

Tamarix Spread, Establishment, and Removal

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Species around the world are becoming known for their ability to uproot food chains, overtake niches, and destroy forests. A species is deemed to be non-native if it is simply introduced to an environment that is not within its natural range. A species is considered to be invasive if it enters a foreign ecosystem, thrives, reproduces, spreads, and has an impact, whether that be low or high, which is generally due to the lack of inhibitory biotic and abiotic factors (insert citation?). Perhaps the most dangerous of all invasive plants would be those classified as weeds. To be an ideal invasive weed, plants must meet a list of criteria established by Herbert George Baker in 1974. This list includes having a large production of seeds by individual plants, the ability for seeds to be spread by water and wind, rapid seedling growth, and hardiness (Natale et al., 2010). *Tamarix*, also known as saltcedar, is a species of invasive shrubs or small trees that exhibit ten out of the thirteen criteria proposed by Baker. Alongside these characteristics, the species' adaptability allows it to overcome abiotic and biotic factors that limit the spread of most invasive plants alongside making it difficult to remove. For this reason, it is important to explore how *Tamarix* is able to thrive in diverse environments and the effect it has on both biotic and abiotic factors post invasion. Furthermore, the removal of *Tamarix* is difficult and complicated, with both positive and negative effects.

The genus *Tamarix* represents a complex web of taxonomic relationships that describe the species that have been introduced to North America and have spread across the continent (Young et al. 2004). In the early 19th century, eight to twelve species of *Tamarix* were introduced to prevent the erosion of soil and for personal garden use (Pearce 2003). *Tamarix*'s native environment includes most of Eurasia, ranging from the Caspian Sea to western China and Korea (Young 2004). Since its introduction to North America, it has invaded most of the Great Plains, ranging from southern Arizona to eastern Montana, going as far east as western Kansas (Sexton 2002). Other invaded locations include Australia, Mexico, and Argentina (Natale et al. 2010). *Tamarix* tends to invade semi-arid ecosystems, or, due to evaporation, climates that receive precipitation slightly below potential transpiration; however it more commonly invades riparian ecosystems, which contain trees and shrubs that can tolerate extremely moist environments (Carter et al. 2012). Originally, *Tamarix* was intentionally spread by humans, but then began to spread uncontrollably through wind, water, and animals (Pearce et al. 2003). Of all the species of *Tamarix* present in North America, *Tamarix ramosissima* is the second most common woody plant found in riparian environments (Friedman et al. 2005). This particular species is particularly adept at invading several environments and has been the focal point of many studies (Sexton 2002). *Tamarix ramosissima* is a facilitative halophyte, meaning it can tolerate environments of varying salinity ranging from standard to high levels (Natale et al., 2010). It is can also tolerate extremely high levels of water including complete submersion, making it a facilitative phreatophyte. These factors not only allow the plant to survive in extreme environments, but they also give the seeds a wide variety of environments and conditions to germinate.

Tamarix seeds, specifically *Tamarix ramosissima* seeds, are able to flower and release seeds during their first year of life (Friedman et al., 2004). At maturity, each plant has the ability to produce half a million seeds per year, with germination percentages varying between 19-51% (Natale et al., 2010). The seed production takes place over a five-and-a-half-month time period with peak production in May and June. The seeds are extremely small and have short hairs that aid in wind dispersal aerodynamics. These features also help with seed buoyancy and anchorage to seedbeds, thus improving water transportation (Young et al., 2004). Germination is almost instantaneous as soon as the seeds come in contact with water (Young et al., 2004). Despite mature plants having a tolerance to salinity, the seeds show considerably less tolerance. *Tamarix ramosissima* in particular has a very low germination percent above about 13,000 ppm of NaCl (Natale et al., 2010). However, the species can still reproduce at higher salinity levels due to the enormous number of seeds it produces every year. Despite the seeds low tolerance to salinity, they are able to germinate successfully at all temperatures except very cold (zero degrees Celsius) or very warm (forty degrees Celsius), with maximum germination at about twenty degrees Celsius (Young et al., 2004). Seeds are most sensitive to water availability and will not germinate in environments that are water deficient (Natale et al., 2010). If conditions are tolerant, the seeds will germinate and undergo an explosive period of growth until maturity, at which time the plants are able to adapt to extreme differences in temperatures.

Plasticity is the ability of the phenotype of a plant to change in response to its environment (Sexton, 2002). As mentioned, the invasion of *Tamarix ramosissima* ranges from Arizona to Montana, making it the most widespread species of *Tamarix* in the United States (Sexton 2002). Plasticity aids its ability to invade a wide range of environments, for, as a seedling, the individual plant's roots and shoots can adjust in mass and length. After multiple generations in the same environment, genetic variation can occur, which alters the genes of the species (Sexton, 2002). If a species exposes itself to a variety of environments that favor different phenotypes, with not one being superior to the rest, then adaptive plasticity is likely to occur (Ghalambor et al., 2007). Seeds taken from the southern most point of *Tamarix ramosissima*'s range, and placed in the northern most point, will germinate and develop considerably shorter shoots that have lower overall mass than their parents. The plants are then able to physically adapt to abiotic factors, which limits their spread. If these environmental pressures produce the same result in all seeds over an extended period of time, then the genotype of the species can change (Sexton, 2007). However, during this time and throughout the rest of the plant's life, it must survive high salinity levels and periods of drought.

Tamarix is able to tolerate high salinity levels by maintaining salt concentrations through non-selective ion exclusion (Carter, Nippert 2010). Excess ions are excreted through foliar glands, which increases salt concentration in the surrounding topsoil (Natale et al., 2010). Despite evolving mechanisms that allow the saltcedar to tolerate high salt concentrations, the plant still experiences the effects of salt. While gas exchange is relatively unaffected, it takes energy to actively transport the salt out of the cells against the concentration gradient (Natale et al., 2010). The plant becomes salt stressed, which affects protein synthesis, inhibits photosynthesis, and alters metabolic processes (Carter et al., 2010). *Tamarix ramosissima* can accumulate

soluble sugars for metabolic use, but synthesizing such sugars requires large amounts of energy and ultimately results in reduced plant growth (Natale et al., 2010). Therefore, as long as it is not unscathed, the plant can tolerate higher salinity levels and survive where many plants cannot. Water deficiencies only amplify the effects of salt stress, but *Tamarix* is capable of surviving completely submerged for up to seventy days (Natale et al., [year]). The plants can also survive extended periods of drought in locations of lower salinity (Pearce 2003). Mature *Tamarix ramosissima* have extremely deep roots, which aids the plant in surviving droughts and in avoiding water sources containing undesirable salinity concentrations (Natale et al., 2010). With this being said, perhaps the trait with the biggest impact on the success of *Tamarix* would be plasticity. Once established, *Tamarix* affects the environment in ways that promote its establishment.

Humans have facilitated the spread of *Tamarix* by altering waterways for irrigation dams, clear land, and groundwater pumping (Tickner et al. 2001, Shafroth et al. 2005). This renovation has both altered and stripped the ecosystems of their native plants, providing open niches for *Tamarix*. Due to their ability to colonize disrupted riverbanks, *Tamarix* has quickly invaded and begun to affect the ecosystem (Tickner et al. 2001). In the riverbanks, the species uses more water than native plants due to evapotranspiration (Shafroth et al. 2005). Furthermore, *Tamarix* has extremely deep roots, which gives it access to sources of water unreachable by native plants and also facilitates a net loss of water by the ecosystem. *Tamarix* stands are extremely dense and trap debris and sediment, causing flash floods that interfere with the survival of shorter rooted plants (Tickner et al. 2001). Thus, not only is *Tamarix* able to invade recently altered ecosystems, but it can also alter the environment to prevent the re-establishment of native plants.

Tamarix can tolerate water sources with higher salinity levels due to its ability to uptake ions together with cellular compartmentation and salt excretion (Tickner et al. 2001). *Tamarix* gets the ability to regulate salt balances through foliar glands (Ladenburger et al. 2006). Generally this secretion is done through the leaves, which then fall and decompose in the soil around the plant (Kennedy and Hobbie, 2004). Additional salt in the soil also decreases the quality of water and causes higher rates of plant transpiration in attempt to regulate osmosis in the cells (Shafroth et al. 2005). This increase in salinity and decrease in water levels causes a decrease in species diversity because native plants and wildlife are unable to survive (Tickner et al. 2001). *Tamarix* also creates pockets of fertility around its roots, which allows it to survive. Native plants, however, have difficulty establishing themselves above and around the soil (Kennedy and Hobbie, 2004). This dissimilarity provides an advantage for *Tamarix* over native species, thus facilitating its invasion (Shafroth et al. 2005). As *Tamarix* replaces native species, it also shifts the ecosystem's previous reliance on autochthonous inputs to allochthonous inputs (Kennedy and Hobbie, 2004). Prior to plant invasions, the ecosystems generally rely on a steady, year-round feed of litter inputs. However, *Tamarix* tends to drop its salt-riddled leaves in the fall, providing a spike of allochthonous input at this time and little to no input during the rest of the year (Kennedy and Hobbie, 2004). This occurrence not only increases salinity levels, but it also affects the soil in ways that native species cannot tolerate. For example, increasing levels of organic acids after a breakdown of litter cause a decrease in pH levels. (Ladenburger et al. 2006). Due to higher salinity, nitrogen levels also become higher and electrical conductivity increases (Ladenburger et al. 2006). These abiotic effects

ultimately result in biotic environmental changes.

The effects of *Tamarix* on wildlife depend on the ecosystem and species involved (Sogge et al. 2008). *Tamarix* tends to invade locations where cottonwood, bulrush, ash, and/or willow are the dominant plants (Shafroth et al. 2005; Kennedy et al. 2005). Bulrush inhabits the beds of streams with the roots of the plant submerging completely. This inhabitation provides a stable area for algae and invertebrates to reproduce, grow, and live (Kennedy and Hobbie 2004). The removal of this algae base brings about negative effects for the native fish population and diversity (Kennedy et al. 2005). For example, an invasion in a Nevada stream caused a significant increase in crayfish and mosquitofish abundances, but at the expense of pupfish and speckled dace abundances (Kennedy et al. 2005). If you were to shift one hundred miles to the north, there would be completely different results based on the community. This concept translates to arthropods as well; bee, wasp, and butterfly abundances have increased since invasion due to the hardy, long-lasting flowers the plant produces and that insects use (Shafroth et al. 2005). Arthropods that are able to use *Tamarix* as a food source tend to do well, while insects that are not generalists tend to experience decreases in populations post invasion (Shafroth et al. 2005). Perhaps, however, *Tamarix* affects the avian populations the most out of all other species.

The effect *Tamarix* invasion has on birds depends solely on the bird species and ecosystem (Sogge et al. 2008). Where one bird might be able to use *Tamarix*, another similar bird might not. However, many birds can successfully breed in *Tamarix* invaded habitats without any negative consequences. Research demonstrates that, overall, species are less abundant despite the increase in total number of birds in comparison with pre-invasion (Sogge et al. 2008). For some species, the structure of the vegetation is more important than the actual species; these species tend to be generalists. In other cases, the effects *Tamarix* has on the environment, such as surface water levels decreasing, provide habitats for birds and more diversity (Sogge et al. 2008). On the flip side, most birds in desert populations cannot use saltcedar for breeding purposes because it does not provide enough shade (Shafroth et al. 2005). If situations are correct, then species' abundances can increase; however, *Tamarix* rarely supports the same species' richness and population sizes as native habitats (Sogge et al. 2008).

Due to *Tamarix* destruction of native habitats, millions of dollars are spent annually in an attempt to remove the species (Shafroth et al. 2005). For eradication to be successful, careful planning must occur about what invaded sections are most likely to be successful, how to remove the *Tamarix*, what to replace the species with, and how to prevent the almost inevitable reinvasion (Shafroth et al. 2008). Because of these questions, it has been debated heavily for decades whether the removal of *Tamarix* can even provide the anticipated ecological and economic benefits (Shafroth et al. 2005). Saltcedar alters the water levels in the ecosystem, lowers pH levels, and changes the cycling of nutrients, all of which are not easily reversed and can prevent the reestablishment of native species (Ladenburger et al. 2006; Tickner et al. 2001). Furthermore, the species of birds that has used the niches *Tamarix* provides will suffer immediately while native species slowly take root once again (Sogge et al. 2008). All of these issues pose crucial questions about the justification of the removal of saltcedar. However, the approach is generally taken that removing saltcedar will increase water yield, improve wild life habitat, restore native vegetation, and even decrease both forest fire and flash flood frequency (Shafroth et al. 2008). This is the long-term goal, which can be reached with the

careful planning mentioned above. Generally a combination of chemical, mechanical, and biological control is used with frequent retreating (Beaugh et al. 2009). Mechanical and chemical control has been used since *Tamarix* establishment, and it provides immediate visible results.

Mechanical and chemical treatments have been used with mixed success for almost half a decade (Shafroth et al. 2008). Mechanical control generally begins with the removal of individual organisms through removal by hand (Beaugh et al. 2009). This technique has been used the longest, but generally has no effect on the overall plant, as *Tamarix* quickly resprouts from the buried, undamaged root system (Shafroth et al. 2005). Cutting by hand is also undesirable since it is physical, time consuming labor and requires that the cut plants be physically removed from the site or burned (Beaugh et al., 2009). Plant mortality has improved to almost one hundred percent with the use of bulldozing, which involves removal of the root crowns followed by burning (Shafroth et al. 2005). Chemical removal tends to have a consistently high success rate without the abrupt change in the ecosystem that bulldozing causes. For dense monotype stands of saltcedar, aerial spraying successfully eliminates *Tamarix* while individual applications are performed in less dense strands (Shafroth et al. 2005). For large monotype stands, removal using a helicopter with specialized nozzles has been used even near water (Beaugh et al. 2009). Generally the herbicides used tend to target defoliation of the plant using a topical application of imazapyr, but *Tamarix* stumps can be individually treated with triclopyr post cutting (Shafroth et al. 2005).

The United States Department of Agriculture Animal and Plant Health Inspection Services (USDA-APHIS) approved the release of beetles to use as biocontrol for *Tamarix* in the western United States (Uselman et al. 2011). Currently, the herbivorous *Diorhabda elongata sensu lato* leaf beetle and the *Diorhabda carinulata* saltcedar leaf beetle are used for control (Pattison et al. 2010; Shafroth et al. 2008). The adult and larval beetles scrape, chew, and even remove entire sections of *Tamarix* leaves, causing immediate discoloration, desiccation, and eventual loss of leaves (Uselman et al. 2011). Ultimately, the plant drops its leaves because its ability to regulate water loss is reduced once damaged (Hultine et al. 2009; Uselman et al. 2011). This is called defoliation: a defense mechanism of the plant. Depending on the severity of the defoliation, photosynthesis by the plant has either stopped completely or is at a lower level (Shafroth et al. 2008). Stem sap flow decreases due to the plant's need to conserve sugar. The loss of leaves limits photosynthesis, so less sugar is made for the plant (Pattison et al. 2010). Because the defoliation is done quickly to prevent further damage, the plant does not have time to reabsorb the nutrients stored in the leaves (Pattison et al. 2010). As a result, the leaf litter input contains higher concentrations of nitrogen and phosphorous (Uselman et al. 2011). There is also a higher phosphorous concentration, a lower carbon-to-nitrogen ratio, and higher concentrations of carbon dioxide due to the decrease in photosynthesis rates (Hultine et al. 2009). Thus, the leaf litter decomposes faster, which increases soil respiration fluxes and loss of carbon to the atmosphere (Hultine et al. 2009). Nitrogen concentrations also increase in conjunction with the effects of defoliation and removal of *Tamarix on the nitrogen cycling* (Hultine et al. 2009; Shafroth et al. 2008). Defoliation may have short-term effects in increasing nitrogen availability, but long-term effects of *Tamarix* removal result in soil erosion and the exportation of nitrogen downstream (Hultine et al. 2009). Severe defoliation will not kill the plants, as they can reverse defoliation in as little as three weeks with little to know long-term damage (Uselman et al. 2011; Pattison et al. 2010). However, if the infestation of the beetles is severe

and complete defoliation repeatedly occurs, than the *Tamarix* will not be able to reverse defoliation and replenish its sugar reserves, resulting in death (Hultine et al. 2009). Once the *Tamarix* is removed, bare land is open for colonization by other species.

Prior to the eradication of *Tamarix*, defoliation produces gaps in the canopy that promotes understory growth (Hultine et al. 2009). Unfortunately, the high levels of nitrogen and bare ground facilitate the invasion of non-native species, such as Russian olive, common pepperweed, Russian knapweed, and thistle (Hultine et al. 2009). Careful planning and planting of native plants post invasion must occur, with frequent mechanical and chemical treatments of remaining or sprouting *Tamarix* (Shafroth et al. 2008). *Tamarix* has also created a specialized environment that select few species can inhabit, making reinvasion likely (Shafroth et al. 2008; Sogge et al. 2008). An experimental technique with controlled flooding has had some success stimulating native species' re-establishment from seeds (Sprenger et al. 2002). However, the question remains: does removal cause more harm than good? Physical removal of *Tamarix* is costly and time-consuming, while the long-term effects of biocontrol have not been seen. Despite extensive laboratory testing, the beetles are also an invasive species and it is not possible to predict all of their effects (Pattison et al. 2010). They may switch hosts, grow out of control, and cause more harm than good (Uselman et al. 2011). Also, *Tamarix* has established itself in several sites for nearly a century now, and wildlife has adjusted to its establishment (Sogge et al. 2008). Some species of endangered birds, such as the Yellow-billed Cuckoo from New Mexico and several species from the Grand Canyon, have grown to rely on *Tamarix*, and its removal may result in the extinction of wildlife populations (Hunter et al. 1988; Sogge et al. 2008). However, the positive long-term results of increased water yield, restoration of native vegetation, and decreases in catastrophic flooding or forest fires need to be considered to justify the risks and initial negative effects (Shafroth et al. 2008).

Tamarix removal is difficult with both positive and negative effects, primarily due to its ability to invade diverse environments, out-compete native species, and alter the composition of the ecosystem. The question remains: should efforts to remove *Tamarix* continue, or should the attention and money be shifted elsewhere? Certain sites are relatively recently invaded, making eradication probable and the eventual return of the natural ecosystem possible, but what prevents a reinvasion? *Tamarix* is hardy and can quickly establish, especially in recently cleared areas. Perhaps the millions of dollars spent annually on mechanical, chemical, and biological control should be shifted to preventing the further spread of *Tamarix*, to targeting less established or adaptive species, or to the prevention of invasion species. It is difficult to quantify the immediate economical benefits versus the long-term benefits or mistakes. These are complicated questions, with no clear or correct answers.

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