks can be used to inform future restoration efforts in Canyon de Chelly. There are many native grassland species that may be useful candidates for restoring tamarisk and Russian olive removal sites. Exotic grasses dominated the vegetation in our sites (Table 4.1). However, native seed additions in removal sites may improve native vegetation compared to my sites where no seed additions occurred (Harms and Hiebert 2006, Shafroth et al. 2008). Our study did not address grazing impacts in Canyon de Chelly, but there is active cattle, horse and sheep grazing occurring throughout Canyon de Chelly, which may have a negative impact on native vegetation. Managers in Canyon de Chelly should continue with cut-stump removal of tamarisk and Russian olive, continue monitoring vegetation in removal sites to track long-term vegetation change and pursue further management actions to facilitate native vegetation establishment such as native seed additions and grazing exclosures.

4.5 LITERATURE CITED

Bay, R. F., and A. A. Sher. 2008. Success of active revegetation after Tamarix removal in riparian ecosytems of the southwestern United States: A quantitiative assessment of past restoration projects. Restoration Ecology **16**:113-128.

Bertrand, L. J., and M. Lalonde. 1985. Invitro-Propagation and Nodulation by Frankia of Actinorhizal Russian Olive (Elaeagnus-Angustifolia L). Plant and Soil **87**:143-152.

Binkley, D., and P. Matson. 1983. Ion-Exchange Resin Bag Method for Assessing Forest Soil-Nitrogen Availability. Soil Science Society of America Journal **47**:1050-1052.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends In Ecology & Evolution **24**:127-135.

Brotherson, J. D., and V. Winkel. 1986. Habitat Relationships of Saltcedar (Tamarix-Ramosissima) in Central Utah. Great Basin Naturalist **46**:535-541.

Cadol, D. D. 2007. Aerial photographic analysis of channel change and riparian vegetation establishment in Canyon de Chelly National Monument, Arizona, 1935-2004. Master's. Colorado State University, Fort Collins.

Cleverly, J. R., C. N. Dahm, J. R. Thibault, D. E. McDonnell, and J. E. A. Coonrod. 2006. Riparian ecohydrology: Regulation of water flux from the ground to the atmosphere in the Middle Rio Grande, New Mexico. Hydrological Processes **20**:3207-3225.

Cooper, D. J., D. C. Andersen, and R. A. Chimner. 2003. Multiple pathways for woody
plant establishment on floodplains at local to regional scales. Journal of Ecology
91:182-196.

Cooper, D. J., D. M. Merritt, D. C. Andersen, and R. A. Chimner. 1999. Factors
controlling the establishment of Fremont cottonwood seedlings on the upper
Green River, USA. Regulated Rivers-Research & Management **15**:419-440.

Crawley, M. J. 2007. The R Book. Jon Wiley and Sons, West Sussex, England.

DeCant, J. P. 2008. Russian Olive, Elaeagnus Angustifolia, Alters Patterns In Soil
Nitrogen Pools Along The Rio Grande River, New Mexico, Usa. Wetlands
28:896-904.

Friedman, J. M., G. T. Auble, P. B. Shafroth, M. L. Scott, M. F. Merigliano, M. D.
Preehling, and E. K. Griffin. 2005a. Dominance of non-native riparian trees in
western USA. Biological Invasions **7**:747-751.

Friedman, J. M., M. L. Scott, and W. M. Lewis. 1995. Restoration of Riparian Forest
Using Irrigation, Artificial Disturbance, and Natural Seedfall. Environmental
Management **19**:547-557.

Goodson, J. M., A. M. Gurnell, P. G. Angold, and I. P. Morrissey. 2001. Riparian seed
banks: structure, process and implications for riparian management. Progress in
Physical Geography **25**:301-325.

Gurevitch, J., S. M. Scheiner, and G. A. Fox. 2002. The Ecology of Plants, Sunderland,
MA.

Harms, R. S., and R. D. Hiebert. 2006. Vegetation response following invasive tamarisk (Tamarix spp.) removal and implications for riparian restoration. Restoration Ecology **14**:461-472.

Hood, W. G., and R. J. Naiman. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecology **148**:105-114.

Hughes, R. F., and J. S. Denslow. 2005. Invasion by a N-2-fixing tree alters function and structure in wet lowland forests of Hawaii. Ecological Applications **15**:1615-1628.

Jaeger, K. 2009. Channel dynamics in Canyon de Chelly National Monument, AZ, with emphasis on the effect of invasive plants. Dissertation. Colorado State University, Fort Collins.

Katz, G. L., and P. B. Shafroth. 2003. Biology, ecology and management of Elaeagnus angustifolia L. (Russian olive) in western North America. Wetlands **23**:763-777.

Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation Of Riparian Ecosystems In The United-States. Wilson Bulletin **100**:272-284.

Nagler, P. L., E. P. Glenn, K. Didan, J. Osterberg, F. Jordan, and J. Cunningham. 2008. Wide-area estimates of stand structure and water use of Tamarix spp. on the Lower Colorado River: Implications for restoration and water management projects. Restoration Ecology **16**:136-145.

Nagler, P. L., K. Morino, K. Didan, J. Erker, J. Osterberg, K. R. Hultine, and E. P. Glenn. 2009. Wide-area estimates of saltcedar (Tamarix spp.) evapotranspiration on the lower Colorado River measured by heat balance and remote sensing methods. Ecohydrology **2**:18-33.

Olano, J. M., I. Caballero, J. Loidi, and A. Eseudero. 2005. Prediction of plant cover from seed bank analysis in a semi-arid plant community on gypsum. Journal of Vegetation Science **16**:215-222.

R Development Core Team. 2009. R: A language and environment for statistical computing. *in*. R Foundation for Statistical Computing, Vienna, Austria.

Richter, R., and J. C. Stromberg. 2005. Soil seed banks of two montane riparian areas: implications for restoration. Biodiversity and Conservation **14**:993-1016.

Rink, G. 2003. Vascular Flora of Canyon de Chelly National Monument, Apache County, Arizona. Master's Thesis. Northern Arizona University, Flagstaff, AZ.

Rood, S. B., J. H. Braatne, and F. M. R. Hughes. 2003. Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. Tree Physiology **23**:1113-1124.

Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, and A. Welter. 2005. Riparian zones increase regional species richness by harboring different, not more, species. Ecology **86**:56-62.

SAS Institute Inc. 2008. SAS. *in*, Cary, North Carolina, USA.

Schade, J. D., and S. E. Hobbie. 2005. Spatial and temporal variation in islands of fertility in the Sonoran Desert. Biogeochemistry **73**:541-553.

Schlesinger, W. H., and A. M. Pilmanis. 1998. Plant-soil interactions in deserts. Biogeochemistry **42**:169-187.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems (vol 77, pg 364, 1996). Ecology **77**:1270-1270.

SCS, U. S. 1934. United States Soil Conservation Service Region Eight Records. *in* U. o. N. Mexico, editor. Center for Southwest Research.

Shafroth, P. B., V. B. Beauchamp, M. K. Briggs, K. Lair, M. L. Scott, and A. A. Sher. 2008. Planning riparian restoration in the context of Tamarix control in western North America. Restoration Ecology **16**:97-112.

Shafroth, P. B., J. R. Cleverly, T. L. Dudley, J. P. Taylor, C. Van Riper, E. P. Weeks, and J. N. Stuart. 2005. Control of Tamarix in the Western United States: Implications for water salvage, wildlife use, and riparian restoration. Environmental Management **35**:231-246.

Sher, A. A., S. Gieck, C. S. Brown, and S. J. Nissen. 2008. First-year responses of cheatgrass following Tamarix spp. control and restoration-related disturbances. Restoration Ecology **16**:129-135.

Simberloff, D. 2005. Non-native species do threaten the natural environment! Journal Of Agricultural & Environmental Ethics **18**:595-607.

Simons, S. B., and T. R. Seastedt. 1999. Decomposition and nitrogen release from foliage of cottonwood (Populus deltoides) and Russian-olive (Elaeagnus angustifolia) in a riparian ecosystem. Southwestern Naturalist **44**:256-260.

Stromberg, J. C., M. K. Chew, P. L. Nagler, and E. P. Glenn. 2009. Changing Perceptions of Change: The Role of Scientists in Tamarix and River Management. Restoration Ecology **17**:177-186.

Taylor, J. P., and K. C. McDaniel. 1998. Restoration of saltcedar (Tamarix sp.)-infested floodplains on the Bosque del Apache National Wildlife Refuge. Weed Technology **12**:345-352.

USDA. 2009. The PLANTS Database, National Plant Data Center, NRCS. *in*. http://plants.usda.gov, Baton Rouge, LA.

Van Hylckama, T. E. A. 1970. Water Use By Salt Cedar. Water Resources Research **6**:728-&.

Vosse, S., K. J. Esler, D. M. Richardson, and P. M. Holmes. 2008. Can riparian seed banks initiate restoration after alien plant invasion? Evidence from the Western Cape, South Africa. South African Journal Of Botany **74**:432-444.

4.6 TABLES

Table 4.1 Top ten herbaceous species ranked by total cover in all sites in Canyon de Chelly, top ten exotic herbaceous species ranked by total cover in all sites, and top ten native herbaceous species ranked by total cover. Native status is indicated by an E (exotic) or N (native).

Rank by total cover	Species	Native status
1	*Bromus tectorum*, cheatgrass	E
2	*Bromus rigidus*, ripgut brome	E
3	*Hordeum murinum*, mouse barley	E
4	*Heterotheca villosa*, hairy false goldenaster	N
5	*Cenchrus longispinus*, mat sandbur	N
6	*Ambrosia acanthicarpa*, flatspine burr ragweed	N
7	*Sporobolus cryptandrus*, sand dropseed	N
8	*Salsola iberica*, prickly Russian thistle	E
9	*Vulpia octoflora*, sixweeks fescue	N
10	*Croton texensis*, Texas croton	N

Exotic species

1	*Bromus tectorum*, cheatgrass	
2	*Bromus rigidus*, ripgut brome	
3	*Hordeum murinum*, mouse barley	
4	*Salsola iberica*, prickly Russian thistle	
5	*Sisymbrium altissimum*, tall tumblemustard	
6	*Polygonum aviculare*, prostrate knotweed	

7	*Erodium cicutarium*, redstem stork`s bill
8	*Portulaca oleracea*, little hogweed
9	*Tribulus terrestris*, puncturevine
10	*Medicago lupulina*, black medick

Native species

1	*Heterotheca villosa*, hairy false goldenaster
2	*Cenchrus longispinus*, mat sandbur
3	*Ambrosia acanthicarpa*, flatspine burr ragweed
4	*Sporobolus cryptandrus*, sand dropseed
5	*Vulpia octoflora*, sixweeks fescue
6	*Croton texensis*, Texas croton
7	*Conyza canadensis*, Canadian horseweed
8	*Artemisia ludoviciana*, white sagebrush
9	*Senecio spartioides*, broomlike ragwort
10	*Opuntia polyacantha*, plains pricklypear

Table 4.2 Top five woody species ranked for total cover in all sites in Canyon de Chelly.

Native status is indicated by an E (exotic) or N (native).

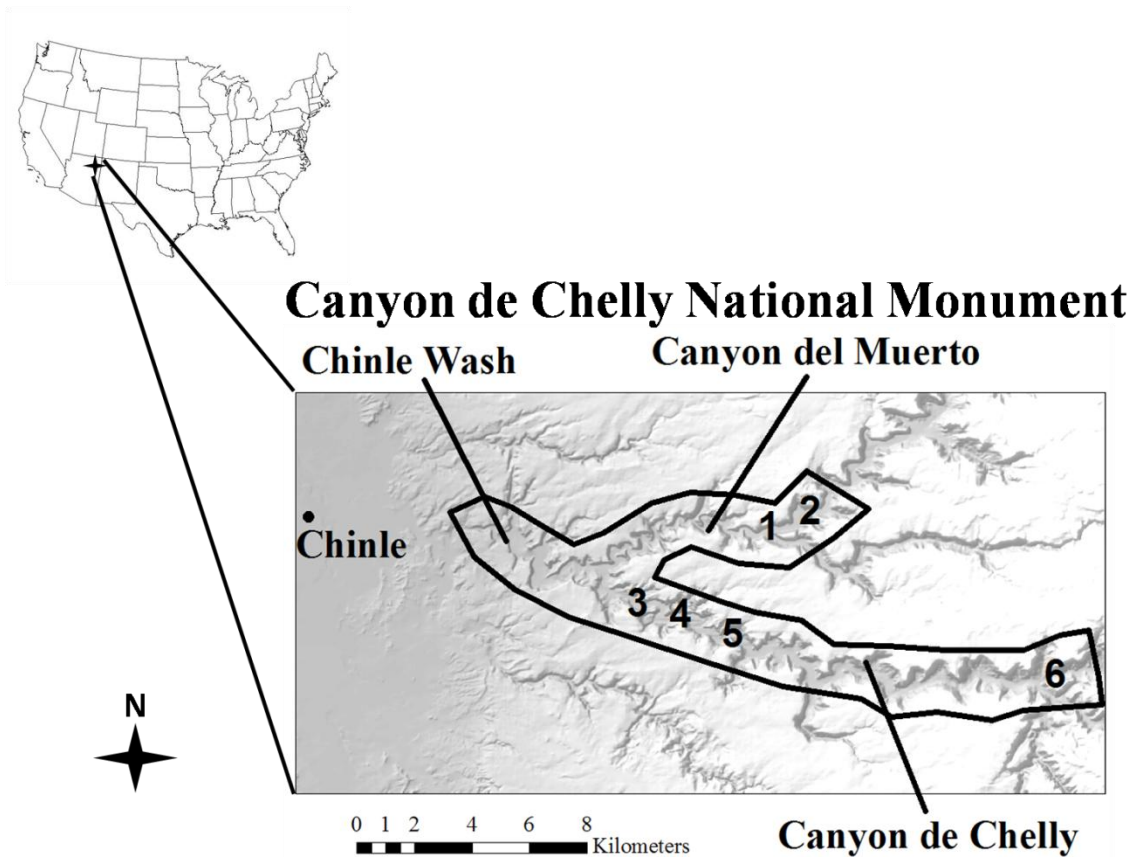| Rank by total cover	Species	Native status
1	*Elaeagnus angustifolia*, Russian olive	E
2	*Populus fremontii*, Fremont cottonwood	N
3	*Tamarix ramosissima*, saltcedar	E
4	*Salix gooddingii*, Goodding`s willow	N
5	*Populus +acuminata*, lanceleaf cottonwood	N

4.7 FIGURES

Figure 4.1 Map of Canyon de Chelly National Monument, Arizona, United States. The cross on the map of the United States indicates the location of Canyon de Chelly and the enlarged area. Exotic plant extraction study sites are indicated by numbers: 1 – Navajo Fortress, 2 – Standing Cow, 3 – Lower White House, 4 – Upper White House, 5 – Sliding Rock and 6 – Spider Rock.
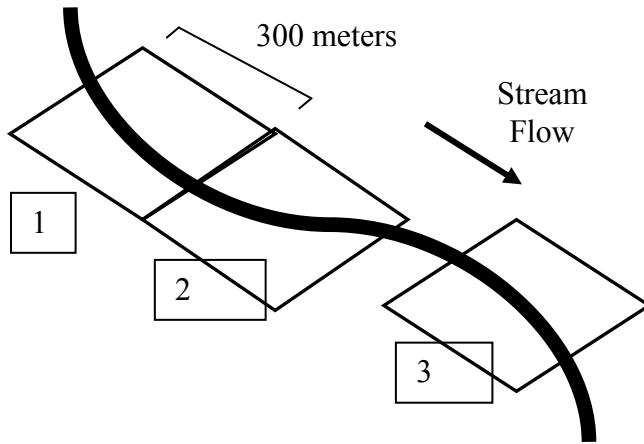
Figure 4.2 Experimental design of exotic plant removal in Canyon de Chelly National Monument. The bold line represents the stream channel, with water flowing from left to right and boxes represent the study block areas: (1) control, (2) above-ground removal w/ herbicide, (3) above-ground removal w/ herbicide.
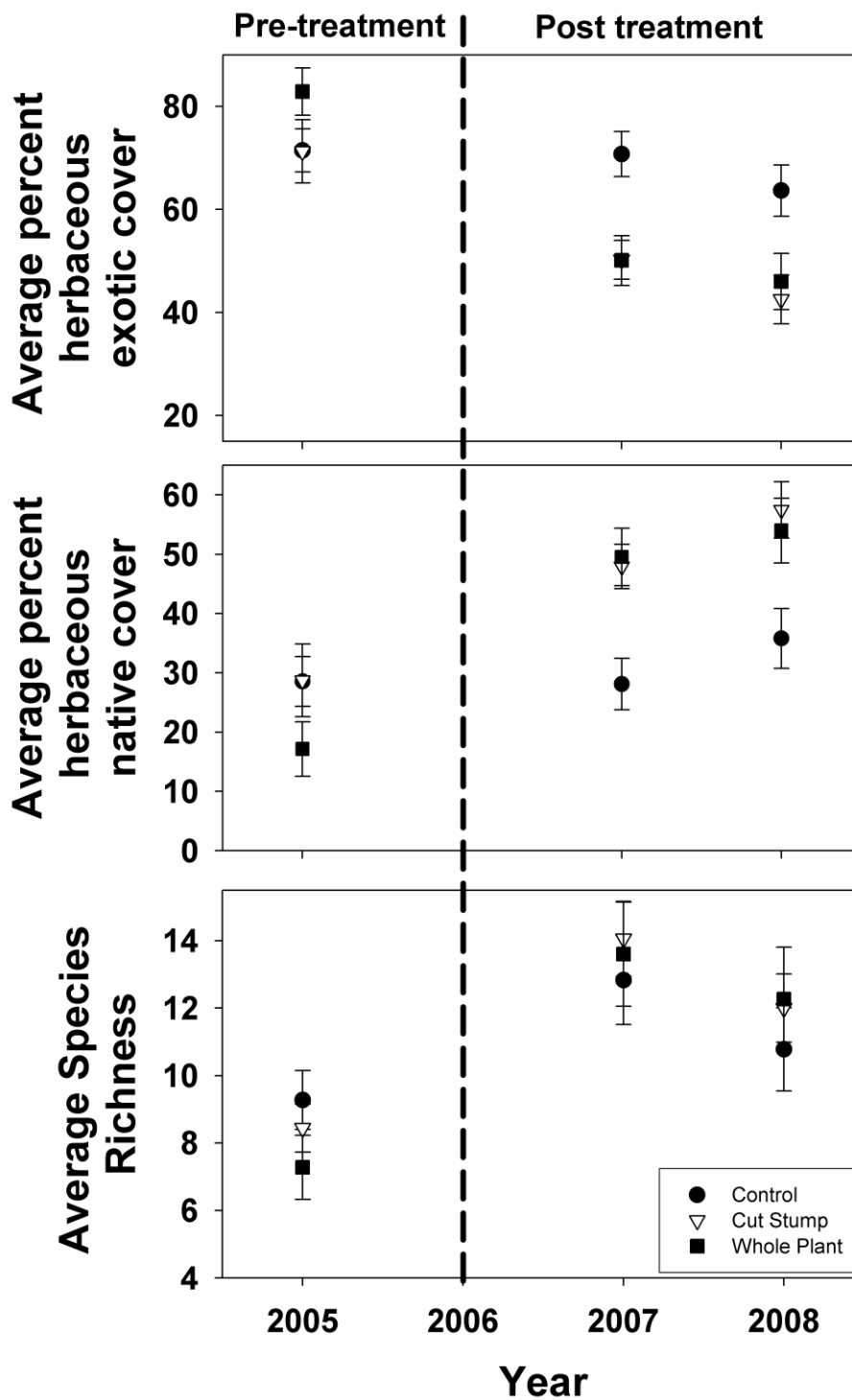
Figure 4.3 Average percent (±SE) herbaceous cover of exotic species (top panel), native

species (middle panel) and total species richness (bottom panel) in each treatment in

years 2005, 2007 and 2008. Treatments are indicated by symbols: control (circle), cut

stump (inverted triangle) and whole plant removal (square). Sampling in year 2005

occurred before the treatments were implemented (pre-treatment), treatments were

completed in 2006, and post treatment sampling occurred in 2007 and 2008.

Figure 4.4 Average percent (±SE) canopy cover of exotic species (top panel) and native

species (bottom panel) in each treatment in years 2005, 2007 and 2008. Treatments are

indicated by symbols: control (circle), cut stump (inverted triangle) and whole plant

removal (square). Sampling in year 2005 occurred before the treatments were

implemented (pre-treatment), treatments were completed in 2006, and post treatment
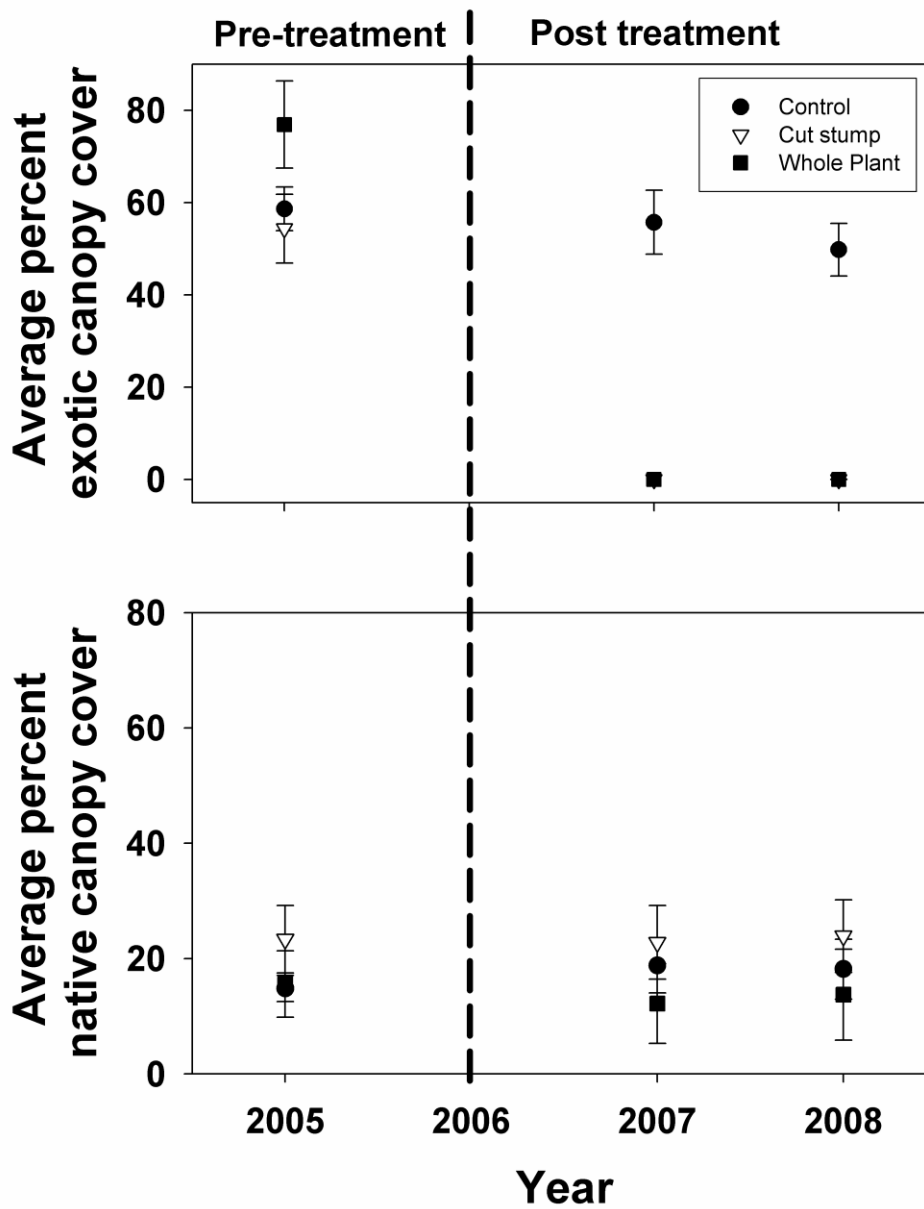
sampling occurred in 2007 and 2008.
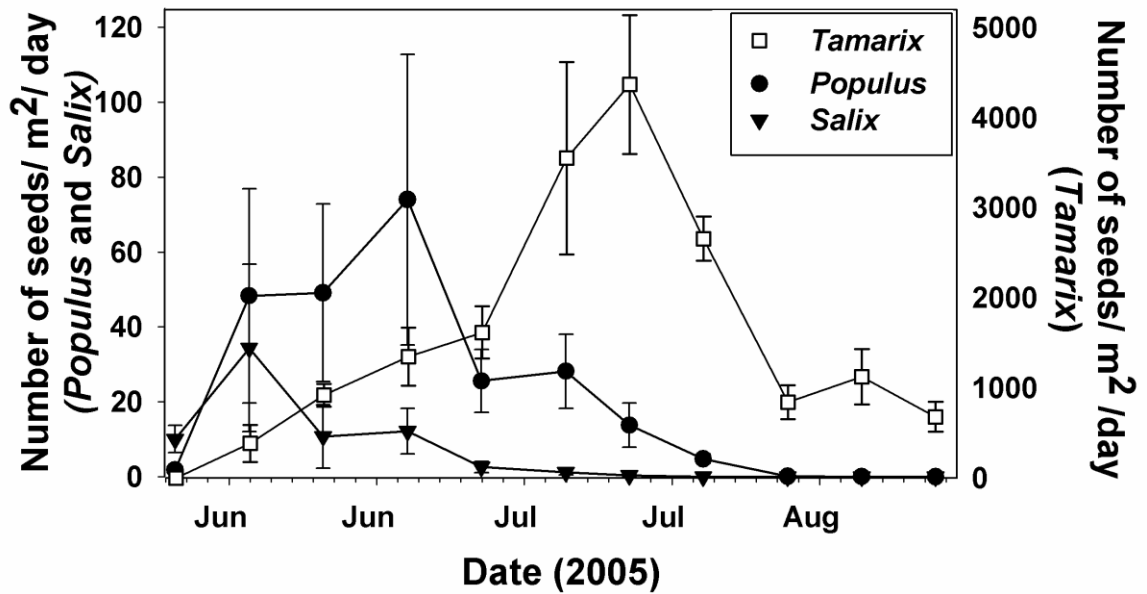
Figure 4.5 The average number of aerially dispersed *Tamarix* (open squares), *Populus* (circles), and *Salix* (inverted triangles) seeds per m^2 per day (± SE) across all pre-treatment sites in Canyon de Chelly during summer of 2005.

Figure 4.6 Top panel: the average number of aerially dispersed *Tamarix* seeds per m^2 per day (± SE) during summer of 2006 in whole plant removal treatments (solid circles), cut stump removal treatments (open circles) and control treatments (inverted triangles).
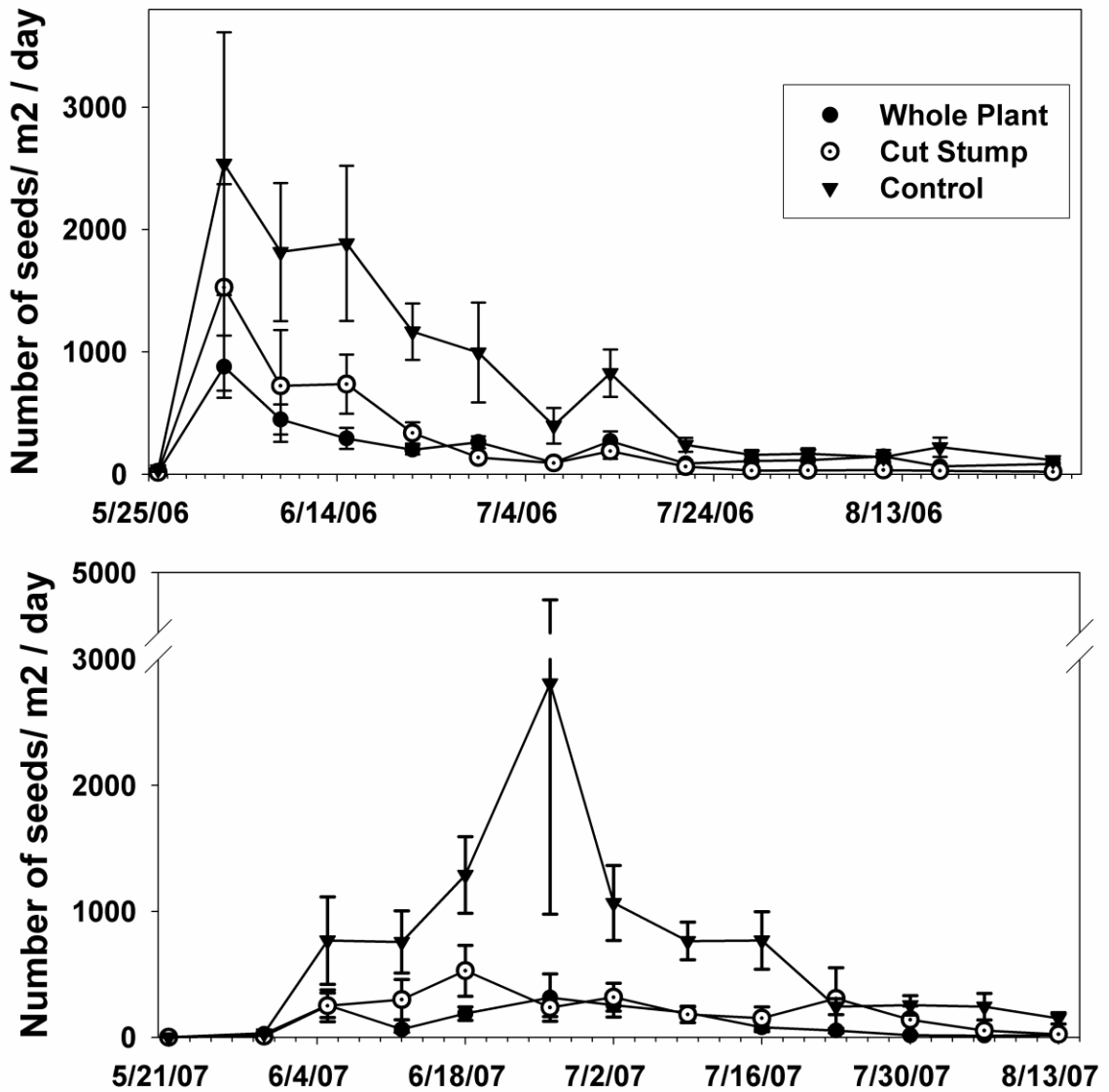
Bottom panel: the average number of aerially dispersed *Tamarix* seeds per m^2 per day (± SE) during summer of 2007 in whole plant removal treatments (solid circles), cut stump removal treatments (open circles) and control treatments (inverted triangles).

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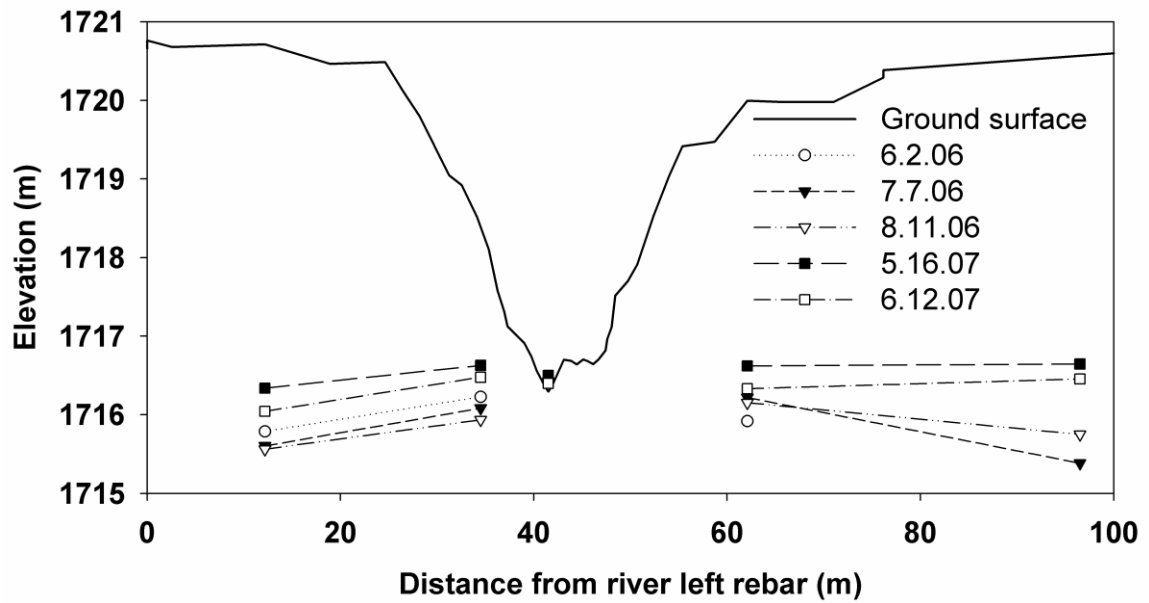
Figure 4.7 Ground water and river stage in the Lower White House Control plot between June 2006 and June 2007. The ground surface channel cross section is indicated by the bold line. Ground water elevations (m) relative to the ground surface elevation are indicated by symbols and hatched lines.
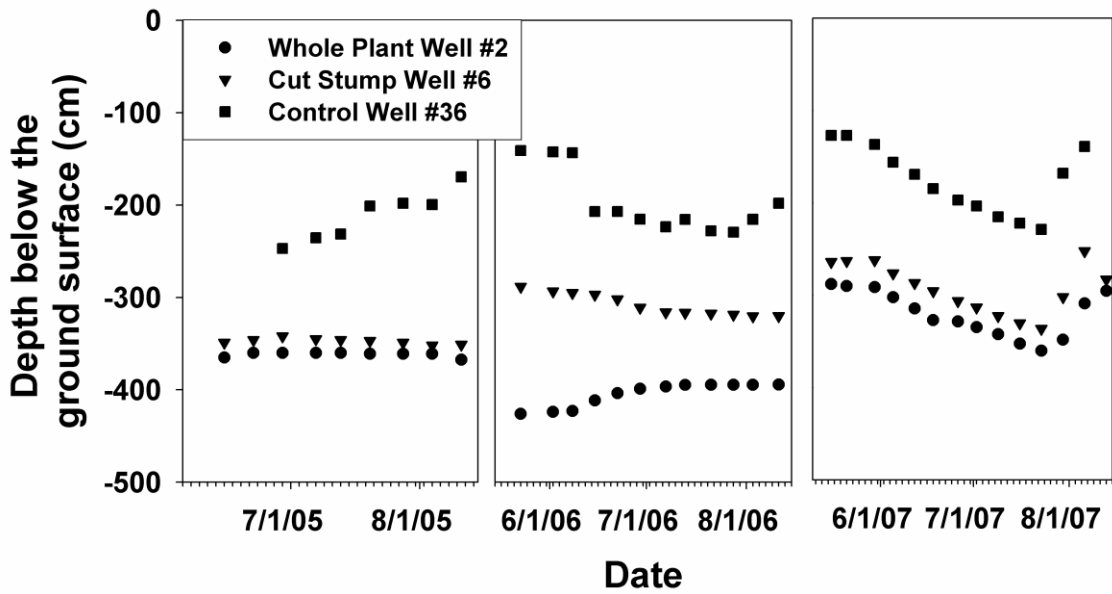
Figure 4.8 Ground water levels (depth below the ground surface, cm) between June 1, 2005 and August 15, 2007 at 3 wells in the Lower White House site: Well #2 (whole plant treatment, circles), Well #6 (cut stump treatment, inverted triangles), and Well #36 (control treatment, squares).
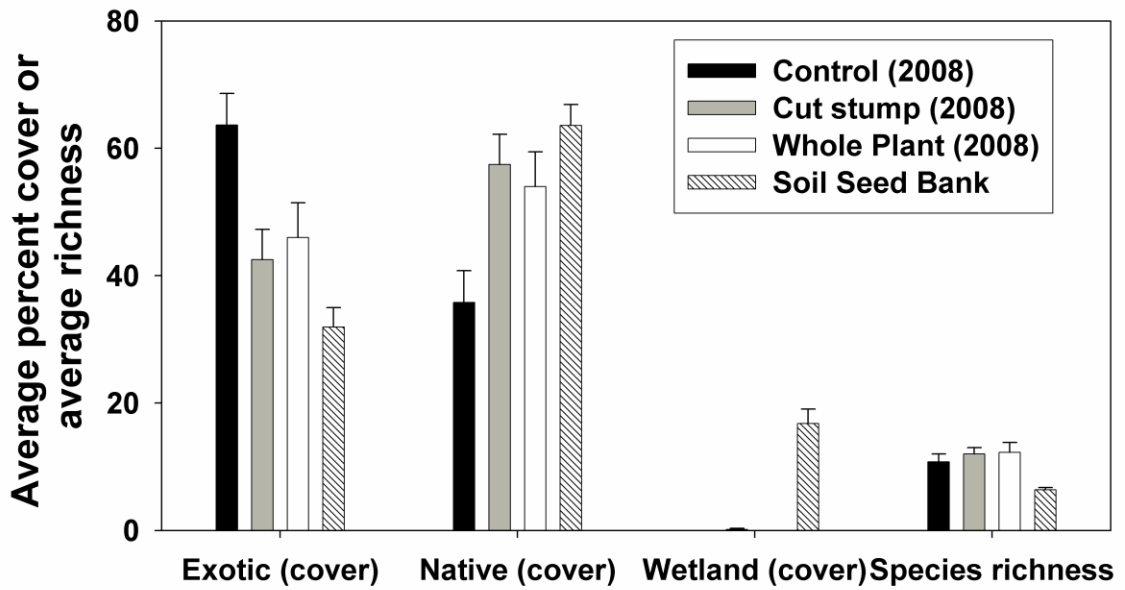
Figure 4.9 Average percent cover or average species richness of exotic species, native species, wetland species and total species richness for herbaceous vegetation in 2008 in removal treatments and soil seed bank: control (black), cut stump (gray), whole plant removal (white), and soil seed bank (hatched).
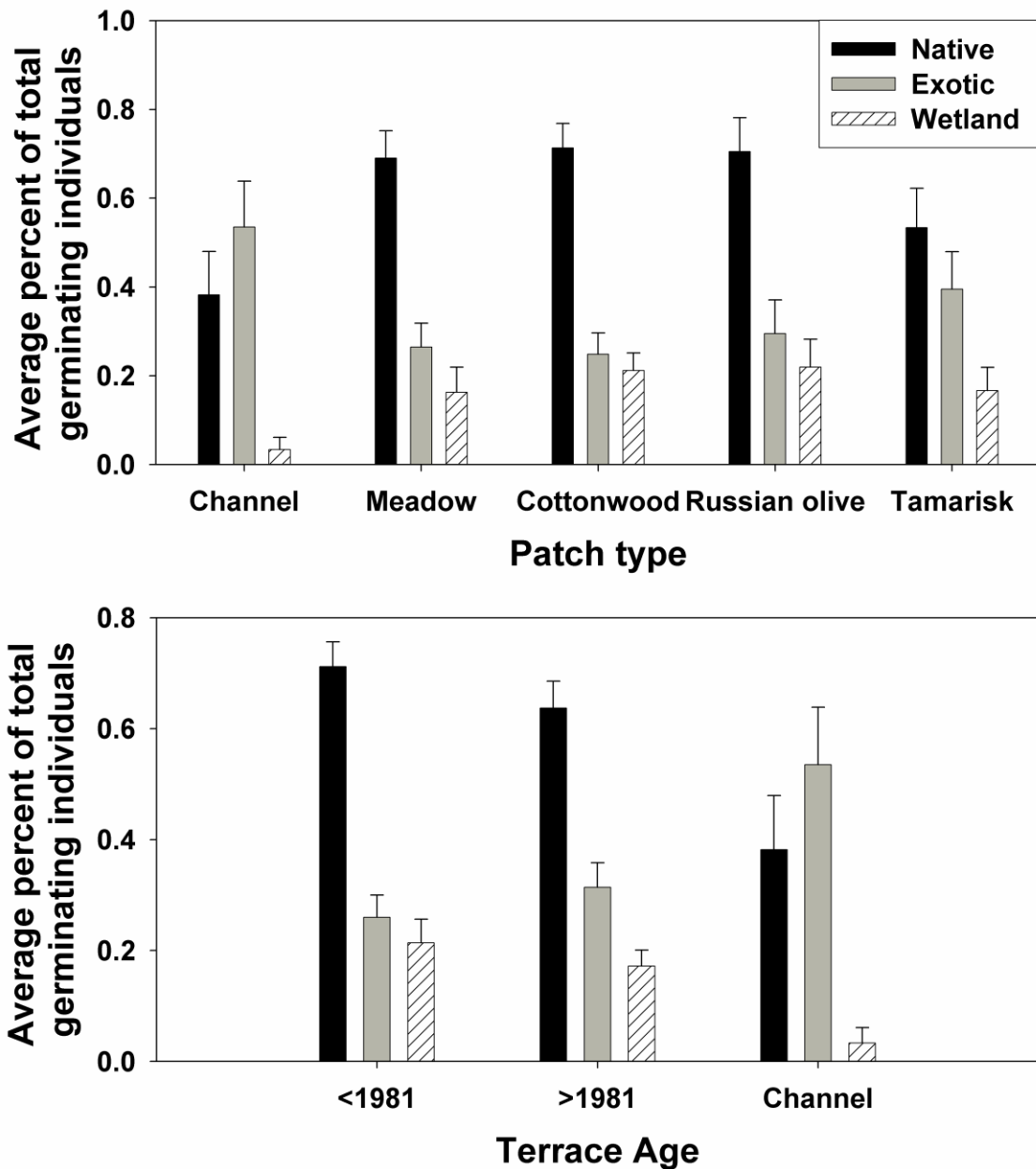
Figure 4.10 Average percent of total number of germinating individuals that were native species (black), exotic species (gray) and wetland species (hatched) in the soil seed bank samples of different patch types (top panel) and on terraces of different ages (bottom panel).
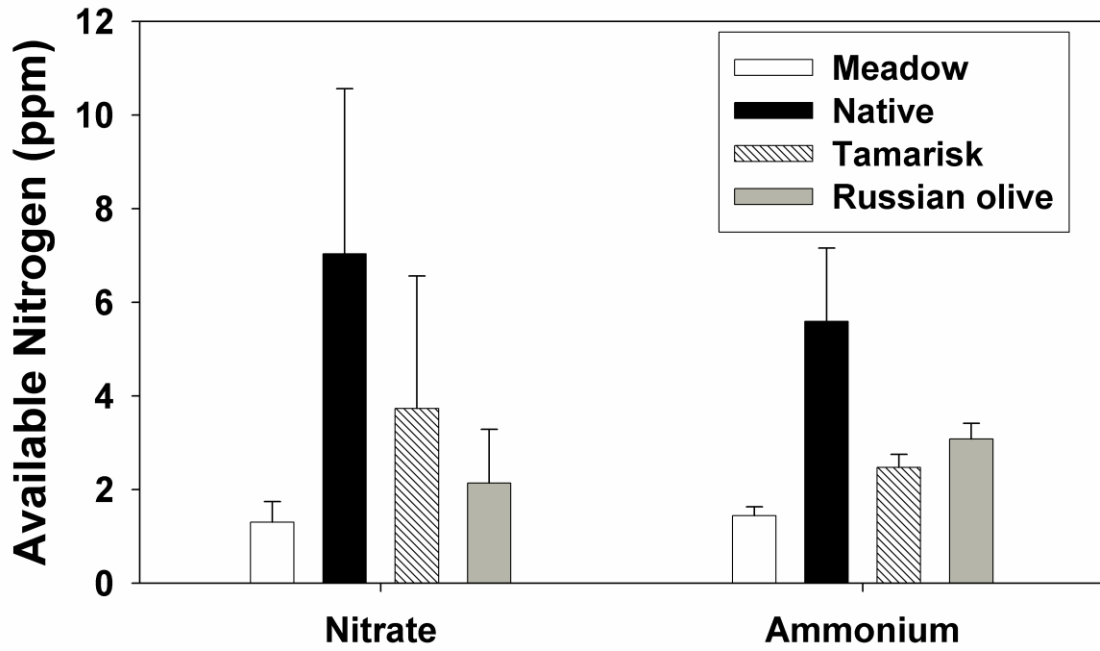
Figure 4.11 Available nitrate and ammonium (ppm) ± SE in different plant communities

(meadow, native riparian trees, tamarisk, and Russian olive) in 2005.
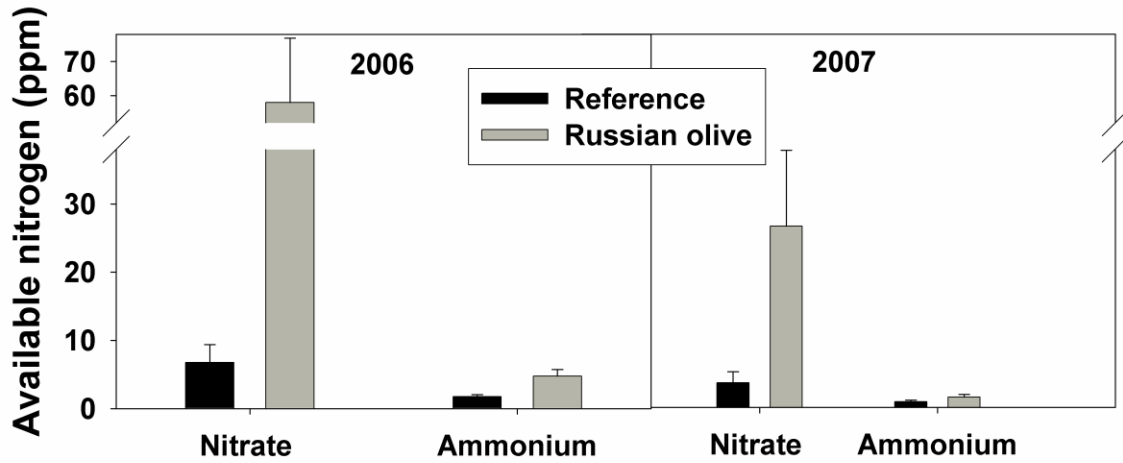
Figure 4.12 Available nitrate and ammonium (ppm) ± SE next to Russian olive stumps (gray bars) and in reference soils without Russian olive roots (black bars) in 2006 (left panel) and 2007 (right panel).
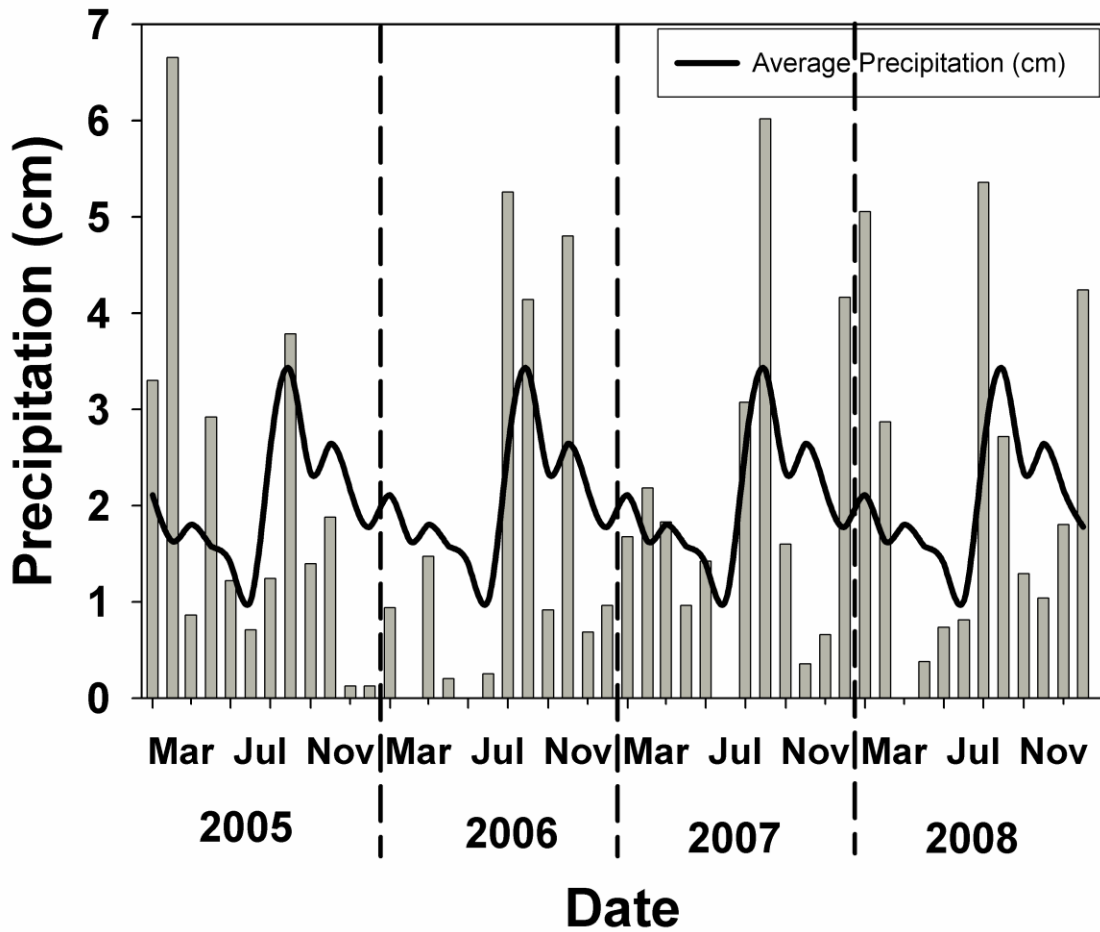
Figure 4.13 Total monthly precipitation (cm) in Chinle, AZ from January 2005 through

December 2008 (gray bars) and average monthly precipitation (cm) for Chinle, AZ for

the period of record 1970-2009 (black line). Precipitation data from the US National

Weather Service, Western Regional Climate Center

(http://www.wrcc.dri.edu/index.html).

5   SYNTHESIS

5.1   CONCLUSIONS

This research examined the patterns, processes, and mechanisms of exotic riparian plant invasion into Canyon de Chelly National Monument and across the southwestern U.S. I studied invasion in the context of three broad subjects: the history of invasion, niche space and invasion facilitation, and how exotic plant removal methods influence future vegetation. My findings are applicable to both ecological theory and land management. These results aid the understanding of how tamarisk and Russian olive have successfully colonized southwestern floodplains, through both climatic and geomorphic drivers. I have addressed current debates in invasion ecology regarding invasion facilitation and niche space, described Russian olive ecology in more detail than has been previously attempted and highlighted the ongoing threat of Russian olive invasion into southwestern riparian habitats. Finally, my research shows that both cut-stump and whole plant removal methods are effective treatments for tamarisk and Russian olive to restore native riparian plant communities.

Results from my study on the history of invasion into Canyon de Chelly suggest that peak Russian olive establishment occurred from 1985-87, which corresponded to above-average monsoon storm precipitation, total precipitation, and high stream flow. However, our best model explained only 12% of variation in plant establishment, suggesting that many other, unmeasured factors influenced Russian olive establishment. In addition, tamarisk establishment was not related to any of the precipitation drivers tested in my models. Although plantings and river regulation by dams probably played a role in tamarisk and Russian olive invasion, my results suggest these species required

hydroclimatic drivers and natural stream bed adjustments for wide-spread establishment. Invasion depended on a sequence of years with above-average precipitation in combination with stream incision that left established plants safe from subsequent flooding.

Controlled experiments and field surveys in my second research study demonstrated that Russian olive has a broader niche than cottonwood and tamarisk. Russian olive appears to be exploiting empty niches among woody riparian vegetation in southwestern ecosystems. It can persist along wide gradients of water and light availability, and its broad habitat tolerances will likely lead to its population increase. As the Russian olive population expands across the western US, it will create shaded habitat where tamarisk and cottonwood cannot establish, potentially leading to their population decline. Although Russian olive invasion is not limited by light availability or the presence of a shallow riparian water table, it appears to be limited by seed dispersal. In further study of niche space in southwestern riparian ecosystems, Russian olive should be planted in xeric habitats to test its niche limitations. Also, more studies should investigate seed dispersal limitations of Russian olive invasion.

In my study of ecosystem response to tamarisk and Russian olive removal, I found that both cut-stump and whole plant removals similarly reduce exotic species cover and increase native species cover after two years. Both removal methods also reduce aerial seed rain inputs of tamarisk seeds, cut-stump removals can increase available nitrogen near dead Russian olive boles within two years of removal, and both treatments seem to have no effect on ground water levels. Although whole-plant removal of exotic woody species provides thorough removal, it is costly in terms of time and money and

our results indicate that it does not provide more benefit to riparian vegetation than cut-stump with herbicide removal methods.

Based on my study of the soil seed bank in Canyon de Chelly, there is great potential for native species and wetland species colonization of these sites from the seed bank. However, most of these sites, although they are riparian, are rarely flooded because the stream channel in Canyon de Chelly has incised 2-4 meters below the adjacent floodplain. Channel incision in the late 1980s left the former floodplains in my study sites abandoned by the stream channel. With the removal of tamarisk and Russian olive, these sites are transitioning to xeric grasslands. Further study in our xeric sites should include active revegetation, where native seeds are added to removal sites, with possible water additions to increase native species cover. Exotic grasses dominated the vegetation in our sites, but native seed additions in removal sites may increase native vegetation cover. Our study did not address grazing impacts in Canyon de Chelly, but there is active cattle, horse and sheep grazing occurring throughout the canyon, which may have a negative impact on native vegetation.

In a concurrent study, Jaeger found that whole plant removal treatments caused greater geomorphic change in the study sites, in the form of channel widening (Jaeger 2009). Therefore, if management goals include returning the channel to a more dynamic, braided channel, whole plant removal may facilitate that process. Managers must weigh the costs and benefits of both methods of removal before proceeding.

The biological control agent tamarisk leaf-eating beetle (*Diorhabda elongata*) has recently been introduced to control tamarisk in Utah and Nevada (Dennison et al. 2009). This beetle has caused widespread damage to large stands of tamarisk in the Moab area

and along the Virgin River in Nevada. Research is in progress to monitor the ecosystem

and landscape-scale effect of these beetles on riparian areas in the west. These beetles

will likely reach Canyon de Chelly within the next ten years and it will be important for

land managers to consider the impact of these beetles. If the beetles can successfully kill

stands of tamarisk in Canyon de Chelly, the dead standing biomass that is left may cause

a significant fire threat. Stands of riparian trees that include dead tamarisk and live

Russian olive may also provide opportunities for more Russian olive invasion as

competition for soil nutrients and water is decreased following beetle kill.

The implications of my research findings should be used in combination with

findings from concurrent geomorphic research in Canyon de Chelly (Cadol 2007, Jaeger

2009) and with perspective on local issues such as grazing, revegetation, possible

tamarisk beetle invasion, and fire management to guide future management goals.

5.2   MANAGEMENT IMPLICATIONS

- Tamarisk and Russian olive require hydroclimatic triggers for establishment. Our

    results indicate that invasion depended on a sequence of years with above-average

    precipitation. Multiple years of above-average precipitation likely led to flooding

    conditions that facilitated Russian olive and tamarisk establishment. High

    precipitation years that lead to large floods along rivers are essential for large

    pulses of tamarisk and Russian olive invasion. Riparian managers should take

    action when flooding exceeds average levels for more than two years in a row and

    remove areas of tamarisk and Russian olive seedlings that establish in the

    available habitat. These flooding conditions will likely be favorable for native

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cottonwood and willow trees as well, thus careful attention to avoid damaging native plants will also be needed.

- Russian olive can establish in drier and shadier habitat than native cottonwood or tamarisk and can invade beneath established cottonwood and tamarisk canopies. Also, Russian olive can establish in response to heavy precipitation events on abandoned floodplains that are disconnected from the riparian water table. Shaded and un-flooded habitats represent areas where Russian olive can establish but cottonwood and tamarisk cannot. These results indicate that large areas of potential Russian olive habitat exist along western rivers. Invasion of Russian olive is only limited by seed dispersal, therefore managers should concentrate control efforts in existing stands of tamarisk and also diligently check unflooded, shaded habitats for Russian olive colonization, even though these habitats are not traditionally thought to be invasible by riparian plants.

- Managers in Canyon de Chelly should continue with cut-stump removal of tamarisk and Russian olive as it has proven to be effective in reducing exotic vegetation and increasing native vegetation cover. Managers should continue monitoring vegetation in removal sites to track long-term vegetation change and pursue further management actions to facilitate native vegetation establishment such as native seed additions and grazing exclosures.

5.3   LITERATURE CITED

Cadol, D. D. 2007. Aerial photographic analysis of channel change and riparian vegetation establishment in Canyon de Chelly National Monument, Arizona, 1935-2004. Master's. Colorado State University, Fort Collins.

Dennison, P. E., P. L. Nagler, K. R. Hultine, E. P. Glenn, and J. R. Ehleringer. 2009. Remote monitoring of tamarisk defoliation and evapotranspiration following saltcedar leaf beetle attack. Remote Sensing of Environment **113**:1462-1472.

Jaeger, K. 2009. Channel dynamics in Canyon de Chelly National Monument, AZ, with emphasis on the effect of invasive plants. Dissertation. Colorado State University, Fort Collins.

APPENDIX A.

SPECIES LISTS FOR VEGETATION AND SOIL SEED BANK SURVEYS IN

CANYON DE CHELLY NATIONAL MONUMENT

Table A.1 Herbaceous plant species in vegetation survey plots 2005-2008. Native status is indicated by an E (exotic) or N (native). Wetland species as defined by USDA PLANTS Database as obligate wetland species in Region 7, which includes the study area, are indicated with a W (USDA 2009).

Species	Native Status	Wetland Status
Achillea millefolium L., common yarrow	N	
Acroptilon repens L., hardheads	E	
Agropyron smithii (Rydb.), western wheatgrass	N	
Agropyron trachycaulum (Link), slender wheatgrass	N	
Alyssum simplex Rudolphi, alyssum	E	
Amaranthus blitoides S. Watson, mat amaranth	E	
Amaranthus retroflexus L., redroot amaranth	N	
Ambrosia acanthicarpa Hook, flatspine burr ragweed	N	
Ambrosia artemisiifolia L., annual ragweed	N	
Artemisia dracunculoides(DC.) Nutt, tarragon	N	
Artemisia filifolia Torr., sand sagebrush	N	
Artemisia ludoviciana Nutt., white sagebrush	N	
Artemisia tridentata Nutt., big sagebrush	N	
Bouteloua barbata Lag., sixweeks grama	N	
Bouteloua gracilis (Willd. Ex Kunth) Lag. ex Griffiths, blue grama	N	
Brickellia californica (Torr. & A. Gray) A. Gray, california brickellbush	N	
Brickellia grandiflora (Hook.) Nutt., tasselflower brickellbush	N	

Bromus racemosus L., bald brome	E	
Bromus rigidus Roth, ripgut brome	E	
Bromus tectorum L., cheatgrass	E	
Capsella bursa-pastoris (L.) Medik., shepherd's purse	E	
Carduus nutans L., musk thistle, nodding plumeless thistle	E	
Carex spp.	N	W
Cenchrus longispinus (Hack.) Fernald, mat sandbur	N	
Centaurea diffusa Lam., white knapweed	E	
Chamaesyce maculata L. Small, spotted sandmat	N	
Chenopodium album L., lambsquarters	N	
Chrysothamnus viscidiflorus (Hook.) Nutt., yellow rabbitbrush	N	
Clematis ligusticifolia Nutt., western white clematis	N	
Cleome serrulata Pursh, rocky mountain beeplant	N	
Convolvulus arvensis L., field bindweed	E	
Conyza canadensis (L.) Cronquist, Canadian horseweed	N	
Croton texensis (Klotzsch) Müll. Arg., Texas croton	N	
Dalea candida Michx. ex Willd., white prairie clover	N	
Datura wrightii Regel, sacred thorn-apple	N	
Descurainia pinnata (Walter) Britton, western tansymustard	N	
Distichlis spicata (L.) Greene, inland saltgrass	N	
Draba cuneifolia Nutt. ex Torr. & A. Gray, wedgeleaf draba	N	
Eleocharis palustris (L.) Roem. & Schult., common spikerush	N	W
Elymus canadensis L., Canada wildrye	N	

Equisetum laevigatum A. Braun, smooth horsetail N

Erigeron speciosus (Lindl.) DC., aspen fleabane N

Erodium cicutarium (L.) L'Hér. ex Aiton, redstem stork's bill E

Galium wrightii A. Gray, wright`s bedstraw N

Gutierrezia sarothrae (Pursh) Britton & Rusby, broom snakeweed N

Halogeton glomeratus (M. Bieb.) C.A. Mey., saltlover E

Helianthus annuus L., common sunflower N

Heterotheca villosa (Pursh) Shinners, hairy false goldenaster N

Hordeum murinum L., mouse barley E

Ipomopsis aggregata (Pursh) V.E. Grant, scarlet gilia N

Ipomopsis longiflora (Torr.) V.E. Grant, flaxflowered ipomopsis N

Juncus articulatus Willd., jointleaf rush N W

Juncus bufonius L., toad rush N W

Kochia scoparia (L.) A.J. Scott, Mexican-fireweed E

Lactuca serriola L., prickly lettuce E

Marrubium vulgare L., horehound E

Medicago lupulina L., black medick E

Medicago sativa L., alfalfa E

Melilotus albus Medik., white sweetclover E

Melilotus officinalis (L.) Lam., yellow sweetclover E

Mirabilis multiflora (Torr.) A. Gray, Colorado four o'clock N

Monroa squarrosa (Nutt.) Torr., false buffalograss N

Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi, N

scratchgrass

Oenothera albicaulis Pursh, whitest evening-primrose	N	
Opuntia polyacantha Haw., plains pricklypear	N	
Opuntia whipplei (Engelm. & Bigelow) F.M. Knuth, whipple cholla	N	
Oryzopsis hymenoides (Roem. & Schult.) Barkworth, indian ricegrass	N	
Panicum dichotomiflorum Michx., fall panicgrass	N	
Phalaris arundinacea L., reed canarygrass	N	W
Phragmites australis (Cav.) Trin. ex Steud., common reed	N	
Physalis hederifolia A. Gray, ivyleaf groundcherry	N	
Physalis longifolia Nutt., longleaf groundcherry	N	
Plantago major L., common plantain	E	
Plantago patagonica Jacq., woolly plantain	N	
Pleuraphis jamesii Torr., James' galleta	N	
Poa pratensis L., kentucky bluegrass	N	
Polygonum aviculare L., prostrate knotweed	E	
Portulaca oleracea L., little hogweed	E	
Ranunculus cymbalaria Pursh, alkali buttercup	N	W
Salsola iberica L., prickly Russian thistle	E	
Senecio douglasii (Hook. & Grev.) Spring, douglas' ragwort	N	
Senecio flaccidus Less., threadleaf ragwort	N	
Senecio spartioides Torr. & A. Gray, broomlike ragwort	N	
Sisymbrium altissimum L., tall tumblemustard	E	

Solanum elaeagnifolium Cav., silverleaf nightshade N

Solidago velutina DC., threenerve goldenrod N

Sphaeralcea coccinea (Nutt.) Rydb., scarlet globemallow N

Sporobolus airoides (Torr.) Torr., alkali sacaton N

Sporobolus cryptandrus (Torr.) A. Gray, sand dropseed N

Taraxacum officinale F.H. Wigg., common dandelion N

Thelesperma megapotamicum (Spreng.) Kuntze,

   Hopi tea greenthread N

Thlaspi arvense L., field pennycress E

Townsendia incana Nutt., hoary townsend daisy N

Tradescantia occidentalis (Britton) Smyth, prairie spiderwort N

Tragopogon dubius Scop., yellow salsify E

Tribulus terrestris L., puncturevine E

Urtica dioica L., stinging nettle N

Verbena bracteata Cav. ex Lag. & Rodr., bigbract verbena N

Vulpia octoflora (Walter) Rydb., sixweeks fescue N

Xanthium strumarium L., rough cockleburr N

Table A.2 Woody plant species in vegetation survey plots 2005-2008. Native status is indicated by an E (exotic) or N (native).

Species	Native status
Acer negundo L., boxelder	N
Elaeagnus angustifolia L., Russian olive	E
Forestiera neomexicana A. Gray, stretchberry	N
Juglans major (Torr.) A. Heller, Arizona walnut	N
Juniperus utahensis (Torr.) Little, Utah juniper	N
Pinus edulis Engelm., two needle pinyon	N
Populus x acuminata Rydb. (pro sp.) [*angustifolia* × *deltoides*], lanceleaf cottonwood	N
Populus fremontii S. Watson, Fremont cottonwood	N
Salix amygdaloides Andersson, peachleaf willow	N
Salix exigua Nutt., narrowleaf willow	N
Salix gooddingii C.R. Ball, Goodding`s willow	N
Salix lucida Muhl., shining willow	N
Tamarix ramosissima Ledebour, *T. chinensis* Loureiro, and hybrids, saltcedar	E
Ulmus pumila L., Siberian elm	E

Table A.3 Species list from soil seed bank study 2007. Native status is indicated by an E (exotic) or N (native). Wetland species as defined by USDA PLANTS Database as obligate wetland species in region 7, which includes the study area, are indicated with a W (USDA 2009).

Species	Native Status	Wetland Status
Acer negundo L., boxelder	N	
Agrostis scabra Willd., rough bentgrass	N	
Amaranth blitoides S. Watson, mat amaranth	E	
Amaranth retroflexus L., redroot amaranth	N	
Ambrosia acanthacarpa Hook, flatspine burr ragweed	N	
Anaphalis margaritacea (L.) Benth., western pearly everlasting	N	
Anemopsis californica (Nutt.) Hook. & Arn., yerba mansa	N	W
Artemesia ludoviciana Nutt., white sagebrush	N	
Astragalus nuttallianus DC., smallflowered milkvetch	N	
Bouteloua barbata Lag., sixweeks grama	N	
Bromus rigidus Roth, ripgut brome	E	
Bromus tectorum L., cheatgrass	E	
Cardus nuutans L., musk thistle, nodding plumeless thistle	E	
Celtis laevigata Willd., sugarberry	N	
Cenchrus longispinus (Hack.) Fernald, mat sandbur	N	
Chamaesyce maculata (L.) Small, spotted sandmat	N	
Clematis ligusticifolia Nutt., western white clematis	N	

Conyza canadensis (L.) Cronquist, Canadian horseweed	N	
Descurainia pinnata (Walter) Britton, western tansymustard	N	
Draba cuneifolia Nutt. ex Torr. & A. Gray, wedgeleaf draba	N	
Elaeagnus angustifolia L., Russian olive	E	
Eleocharis palustris (L.) Roem. & Schult., common spikerush	N	W
Elymus trachycaulus (Link), slender wheatgrass	N	
Epilobium ciliatum Raf., fringed willowherb	N	
Eragrostis cilianensis (All.) Vign. ex Janchen, stinkgrass	E	
Eragrostis pectinacea (Michx.) Nees ex Steud., tufted lovegrass	N	
Eragrostis pilosa (L.) P. Beauv., Indian lovegrass	N	
Erigeron colomexicanus A. Nelson, running fleabane	N	
Erigeron pumilus Nutt., shaggy fleabane	N	
Erigeron speciosus (Lindl.) DC., aspen fleabane	N	
Erodium cicutarium (L.) L'Hér. ex Aiton, redstem stork's bill	E	
Gutierrezia sarothrae (Pursh) Britton & Rusby, broom snakeweed	N	
Halogeton glomeratus (M. Bieb.) C.A. Mey., saltlover	E	
Helianthus annuus L., common sunflower	N	
Heterotheca villosa (Pursh) Shinners, hairy false goldenaster	N	
Hordium murinum L., mouse barley	E	
Ipomopsis aggregata (Pursh) V.E. Grant, scarlet gilia	N	

Ipomopsis longiflora (Torr.) V.E. Grant,

    flaxflowered ipomopsis   N

Juncus articulatus Willd., jointleaf rush   N   W

Juncus bufonius L., toad rush   N   W

Juncus confusus Coville, Colorado rush   N   W

Juncus ensifolius Wikstr. var. *montanus*

    (Engelm.) C.L. Hitchc.*,* Rocky mountain rush   N   W

Juncus mexicanus Willd. ex Schult. & Schult. f.,

    Mexican rush   N   W

Juncus saximontanus A. Nelson, Rocky Mountain rush   N   W

Kochia scoparia (L.) A.J. Scott, Mexican-fireweed   E

Lepidium densiflorum Schrad., common pepperweed   N

Lupinus brevicaulis S. Watson, shortstem lupine   N

Medicago lupulina L., black medick   E

Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi,

    scratchgrass   N

Muhlenbergia richardsonis (Trin.) Rydb., mat muhly   N

Munroa squarrosa (Nutt.) Torr., false buffalograss   N

Oenothera albicaulis Pursh, whitest evening-primrose   N

Opuntia whipplei (Engelm. & Bigelow) F.M. Knuth,

    whipple cholla   N

Panicum capillare L., witchgrass   N

Phalaris arundinacea L., reed canarygrass   N   W

Physalis crassifolia Benth., yellow nightshade groundcherry N

Physalis hederifolia A. Gray, ivyleaf groundcherry N

Plantago major L., common plantain E

Plantago patagonica Jacq., woolly plantain N

Poa annua L., annual bluegrass E

Poa canbyi (Scribn.) Howell N

Poa compressa L., Canada bluegrass E

Polypogon monspeliensis (L.) Desf., annual rabbits foot

grass E

Populus fremontii S. Watson, Fremont cottonwood N

Portulaca oleracea L., little hogweed E

Ranunculus cymbalaria Pursh, alkali buttercup N W

Salix spp. N

Salsola collina Pall., slender Russian thistle E

Salsola iberica L., prickly Russian thistle E

Scirpus spp. N W

Senecio douglasii (Hook. & Grev.) Spring,

   Douglas' ragwort N

Senecio spartoidies Torr. & A. Gray, broomlike ragwort N

Spergularia salina J. Presl & C. Presl, salt sandspurry N W

Sporabolus cryptandrous (Torr.) A. Gray, sand dropseed N

Tamarix ramosissima Ledebour, *T. chinensis* Loureiro,

   and hybrids, saltcedar E

Taraxacum officinale F.H. Wigg., common dandelion   N

Tribulus terrestris L., puncturevine   E

Verbena bracteata Cav. ex Lag. & Rodr., bigbract verbena   N

Veronica anagallis-aquatica L., water speedwell   N   W

Vulpia octiflora (Walter) Rydb., sixweeks fescue   N