

Environmental tolerance of an invasive riparian tree and its potential for continued spread in the southwestern US

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Abstract

Questions: Exotic plant invasion may be aided by facilitation and broad tolerance of environmental conditions, yet these processes are poorly understood in species-rich ecosystems such as riparian zones. In the southwestern United States (US) two plant species have invaded riparian zones: tamarisk (*Tamarix ramosissima*, *T. chinensis*, and their hybrids) and Russian olive (*Elaeagnus angustifolia*). We addressed the following questions: (1) is Russian olive able to tolerate drier and shadier conditions than cottonwood and tamarisk? (2) Can tamarisk and cottonwood facilitate Russian olive invasion?

Location: Arid riparian zones, southwestern US.

Methods: We analyzed riparian tree seedling requirements in a controlled experiment, performed empirical field studies, and analyzed stable oxygen isotopes to determine the water sources used by Russian olive.

Results: Russian olive survival was significantly higher in dense shade and low moisture conditions than tamarisk and cottonwood. Field observations indicated Russian olive established where flooding cannot occur, and under dense canopies of tamarisk, cottonwood, and Russian olive. Tamarisk and native riparian plant species seedlings cannot establish in these dry, shaded habitats. Russian olive can rely on upper soil water until 15 years of age, before utilizing groundwater.

Conclusions: We demonstrate that even though there is little evidence of facilitation by cottonwood and tamarisk, Russian olive is able to tolerate dense shade and low moisture conditions better than tamarisk and cottonwood. There is great potential for continued spread of Russian olive throughout the southwestern US because large areas of suitable

habitat exist that are not yet inhabited by this species.

Keywords: Exotic plant species; Floodplains; Invasion; Invasive species; Russian olive.

Nomenclature: USDA, NCRS (2010).

Introduction

Exotic invasive species are organisms that expand or are introduced into new ranges and undergo dramatic population growth (Elton 1958). 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 the 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 & O'Dowd 2009). Invasions may also occur when species exploit unused resources, such as shaded habitat in an ecosystem where few species are shade-tolerant (Davis et al. 2000; Tilman 2004; Fridley 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 zones, characterized by periodic flooding, support diverse habitat types and contribute significantly to regional biodiversity (Naiman et al. 1993; Naiman & Decamps 1997; Sabo et al. 2005). In the western United States (US), riparian zones cover <1% of the land area but support up to 80% of breeding bird species (Knopf et al. 1988). Flooding regimes tend to create a disturbance gradient from the river to the adjacent riparian zone. Lower surfaces close to the channel are more frequently flooded than sites at higher elevations and greater distances from the channel (Leopold et al. 1964). Flood disturbances also create opportunities for exotic plant invasions into riparian zones, which have experienced unusually high levels of invasion relative to other habitats worldwide (Stohlgren et al. 1998; Hood & Naiman 2000).

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The two dominant riparian invaders in the southwestern US are the woody species tamarisk (*Tamarix ramosissima* Ledebour, *T. chinensis* Lour-eiro, and their hybrids) and Russian olive (*Elaeagnus angustifolia* L.) (Friedman et al. 2005). Tamarisk was introduced to 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 yr (Friedman et al. 2005). Historically, southwestern riparian zones 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 & 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 & Shafroth 2003). Also, mature tamarisk and Russian olive plants may tolerate long periods without available groundwater, while cottonwood trees cannot (Brotherson & Winkel 1986; Katz & Shafroth 2003).

The establishment requirements of Russian olive seedlings remain poorly understood, yet are essential to its invasion success (Katz & Shafroth 2003). Russian olive trees have been observed growing in densely shaded areas above the limits of flooding where cottonwood and tamarisk cannot establish (Katz et al. 2005). Two small-scale experiments showed Russian olive to be more shade-tolerant and less flood-dependent than native riparian trees (Shafroth et al. 1995; Katz et al. 2001). Shaded and unflooded riparian habitats may represent suitable habitat for Russian olive, while few native species can exploit these harsh conditions (Katz et al. 2005; DeWine & Cooper 2009).

Most studies of riparian tree establishment have included only one spatial scale and limited experimental treatments. Facilitation of invasive riparian trees by native species has been suggested by observational studies, but never tested experimentally, and the importance of facilitation to the success of invasive riparian species on a regional scale remains unknown (Lesica & Miles 1999, 2004). The current state of research leaves many questions regarding the limits to Russian olive invasion (Friedman et al. 2005). Tamarisk invasion in the southwestern US may be slowing because it has filled most suitable riparian habitats (Friedman et al. 2005). In contrast to tamarisk, an abundance of suitable habitats for Russian olive may exist in these mature riparian stands.

We tested mechanisms and water requirements for tamarisk, cottonwood, and Russian olive seed-

lings that could drive Russian olive invasion in southwestern riparian ecosystems by addressing two questions: (1) is Russian olive able to tolerate drier and shadier conditions than cottonwood and tamarisk, enabling it to grow in places the other two species cannot? (2) can cottonwood and tamarisk facilitate Russian olive invasion by providing shaded habitat? We used controlled light experiments and field studies to identify habitats in which each species can establish.

Methods

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 US National Hydrologic Unit System (http://nationalatlas.gov/articles/water/a_hydrologic.html, Fig. 1). See *Regional Sampling* section below for details on sample site selection. 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 (Fig. 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 average of 23 cm of precipitation per year, largely from late summer monsoon storms (Arizona Climate Summaries, Western Regional Climate Center 2009, <http://www.wrcc.dri.edu/index.html>). 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 (Ely et al. 1993).

During the years 1934-1937, the US Soil Conservation Service planted tamarisk and Russian olive in Canyon de Chelly to protect ancient Puebloan ruins and modern farms from riverbank 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 two tributary canyon

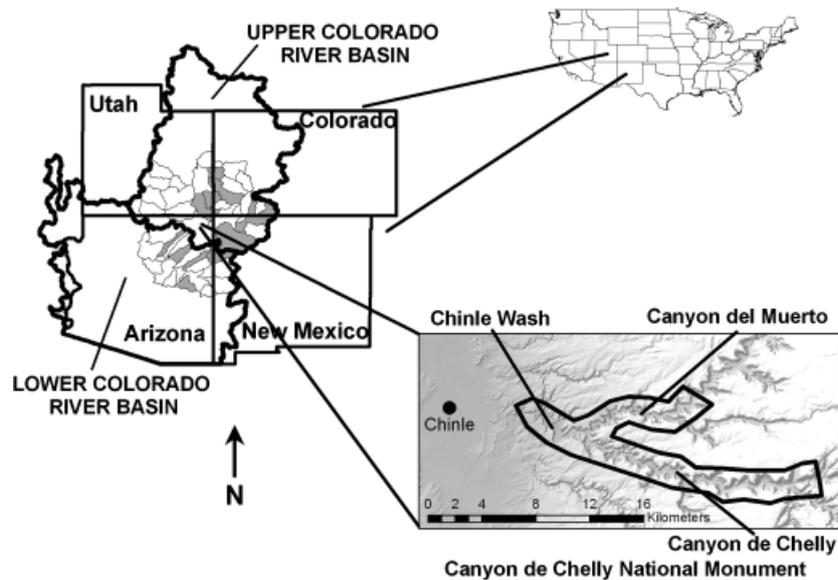


Fig. 1. Maps of Canyon de Chelly National Monument (lower right panel) and regional sampling area (upper left panel). The bold line denotes Canyon de Chelly study area, and its location on the regional map is identified with a cross. Our regional sampling area included 42 Colorado River sub-basin units depicted by small basin outlines. We randomly selected 11 sub-basins (gray-filled) for study.

streams have become incised to 1-8-m deep over the last 50 yr (Rink 2003; Cadol 2007).

Seedling survival experiment

We compared tamarisk, Russian olive, and cottonwood seedling survival using a split-split plot design experiment. Seeds were collected in May and June 2007 from five different parent trees for each species. Each parent tree was at least 1 km from each other parent tree. Tamarisk and cottonwood seeds were collected directly from parent trees as they dispersed in early summer. Russian olive seeds ripen in late summer and require stratification during freezing winter temperatures; therefore, seeds were collected from the 2006 crop that had over-wintered on parent trees and fallen to the ground directly below parent trees. Seeds were germinated on coarse sandy soils under saturated soil conditions, seedlings were grown for 4 weeks and then transplanted individually into 5 cm × 5 cm × 25 cm tall pots filled with soil collected from Chinle Wash. All soils 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 enclosure outside in full sun in Chinle, AZ.

We used four water treatments (shallow water table without rain addition, 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 our experiment. Shade levels were chosen based on previous research showing that tamarisk and cottonwood can survive *in situ* under 0-90% shade (DeWine & 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. 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. Most monsoon rainstorms occur from July through September, and precipitation typically falls in a few hours (Gochis et al. 2006). We applied rain quantities based on average rainfall in Chinle during the monsoon seasons of 1980 through 2006. We 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 3-5% volumetric water

content (VWC) (Kramer & Boyer 1995). Our treatments produced average VWC of $4.53 \pm 0.19\%$ (low rain, ± 1 SE), $4.93 \pm 0.07\%$ (average rain), $5.53 \pm 0.13\%$ (high rain) and $42.67 \pm 0.71\%$ (shallow water table). Ambient rain was measured at our experimental site with a direct-reading rain gauge. During the period of study, approximately 121 mm of ambient rain fell during 13 different precipitation events, averaging 9 ± 3 mm per event. After each precipitation event, the next scheduled water application was skipped or decreased to maintain the water application rates for our treatments. Seedling survival and each plant height (mm) was measured weekly for 10 weeks from July to September 2007.

We 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 our ability to detect a three-way interaction was hindered by excess zeros. Therefore, we 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. We 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.

Seedling transects in Canyon de Chelly

We 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 (Fig. 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 2 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. Elevation (height above the thalweg) was measured at least every 10 m and more often where elevation changed rapidly or slope was greater than zero, for example at channel banks and at edges between floodplain terraces. Distance from the nearest seed source and photosynthetically active radiation (PAR) in $\mu\text{mol m}^{-2}\text{s}^{-1}$ using a Li-Cor 189 was measured for each seedling and also 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 were considered as non-independent. The model adjusted for count data by using a Poisson error structure that excluded the possibility of negative counts, and accounted for non-normal errors and a large number of zeros in the population (Crawley 2007). We fitted random coefficients models with Poisson errors for transect-year combinations of cottonwood and tamarisk, excluding transect-years where no seedlings were found.

Regional sampling

To analyze tamarisk, Russian olive, and cottonwood seedling establishment requirements at a regional scale, we sampled rivers in the region surrounding Canyon de Chelly. We used the US National Hydrologic Unit System to identify 42 sub-basins in the Upper and Lower Colorado River Basins in the Canyon de Chelly region and randomly selected 11 sample sub-basins; sub-basins at high and low elevations outside the known range limits of Russian olive were excluded (Friedman et al. 2005, http://nationalatlas.gov/articles/water/a_hydrologic.html, Fig. 1). Randomly selected sub-basins 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 (Fig. 1).

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 sub-basin. We 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 (1-5 yr old) in one randomly established 1-m² subplot within each vegetation type. The number of 1-m² subplots varied based on the number of plant community types at each site; there were two to five subplots per site. A total of 30 subplots were established across all sites. We estimated percentage canopy cover and PAR of the

overstory in each subplot. We 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.

Russian olive water use

To determine if Russian olive can establish and persist on terraces with deep riparian water tables, we analyzed Russian olive water sources using stable oxygen isotope ratios of xylem water, soil water, and groundwater. 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 8 m above the incised Canyon de Chelly wash. This site was chosen because it included Russian olive of multiple ages persisting at a great height above the riparian water table. 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. We collected three 1-2-kg soil samples from 10-cm to 30-cm deep (upper soil), and four samples from 40-cm to 70-cm deep (lower soil) to represent soil water within 1 m of the surface. Water samples were collected from groundwater monitoring wells near the sample site by bailing the well dry at least three times, and collecting fresh inflowing groundwater. Groundwater at the site is more than 8 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 groundwater samples were determined

by CO₂ equilibration using a VG Microgas Injector (packed column GC) coupled to a VG Optima Stable Isotope Ratio Mass Spectrometer (Isoprime Inc., Manchester, UK). Oxygen isotope ratios of the samples were calculated relative to a standard:

$$\delta^{18}\text{O}(\text{‰}) = \left[\frac{(^{18}\text{O})/(^{16}\text{O})_{\text{sample}}}{(^{18}\text{O})/(^{16}\text{O})_{\text{standard}}} \right] \times 100$$

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

Plant samples were divided into two groups: plants 15 yr and older ($n = 9$) and plants < 15 yr old ($n = 8$). We conducted an analysis of covariance on the oxygen isotope ratios of all plants ($N = 17$) with respect to age and group (≥ 15 yr or < 15 yr). Within group, there was no evident age trend; therefore we conducted t -tests for unequal variance on the oxygen isotope ratios between the two soil layers, groundwater, and the two age groups of plants. We used a Bonferroni adjustment for multiple comparisons ($k = 10$) to determine significance of the t -test P -values. 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).

Results

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 ($F = 25.46$, $P < 0.0001$) (Fig. 2). Survival of Russian

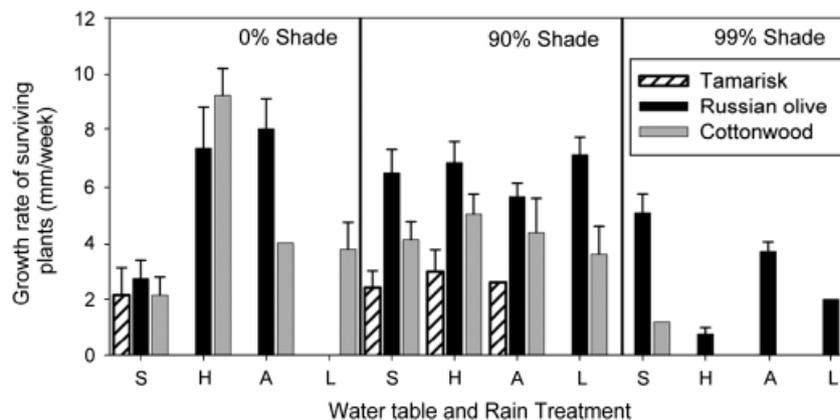


Fig. 2. Growth rate of surviving plants after 10 weeks of shade and water treatments (mm/week \pm SE). Bars without SE indicate treatments where only one plant survived. Shade treatments are the large boxes: 0% shade, 90% shade, and 99% shade. Water treatments are indicated along the x -axis: S = shallow water table, H = high rain, A = average rain, and L = low rain. Species are indicated by shaded bars.

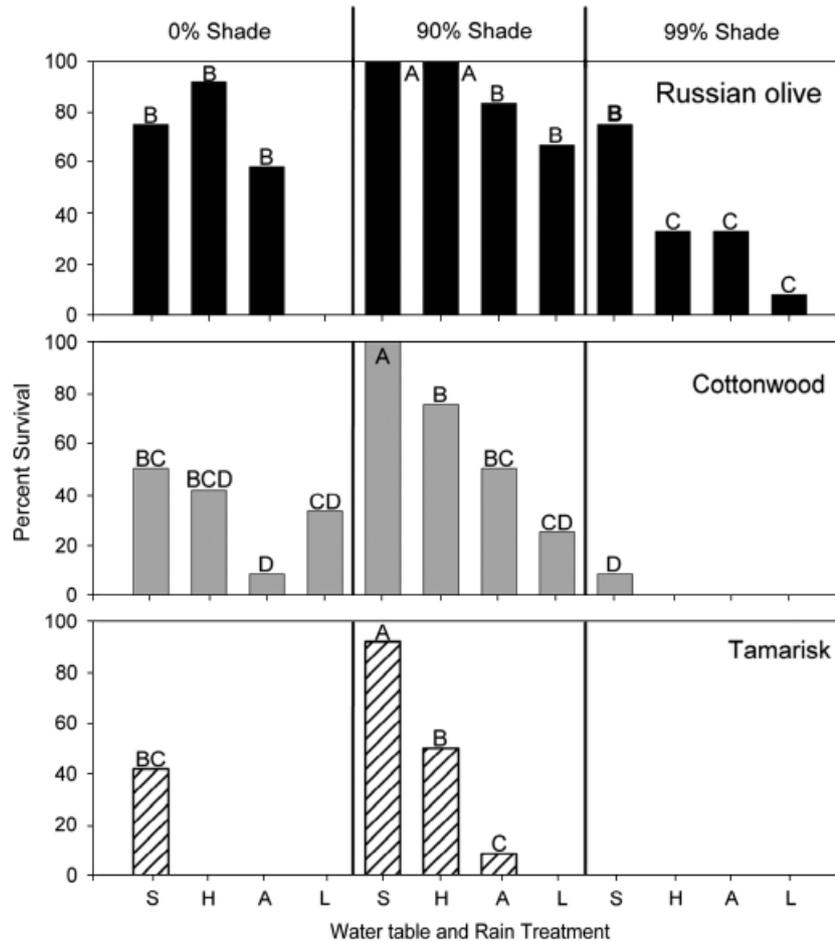


Fig. 3. Percentage survival of Russian olive (top), cottonwood (middle), and tamarisk (bottom) for each shade and water treatment. Shade treatments are the large boxes: 0% shade, 90% shade, and 99% shade. Water treatments are indicated along the *x*-axis: S = shallow water table, H = high rain, A = average rain, and L = low rain. Different letters indicate significantly different survival rates, pooling variance with alpha level 0.05.

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 (Fig. 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 survived in low water and low light treatments, the 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 (Fig. 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 the response to the water treatment varied according to shade treatment (Fig. 3). Shade and water significantly influenced tamarisk survival ($\chi^2 = 11.54_1$, $P < 0.001$ and $\chi^2 = 24.4_2$, $P < 0.001$), 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 (Fig. 3).

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 8 m above the thalweg and along a PAR gradient from 10 to 2200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 4). Russian olive seedling presence was negatively related to distance from seed source (Table 1). These patterns were 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 1), and distance from seed source was nearly significant ($Z = -1.833$, $P = 0.0598$, Table 1). Russian olive seedlings survived from 2006 to 2007 on two transects: 39 seedlings at 0.5 m above the thalweg and one seedling 5 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 1 m in elevation above the channel thalweg and under high light conditions of 1200–2200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 4). Height above thalweg was a significant factor in the cottonwood random coefficients model ($Z = -2.99$, $P = 0.003$, Table 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 1). One cottonwood seedling was found in deep shade

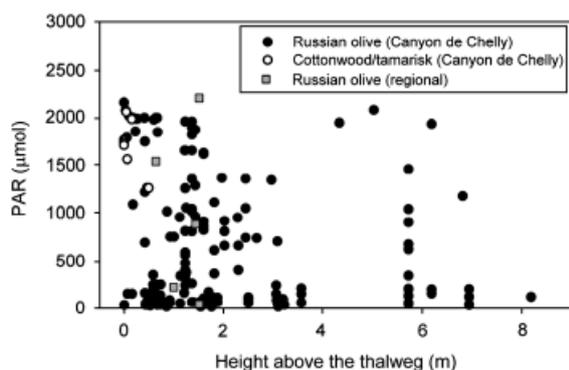


Fig. 4. Presence of seedlings along a height above thalweg (m, x-axis) and PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$, y-axis) gradients. Zero $\mu\text{mol m}^{-2} \text{s}^{-1}$ is 100% shade and 2200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ is full sun. Seedlings of Russian olive were sampled in Canyon de Chelly (black circles) and regionally (gray squares). Seedlings of tamarisk and cottonwood (white circles) were only sampled in Canyon de Chelly.

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, we could not develop a random coefficients model.

Regional sampling

Tamarisk occurred along all 11 rivers sampled, with cottonwood and Russian olive on five rivers each, 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 in five subplots on three different river reaches, with an average of 65.4 ± 46.3 (± 1 SE) seedlings for these five plots. Russian olive seedlings were found 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 seedlings occurred at light levels of $1223.2 \pm 404.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ (mean canopy cover of 55.6 ± 18.4 , ± 1 SE, Fig. 4).

Plant water use

Analysis of covariance for $\delta^{18}\text{O}$ 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 $\delta^{18}\text{O}$ ($t = 4.064$, $P = 0.0012$). The t -tests between plants < 15 yr and those ≥ 15 yr, upper soil (10–30-cm depth), lower soil (40–70-cm depth), and groundwater indicated that significant differences existed between all groups except the two soil layers and plants < 15 yr old (Table 2, Fig. 5).

Discussion

Our controlled experiments and field surveys demonstrated that Russian olive has broader environmental tolerances than cottonwood and tamarisk. We 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,

Table 1. Results of a random coefficients model analysis where number of seedlings was the dependent variable and height above the thalweg (m, height), distance from seed source (m, seed source), and amount of light ($\mu\text{mol m}^{-2} \text{s}^{-1}$, 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

Table 2. T -values and P -values (t -value, P -value) from t -tests for difference in means between the oxygen isotope ratios of upper soil layers of 10-30-cm depth, lower soil layers of 40-70-cm depth, Russian olive plants <15 yr old, Russian olive plants \geq 15 yr old, and groundwater. A Bonferroni adjustment for multiple comparisons ($k = 10$) was used to determine significance of the P -values. Significant values are indicated in bold.

	Upper soil	Lower soil	Plants <15 yr	Plants \geq 15 yr
Lower Soil	3.99, 0.100			
Plants <15	2.31, 0.702	2.06, 0.669		
Plants \geq 15	-9.9, 0.001	-5.95, 0.001	8.67, < 0.001	
Groundwater	-18.55, 0.001	-14.61, < 0.001	-18.76, < 0.001	-8.50, < 0.001

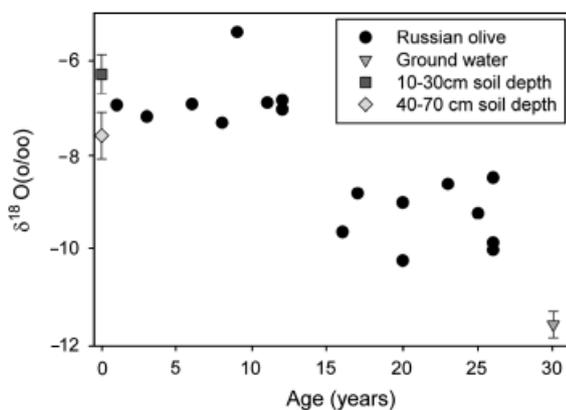


Fig. 5. Average $\delta^{18}\text{O}$ (‰) for Russian olive of different ages (black circles), groundwater (gray inverted triangle), soil of 10-30-cm depth (gray square) and soil of 40-70-cm depth (gray diamond). Error bars indicate ± 1 SE.

cottonwood, or in our shade experiments. Our results clearly demonstrate the potential for continued invasion by Russian olive into shadier and drier habitats than those that tamarisk and cottonwood can tolerate.

We found Russian olive establishing up to 8 m above the stream channel in riparian zones where flooding cannot occur and soils are wetted only by precipitation. This confirms that Russian olive establishment is not solely flood-dependent (Katz et al. 2001). Our oxygen isotope analysis showed that Russian olive could persist on soil water for up to 15 yr before the roots reach the riparian water

table and utilize groundwater. Although our isotope sampling occurred at one site and one time, it represented typical summer conditions and suggests the potential for Russian olive in our study area to establish and survive on soil water. In contrast, tamarisk and cottonwood seedlings established only in environments wetted by floodwater and in areas lacking dense shade (Shafroth et al. 1995; Sher et al. 2002). Russian olive was the only species to survive in our experiments in all 99% shade treatments, and even 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.

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 (*Salix exigua* Nutt.) being the most common (Friedman et al. 2005). The only shade-tolerant native riparian tree is box elder (*Acer negundo* L.), which ranks as seventh in frequency along western US rivers (Friedman et al. 2005). Although Russian olive occurs almost as frequently as cottonwood and tamarisk, it does not yet cover as large an area (Friedman et al. 2005). Mature tamarisk and cottonwood stands are not self-replacing because establishment rarely occurs under closed-canopy forests (DeWine & Cooper 2009). However, Russian olive can create self-replacing stands that ensure its persistence under

unflooded conditions whereas mature stands of cottonwood and tamarisk will eventually senesce and die without flooding disturbance to create seedling habitat (Cooper et al. 1999; Sher & Marshall 2003). Under current management regimes imposed on regulated rivers in the southwestern US, large and widespread flooding occurs less frequently than under historic flow regimes, thus reducing suitable habitat for cottonwood and tamarisk seedlings (Poff et al. 1997; Stromberg et al. 2007a, b). Climate change over the last century has also led to reduced flooding along western rivers, and climate projections for future flow regimes also predict smaller floods due to reductions in discharge (Christensen & Lettenmaier 2007; Rood et al. 2008). The combination of reduced flooding along southwestern rivers and the broad environmental tolerances of Russian olive may lead to decreases in cottonwood and tamarisk populations and increases in Russian olive populations (Webb & Leake 2006; Stromberg et al. 2007a, b).

Although neither cottonwood nor tamarisk seedlings survived the 99% shade treatment in our controlled experiment, these high light-loving species both had higher survival in 90% than 0% shade. These unexpected results suggest: (1) shade reduces water stress, thereby increasing seedling survival, and (2) 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 & Cooper 2009).

In addition to exceeding expectations under moderate shade, cottonwood seedlings were also able to survive under relatively low water conditions of two to four rain events per week. However, it is unlikely that cottonwood seeds could germinate or seedlings survive to maturity under such low water conditions (Mahoney & Rood 1998; Cooper et al. 1999). Cottonwood seedlings had higher survival and growth rates than tamarisk under a variety of light and water conditions. Cottonwood is known to outperform tamarisk under flooded, high light conditions, and our results strengthen this evidence, showing that cottonwood seedlings also tend to be superior under drier and shadier conditions (Cooper et al. 1999; Sher & 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 be-

hind cottonwood and tamarisk wind-borne seeds. Large seeds may provide increased resources during the early stages of seedling establishment, allowing seedlings to withstand dry soil conditions and maintain high growth rates. However, the trade-off for increased seed resources is slower dispersal rates. Successful invasions are often associated with species that have small, rapidly dispersing seeds (Rejmanek & Richardson 1996). Species with slow colonization rates are frequently overlooked, even though they may be successful invaders (Martin et al. 2009). Like other invasive species that are slow-dispersers or in the early stages of invasion, Russian olive may be more common near human settlements where it has been planted horticulturally (Stohlgren et al. 2005). Further study is needed to understand the benefits of large seed size and how Russian olive dispersal influences invasion patterns on a large scale.

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 Russian olive potential habitat in the western US is vast. It appears to be exploiting habitat unused by tamarisk and cottonwood due to harsh environmental conditions. The ability to persist along wide gradients of water and light availability will likely lead to a continued increase of Russian olive, while reduced flooding due to river regulation and climate change may cause a decline in tamarisk and cottonwood populations.

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References

- Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielborger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E.,

- Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B. & Michalet, R. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96: 18–34.
- Brotherson, J.D. & Winkel, V. 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*. MS Thesis, Colorado State University, Fort Collins, Colorado, US.
- Cavieres, L.A., Quiroz, C.L. & Molina-Montenegro, M.A. 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.
- Christensen, N.S. & Lettenmaier, D.P. 2007. A multimodel ensemble approach to assessment of climate change impacts on the hydrology and water resources of the Colorado River Basin. *Hydrology and Earth System Sciences* 11: 1417–1434.
- Cooper, D.J., Merritt, D.M., Andersen, D.C. & Chimner, R.A. 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, Chichester, UK.
- Davis, M.A., Grime, J.P. & Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–534.
- DeWine, J.M. & Cooper, D.J. 2009. Habitat overlap and facilitation in tamarisk and box elder stands: implications for tamarisk control using native plants. *Restoration Ecology* 17, doi: 10.1111/j.1526-100X.2008.00494.x.
- Ehleringer, J.R. & Osmond, C.B. 1989. Stable Isotopes. In: Percy, R.W., Ehleringer, J.R., Mooney, H.A., & Rundel, P.W. (eds.) *Plant Physiological Ecology Field Methods and Instrumentation*, pp. 281–300. Chapman and Hall, New York, NY, US.
- Elton, C.S. 1958. *The ecology of invasions by animals and plants*. The University of Chicago Press, Chicago, IL, US.
- Ely, L.L., Enzel, Y., Baker, V.R. & Cayan, D.R. 1993. A 5000-year record of extreme floods and climate-change in the Southwestern United States. *Science* 262: 410–412.
- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. & Von Holle, B. 2007. The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88: 3–17.
- Friedman, J.M., Auble, G.T., Shafroth, P.B., Scott, M.L., Merigliano, M.F., Preehling, M.D. & Griffin, E.K. 2005. Dominance of non-native riparian trees in western USA. *Biological Invasions* 7: 747–751.
- Gochis, D.J., Brito-Castillo, L. & Shuttleworth, W.J. 2006. Hydroclimatology of the North American monsoon region in northwest Mexico. *Journal of Hydrology* 316: 53–70.
- 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. & Naiman, R.J. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. *Plant Ecology* 148: 105–114.
- Katz, G.L. & Shafroth, P.B. 2003. Biology, ecology and management of *Elaeagnus angustifolia* L. (Russian olive) in western North America. *Wetlands* 23: 763–777.
- Katz, G.L., Friedman, J.M. & Beatty, S.W. 2001. Effects of physical disturbance and granivory on establishment of native and alien riparian trees in Colorado, USA. *Diversity and Distributions* 7: 1–14.
- Katz, G.L., Friedman, J.M. & Beatty, S.W. 2005. Delayed effects of flood control on a flood-dependent riparian forest. *Ecological Applications* 15: 1019–1035.
- Knopf, F.L., Johnson, R.R., Rich, T., Samson, F.B. & Szaro, R.C. 1988. Conservation of riparian ecosystems in the United States. *Wilson Bulletin* 100: 272–284.
- Kramer, P.J. & Boyer, J.S. 1995. *Water relations of plants and soils*. Academic Press, London, UK.
- Leopold, L.B., Wolman, M.G. & Miller, J.P. 1964. *Fluvial processes in geomorphology*. W. H. Freeman & Sons, San Francisco, CA, US.
- Lesica, P. & Miles, S. 1999. Russian olive invasion into cottonwood forests along a regulated river in north-central Montana. *Canadian Journal of Botany – Revue Canadienne De Botanique* 77: 1077–1083.
- Lesica, P. & Miles, S. 2004. Beavers indirectly enhance the growth of Russian olive and tamarisk along eastern Montana rivers. *Western North American Naturalist* 64: 93–100.
- Mahoney, J.M. & Rood, S.B. 1998. Streamflow requirements for cottonwood seedling recruitment – an interactive model. *Wetlands* 18: 634–645.
- Martin, P.H., Canham, C.D. & Marks, P.L. 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.
- Naiman, R.J. & Decamps, H. 1997. The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics* 28: 621–658.
- Naiman, R.J., Decamps, H. & Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3: 209–212.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B.D., Sparks, R.E. & Stromberg, J.C. 1997. The natural flow regime. *Bioscience* 47: 769–784.

- Rejmanek, M. & Richardson, D.M. 1996. What attributes make some plant species more invasive? *Ecology* 77: 1655–1661.
- Rink, G.R. 2003. *Vascular flora of Canyon de Chelly National Monument, Apache County, Arizona*. MS Thesis, Northern Arizona University, Flagstaff, AZ, US.
- Rood, S.B., Pan, J., Gill, K.M., Franks, C.G., Samuelson, G.M. & Shepherd, A. 2008. Declining summer flows of Rocky Mountain rivers: changing seasonal hydrology and probable impacts on floodplain forests. *Journal of Hydrology* 349: 397–410.
- Rowles, A.D. & O'Dowd, D.J. 2009. New mutualism for old: indirect disruption and direct facilitation of seed dispersal following Argentine ant invasion. *Oecologia* 158: 709–716.
- Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Heffernan, J., Jani, A., Katz, G., Soykan, C., Watts, J. & Welter, A. 2005. Riparian zones increase regional species richness by harboring different, not more, species. *Ecology* 86: 56–62.
- Shafroth, P.B., Auble, G.T. & Scott, M.L. 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.
- Sher, A.A. & Marshall, D.L. 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., Marshall, D.L. & Taylor, J.P. 2002. Establishment patterns of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix*. *Ecological Applications* 12: 760–772.
- Simberloff, D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters* 9: 912–919.
- Stohlgren, T.J., Bull, K.A., Otsuki, Y., Villa, C.A. & Lee, M. 1998. Riparian zones as havens for exotic plant species in the central grasslands. *Plant Ecology* 138: 113–125.
- Stohlgren, T.J., Barnett, D., Flather, C., Kartesz, J. & Peterjohn, B. 2005. Plant species invasions along the latitudinal gradient in the United States. *Ecology* 86: 2298–2309.
- Stromberg, J.C., Beauchamp, V.B., Dixon, M.D., Lite, S.J. & Paradzick, C. 2007a. Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in and south-western United States. *Freshwater Biology* 52: 651–679.
- Stromberg, J.C., Lite, S.J., Marler, R., Paradzick, C., Shafroth, P.B., Shorrock, D., White, J.M. & White, M.S. 2007b. Altered stream-flow regimes and invasive plant species: the *Tamarix* case. *Global Ecology and Biogeography* 16: 381–393.
- Tecco, P.A., Gurvich, D.E., Diaz, S., Perez-Harguindeguy, N.P. & Cabido, M. 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 USA* 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, 1–20.
- USDA, NCRS. 2010. *The PLANTS Database*. Available at <http://plants.usda.gov>. National Plant Data Center, Baton Rouge, LA, US.
- Webb, R.H. & Leake, S.A. 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.

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