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TAMARISK GROWTH AT THE NORTHERN MARGIN OF ITS NATURALIZED RANGE IN MONTANA, USA

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Abstract: Tamarisk (*Tamarix spp.*), an introduced shrub or small tree, has invaded riparian areas throughout the western United States. Tamarisk invasion has been studied extensively in the Southwest, but there is little information on its performance at the northern margin of its naturalized range. We measured the canopy cover, density, height and age of tamarisk and plains cottonwood (*Populus deltoides*) in 50 plots at 25 sites along the Bighorn, Powder, and Yellowstone rivers in southeast Montana near the northern edge of tamarisk's western North American range. Tamarisk commonly formed thickets on open, low terraces and along overflow channels but was less dense beneath a cottonwood canopy. Tamarisk stems routinely died back to the ground, and the oldest live stems were generally much younger than the plants. Tamarisk 30 to 40 years old in our study area usually attained heights of only 4 m or less. Height and number of live stems of tamarisk plants were 16% and 44% lower respectively under a tall cottonwood canopy. Cottonwood grows faster than tamarisk, eventually shading it and causing its decline. We believe that tamarisk will be only an understory shrub in most eastern Montana riparian forests, declining as cottonwoods form a closed canopy. Minimizing the spread of tamarisk in riparian areas in Montana can best be accomplished by managing for cottonwood.

Key Words: tamarisk, *Tamarix*, cottonwood, marginal populations, Montana

INTRODUCTION

Introductions of exotic species often have profound effects on the composition and functioning of native ecosystems (de Waal et al. 1994). However, most introduced species do not become problematic (Williamson 1993), while many others cause significant disruption only in particular ecological contexts (Mack 1996). Knowledge of geographic variation in performance in their introduced range is incomplete for most exotic species. Such knowledge allows more accurate prediction of the effects of exotic invasions and helps direct prevention and control efforts (Cousens and Mortimer 1995).

Tamarisk or saltcedar (*Tamarix ramosissima* Ledeb., *T. chinensis* Lour., *T. gallica* L.) is a shrub or small tree native to Europe and Asia. It was first introduced into North America for horticultural purposes in the early 1800s and became a problem weed along rivers and streams in southwestern U.S. by the 1920s (Robinson 1965). Tamarisk was present along the Bighorn River in Montana, at the northern margin of its introduced range, by 1960 (Robinson 1965). By the 1980s tamarisk was known from eight counties in the southeast portion of the state, as well as along the Missouri River further north (Swenson et al. 1982).

Tamarisk colonizes riverbanks (Everitt 1980). It establishes with native cottonwood (*Populus* spp.) and willow (*Salix* spp.) (Irvine and West 1979, Stromberg 1997) but is more tolerant of high salt concentrations (Carman and Brotherson 1982, Busch and Smith 1995, Shafroth et al. 1995). In addition, tamarisk is able to survive lowered floodplain water tables associated with anthropogenic flow regulation and reduction better than native cottonwood and willow (Busch and Smith 1995, Cleverly et al. 1997). For these reasons, tamarisk is replacing native woody vegetation along rivers in the Southwest with high salt concentrations and/or reduced flows (Turner 1974, Howe and Knopf 1991, Cleverly et al. 1997, Smith et al. 1998, but see Stromberg 1998a). The interactions between native cottonwoods and tamarisk at the northern edge of its naturalized range are unknown. The purpose of our study was to gain insights into the ways tamarisk affects the dynamics of native riparian forest succession in southeast Montana. In particular, we ask three questions: (1) How well does tamarisk grow at the northern edge of its introduced range? (2) How strongly can tamarisk compete with plains cottonwood (*Populus deltoides* Marsh) during riparian succession? (3) Will tamarisk displace cottonwood as the dominant woody plant along major rivers in southeast Montana? Knowledge of how tamarisk behaves at the northern edge of its North American range will help predict the

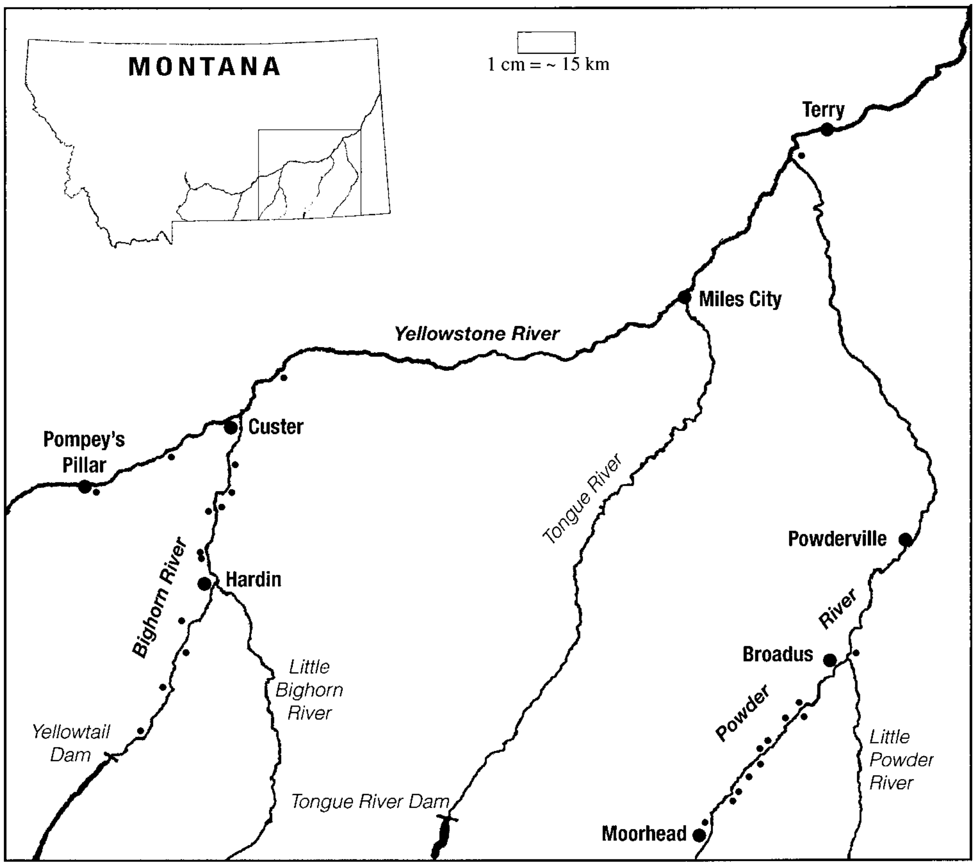

Figure 1. Location of study sites on the Bighorn, Powder, and Yellowstone rivers in southeast Montana.

long-term effects of tamarisk and direct control efforts in riparian areas of the Northern Great Plains and the Northern Rocky Mountains.

TAMARISK LIFE HISTORY

Tamarisk or saltcedar (*Tamarix ramosissima* and *T. chinensis*) is naturalized throughout much of temperate North America (Robinson 1965); species of tamarisk have been collected as far north as southern British Columbia, Manitoba, and Ontario (Baum 1967). In the southwestern U.S. it attains heights of 10–12 m (Campbell and Dick-Peddie 1964, Graf 1978, Everitt 1980). Tamarisk produces copious small, wind-dispersed seeds throughout much of the growing season (Merkel and Hopkins 1957). Seeds are short-lived and can germinate immediately upon wetting (Merkel and Hopkins 1957). Tamarisk seedlings establish on bare, fresh, alluvial deposits or other moist, disturbed soil (Stromberg 1997, Taylor et al. 1999). Tamarisk develops a deep taproot that extends to the water table (Merkel and Hopkins 1957, Gary 1963). However, it is a facultative phreatophyte, not entirely dependent on root contact with the water table and able to tolerate extended periods of drought (Busch et al. 1992, Cleverly et al. 1997, Shafroth et al. 2000). Tamarisk branches near the base, often in the first year of growth. Alluvial deposition can bury branches of established plants, which can then develop new plants along their length (Merkel and Hopkins 1957, Everitt 1980), sometimes forming clonal colonies. Tamarisk and cottonwood are both early successional species with similar dispersal strategies and habitat requirements (Merkel and Hopkins 1957, Bradley and Smith 1986, Stromberg 1997).

We follow Welsh et al. (1987) in calling all of our plants *T. ramosissima.* These plants are difficult to distinguish from *T. chinensis* and *T. gallica* L. (Brock 1994) and have also been incorrectly called *T. pentandra* Pall. (Baum 1967).

STUDY SITES

We conducted our study along the Bighorn, Powder, and Yellowstone rivers in southeast Montana, USA (Figure 1), the portion of the state where tamarisk is most common (Grubb et al. 1997). The Bighorn River has its headwaters in the Bighorn and Absaroka mountains of northwest Wyoming and flows north through Wyoming's Bighorn Basin into Bighorn Canyon. Yellowtail Dam was constructed in 1965 at the north end of Bighorn Canyon. Below the dam, the Bighorn River flows north and northeast for ca. 135 km into the Yellowstone River near the town of Custer. Annual mean flow for the Bighorn River at the upper end of the study reach is 105 m^3/sec. The Powder River also has its headwaters in the Bighorn Mountains and flows unobstructed northeast into the Yellowstone River just above the town of Terry. Annual mean flow of the Powder River at the upper end of the study reach is 13 m^3/sec. In Montana, both rivers cut through plains underlain by Cretaceous sandstone and shale (Alt and Hyndman 1986). Surface elevations on the Bighorn River at Yellowtail Dam and Custer are 916 m and 860 m, respectively, while elevations at Moorhead and Powderville on the Powder River are 975 m and 870 m, respectively.

Climate of the region is semi-arid and continental. Mean annual precipitation at Hardin and Broadus in 1950–1980 was 31–32 cm, with ca. 80% falling in April through October. Mean January minimum and July maximum temperatures were −15° and 32°C, respectively (NOAA 1982).

Natural vegetation of highest riparian terraces is dominated by silver sagebrush (*Artemisia cana* Pursh), western wheatgrass (*Agropyron smithii* Rydb.), prairie sandreed (*Calamovilfa longifolia* (Hook) Scribn.), and green needlegrass (*Stipa viridula* Trin.); however, extensive areas of upper terrace have been converted for agricultural crops. Terraces closer to the river channel support riparian vegetation dominated by plains cottonwood (hereafter referred to as cottonwood), sandbar willow (*Salix exigua* Nutt.), hydrophytic grasses and sedges, especially Eurasian meadow grasses that were seeded or escaped from pasture plantings (Lesica and Miles 2000).

METHODS

Field Methods

We located 93 potential study sites along the entire reach of the Bighorn River, from Yellowtail Dam to its confluence with the Yellowstone River and along the Powder River on lands administered by the Bureau of Land Management in Powder River County. Potential study sites supported large (≥1 ha) populations of tamarisk with at least two distinct size classes present. Many sites also supported populations of cottonwood. Of these, we randomly selected 21 sites for study. We also studied four sites previously known to us in this same part of the state, three on the Yellowstone River and one on the Powder River at its confluence with the Yellowstone (Figure 1).

At each site, we sampled a representative plot subjectively located in each distinct habitat that supported tamarisk. Each site had 1–3 sample plots for a total of 50 plots, 11 on alluvial bars and 39 on terraces. Alluvial bars were areas of deposition on which the oldest woody plants were <5 years old. Terraces were generally higher, with better developed soil and older woody plants. Sample plots were 500 m^2 and circular or rectangular, depending on the shape of the stands being sampled.

For each sample plot, we estimated tall-cottonwood (≥10 m high) canopy cover with a spherical densiometer at plot center in circular plots or at the centers of the two halves of rectangular plots. We recorded the number of cottonwood trees in each of four size classes: seedling— <135 cm high or <2.5 cm diameter at ground level (dgl); sapling— ≥135 cm high and 2.5–13 cm dgl; pole— 13–23 cm dgl; and mature— >23 cm dgl. We recorded the number of tamarisk plants in each of three size classes: small— <0.5 m high; medium— 0.5–1.0 m high; large— >1.0 m high. When plant density was high (≥1/m^2), we obtained estimates of tamarisk and cottonwood density from five evenly spaced, circular microplots 0.8–12.5 m^2. Microplot size was adjusted to obtain an easily countable number of stems per plot. Otherwise, we counted all plants of these species in the macroplot. We estimated the height of cottonwood trees to the nearest meter with a 3-m gauging pole. For tamarisk, we measured the tallest stem to the nearest decimeter with a gauging pole and counted the number of live and dead stems still attached to the live plant.

In terrace plots, we obtained age estimates for three representative plants in the dominant size classes and at least one plant in subordinate classes for cottonwood and tamarisk. Cottonwood ages were derived from cross-sections or increment cores taken just above ground level. The number of annual rings was counted using a 10–20X microscope. Age estimates of cottonwood were likely to be less than the actual age because current ground level is often not the establishment surface (Bradley and Smith 1986, Scott et al. 1997). Additionally, some cottonwood trees had rotten centers, making age determination inaccurate. In eastern Montana, tamarisk has a shrub growth form. New branches and roots often arise from older branches that have been buried by sediment (Everitt 1980). We excavated tamarisk plants and obtained a cross-section from the point just below the union of the lowest stems. However, some tamarisk plant age estimates may be inaccurate because it was not always possible to exactly determine the level where establishment took place. We also recorded the age of the oldest above-ground stem for each plant by counting growth rings of severed stems in the field.

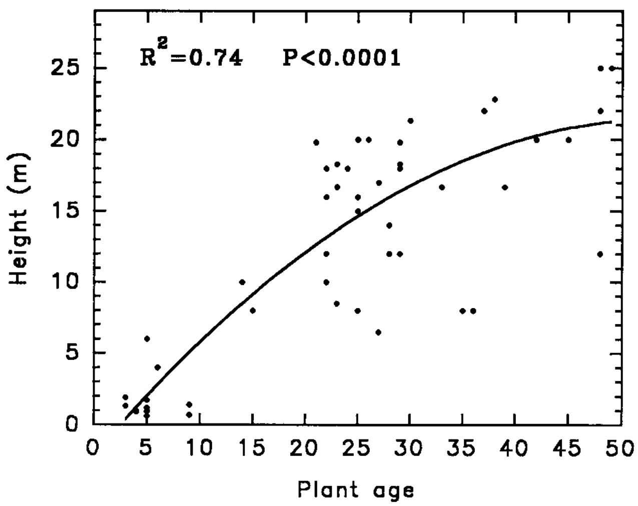

Figure 2. Relationship of height to age for undamaged cottonwood trees in terrace plots.

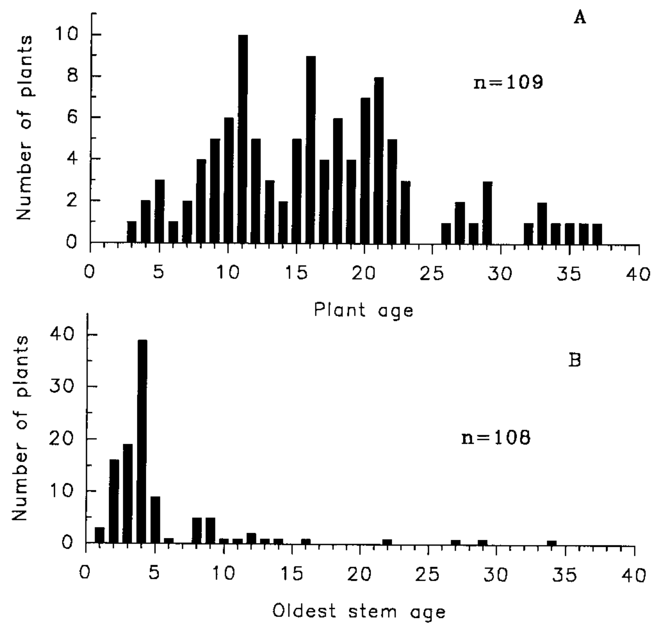

Figure 3. (A) Age distribution of tamarisk plants sampled in terrace plots and (B) Age distribution of oldest live stems for these plants.

Data Analyses

We analyzed tamarisk growth using height (of tallest stem) and number of live stems. We used residuals from linear regression of height and stem number on plant age as measures of relative growth rates for these two variables; i.e., they are surrogates for growth rates corrected for age. A plant with a large positive residual has grown much faster than the average plant of that age. Only plants with unambiguous age determinations were used in regression models.

We used regression analysis to test for significant relationships between tamarisk density and cottonwood canopy cover and between tamarisk age and number of live stems and number of dead stems. We used non-linear regression analysis to assess the relationship between cottonwood height and age. We used analysis of variance (ANOVA) with tamarisk age and number of live stems as covariates to test the effect of a cottonwood canopy on the number of dead stems per tamarisk plant. We used ANOVA with stand age as a covariate to test the effect of cottonwood canopy on tamarisk density. Density was log-transformed to comply with the assumptions of the tests. We used t-tests to assess the differences in tamarisk growth rates between plots with and without cottonwood canopy. Probability values were not adjusted for multiple tests (Stewart-Oaten 1995).

RESULTS

Cottonwood occurred in all 11 alluvial bar plots and in 27 of the 39 terrace plots distributed throughout the study reaches of all three rivers. Terrace cottonwood stands with tamarisk ranged from 5 to 49 years old, with 38% less than ten years old. Density varied from 100 to 101,000 plants/ha. Height of undamaged cottonwood trees increased with age ($R^2=0.70$, $P<0.001$; Figure 2), and trees greater than 10 years old were generally taller than 8 m (Figure 2). Tall cottonwood (≥10 m high) canopy cover occurred in 14 terrace plots and ranged from 5 to 66%.

Tamarisk commonly formed thickets on open, low terraces and along overflow channels but was more sparsely distributed in cottonwood forests. There was a tendency for tamarisk density to decrease with stand age ($R^2=0.08$, $P=0.09$). Mean density of tamarisk in terrace plots was 8300 plants/ha (SE=1600) in full sun but only 700 plants/ha (SE=200) under a cottonwood canopy. This difference was significant after accounting for tamarisk stand age ($F_{1,36}=5.7$, $P=0.02$).

The mean age of tamarisk sampled in terrace plots was 16.7 years, and all plants were between 3 and 37 years of age (Figure 3). Older plants were more likely to have older live above-ground stems ($R^2=0.42$, $P<0.001$). However, the ages of the oldest live above-ground stems were strongly skewed, with 95% younger than 16 years old and 76% under seven years of age (Figure 3). Plants with live stems greater than four years old were at least 11 years old, with a mean age of 22 years. On the Powder River, 94% of the plants had oldest live stems less than seven years old (n=53), and 79% had oldest stems of four years or less.

The mean number of live stems per tamarisk plant was 10 (SE=1) and ranged from 1 to 70 in a strongly skewed distribution with 82% having 1–15 live stems. Dead stems were evident on most terrace tamarisk

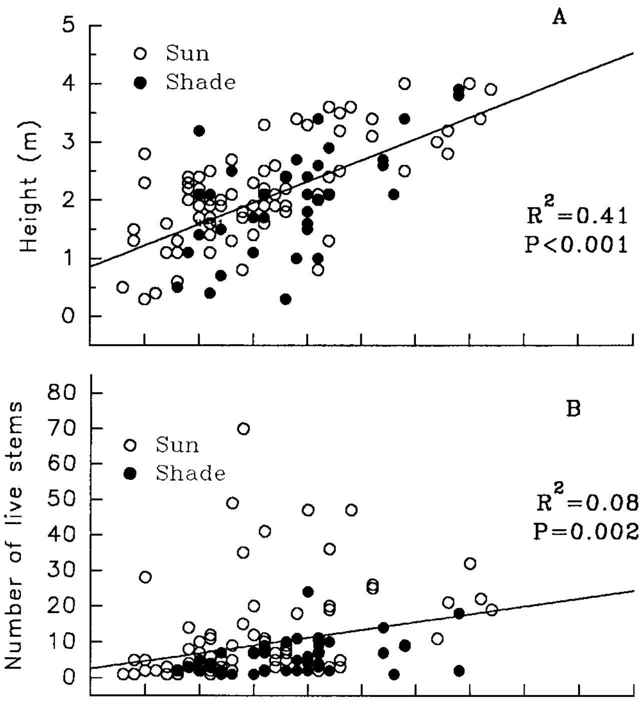

Figure 4. Relationship of sampled tamarisk (A) height and (B) number of live stems with age in terrace plots. Open circles represent plants growing in sun (<5% tall cottonwood canopy); filled circles represent shaded plants. Regression lines represent the average height and live stem number per age. Note that shaded plants are mostly below average for stem number.

plants. On average, 49% (SE=2%) of the stems still attached to the plants were dead, and the number of dead stems increased with both age (R^2=0.37, P<0.001) and number of live stems (R^2=0.19, P<0.001). Number of dead stems per tamarisk plant was not higher under a forest canopy (>5% cover) after age and size had been accounted for ($F_{1,116}$=0.5, P=0.82).

The mean height of tamarisk sampled in terrace plots was 2.1 m, and 95% of all plants were between 0.5 m and 4.0 m tall. We never observed a plant greater than 5.0 m tall in any of our stands.

There were significant positive relationships between tamarisk age and height (R^2=0.41, P<0.001) and number of live stems (R^2=0.08, P=0.002). Residuals from these regression models are measures of relative growth rates (Figure 4; see Methods). A greater proportion of tamarisk plants growing under a cottonwood canopy (>5% cover) had negative residuals compared to those growing in the open. On average, tamarisk plants beneath a cottonwood canopy (>5% cover) grew 84% as high and had 56% as many live stems compared to open-grown plants of the same age, and these difference were significant for both variables (t>2.5, P<0.02).

DISCUSSION

Tamarisk plants were one to nearly 40 years old in our study reaches, indicating that tamarisk invasion began no later than 1960 (Swenson et al. 1982) and is ongoing. Tamarisk established at high densities on freshly deposited alluvium of point bars or side channels. Older stands occurred on moist river terraces. Many of these stands were dominated by cottonwood 5 to 49 years old.

Tamarisk does not appear to be fully hardy in southeast Montana. Stems commonly die back to the ground; the oldest live stems were generally much younger than the plants (Figure 3). The majority of young tamarisk with oldest stems four years old suggests that many young plants died back to the ground between the growing seasons of 1995 and 1996 and may be susceptible to sporadic, harsh, climate-driven events such as freezing, flooding, or ice scour. Frequent dieback appears to curtail the size of plants and may help explain why tamarisk 30–40 years old in our study area usually attained heights of only 4 m or less, while plants of similar age in southwestern states regularly attain heights of 7–12 m (Campbell and Dick-Peddie 1964, Graf 1978, Everitt 1980, Stromberg 1998b). In Arizona, tamarisk plants were less branched at the base compared to Montana (Sexton 2000) and had ca. 33% dead stems on the San Pedro River (Stromberg 1998b) compared to nearly 50% in our study areas. Tamarisk growth rates may also be reduced in Montana's cooler climate. Stromberg (1998a) found that growth of plants occurring at ca. 1130–1300 m in southern Arizona was substantially lower than at ca. 1000 m.

Tamarisk is apparently intolerant of shade. Plants growing in the shade of cottonwood were only a little shorter but had many fewer live stems compared to plants in full sun. Growth rates of tamarisk were lower under a cottonwood canopy.

The smaller size and lower growth rates of shaded tamarisk appears to result mainly from a decline in the initiation of new stems. Shaded plants were only a little shorter and had less than half as many lives stems but no fewer dead stems than sun plants when adjusted for age. These results suggest that tamarisk plants beneath a cottonwood canopy do not die back more than sun plants but fail to produce as many new stems.

Both tamarisk and cottonwood are early successional phreatophytes that establish on sparsely vegetated alluvium. However, cottonwood seedlings grow more quickly than tamarisk (Sher et al. 2000), and tamarisk suffers appreciable dieback. In Montana, undamaged cottonwoods become taller than the largest tamarisk before they are 10 years old. By growing faster, cottonwood can outcompete tamarisk for light (Sher et al.

2000), presumably the limiting factor for phreatophytes. In the absence of herbivory, cottonwood quickly overtops tamarisk when they establish together (compare height-age regressions in Figures 2 and 4). Established cottonwood stands cast appreciable shade, causing tamarisk plants in the understory to decline.

Some researchers view tamarisk as an aggressive invader of riparian areas, capable of displacing native vegetation (Turner 1974, Brotherson and Field 1987, Grubb et al. 1997). Others believe that tamarisk is a poor competitor but opportunistic, colonizing early successional habitat created by human-induced changes such as reduced flows on regulated rivers (Everitt 1998). Our results suggest the latter view is correct in eastern Montana. The inability of tamarisk to achieve the height and presumably the leaf area (Sala et al. 1996) attained in the Southwest will lower its competitive ability at the northern margin of its introduced range. Although new stands of tamarisk will continue to establish with cottonwood in alluvial bar habitat along free-flowing rivers, we believe it will usually be an understory shrub, declining as the cottonwoods mature and form a closed canopy. Even when tamarisk occupied a site before cottonwood, it appeared unable to suppress cottonwood dominance. At six study sites we observed vigorous cottonwood plants 3–5 years old growing up in dense stands of tamarisk 10–23 years old.

Tamarisk is currently common on the regulated Bighorn River; however, there were few stands younger than 15 years old. This is consistent with Everitt's (1998) hypothesis that tamarisk is an opportunist, increasing with channel narrowing following upstream impoundment or diversion, although it may also indicate that tamarisk establishment is episodic. Tamarisk will persist along the unregulated Powder and Yellowstone rivers as flood flows create new habitat on point bars and low terraces, although we believe it will be unable to replace native cottonwood. Tamarisk may dominate these habitats where cottonwood fails to establish. Our results suggest that tamarisk invasion can best be curtailed by promoting the more competitive, native cottonwoods through minimizing livestock damage and maintaining flood flows timed to initiate cottonwood recruitment (Sher et al. 2000).

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