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# 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).

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## 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).

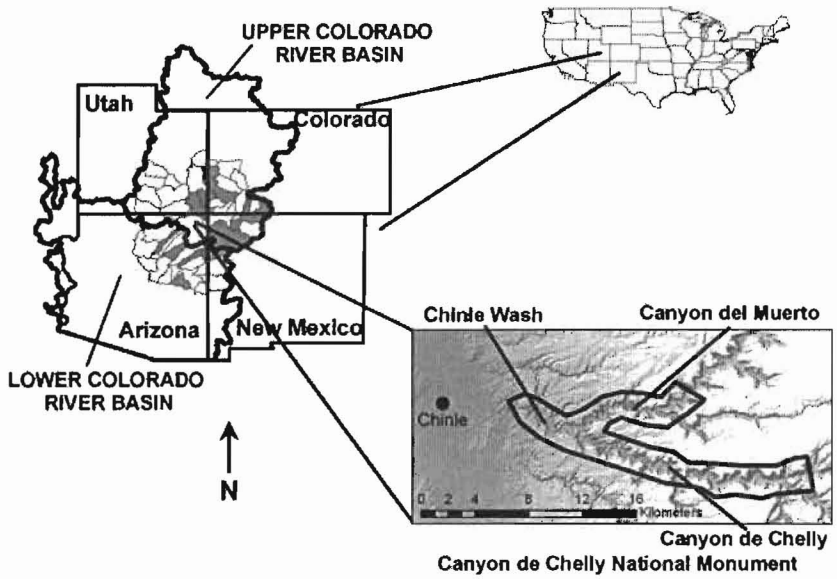


**Fig. 1.** Maps of Canyon de Chelly National Monument (lower right panel) and regional sampling area (upper left panel). The bold line denotes Canyon de Chelly study area, and its location on the regional map is identified with a cross. Our regional sampling area included 42 Colorado River sub-basin 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

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 $CO_2$ 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:

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

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

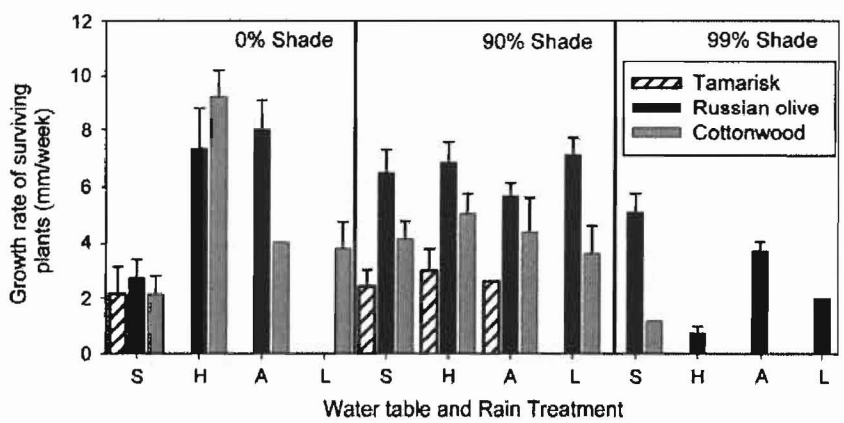


**Fig. 2.** Growth rate of surviving plants after 10 weeks of shade and water treatments (mm/week ± SE). Bars without SE indicate treatments where only one plant survived. Shade treatments are the large boxes: 0% shade, 90% shade, and 99% shade. Water treatments are indicated along the $x$-axis: S =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

*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 $\mu mol\, m^{-2}\, s^{-1}$ (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 $\mu mol\, m^{-2}\, s^{-1}$ (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

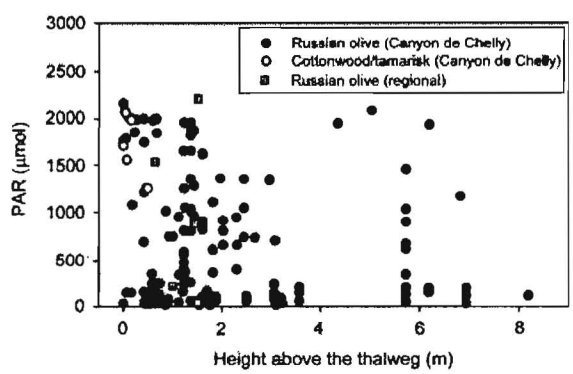


**Fig. 4.** Presence of seedlings along a height above thalweg (m, $x$-axis) and PAR ($\mu mol\, m^{-2}\, s^{-1}$, $y$-axis) gradients. Zero $\mu mol\, m^{-2}\, s^{-1}$ is 100% shade and 2200 $\mu mol\, m^{-2}\, s^{-1}$ is full sun. Seedlings of Russian olive were sampled in Canyon de Chelly (black circles) 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 ± 404.8 $\mu mol\, m^{-2}\, s^{-1}$ (mean canopy cover of 55.6 ± 18.4, ± 1 SE, Fig. 4).

*Plant water use*

Analysis of covariance for $\delta^{18}O$ 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 $\delta^{18}O$ ($t = 4.064$, $P = 0.0012$). The $t$-tests between plants $< 15$ yr and those $\geq 15$ 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,

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 behind 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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