BEAVERS INDIRECTLY ENHANCE THE GROWTH OF RUSSIAN OLIVE AND TAMARISK ALONG EASTERN MONTANA RIVERS

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ABSTRACT.—Russian olive and tamarisk are introduced woody plants invading western North American riparian communities. Beavers can play an important role in structuring these communities by removing the dominant cottonwood trees. Our study explored the way in which beavers interact with cottonwood, Russian olive, and tamarisk along 4 rivers on the Great Plains of eastern Montana. We sampled cottonwood stands that supported populations of 1 or both exotic species, recording beaver damage and density in addition to size and age of cottonwood, Russian olive, and tamarisk. In stands where beaver had been present, they felled an average of 80% of cottonwood trees while rarely using Russian olive or tamarisk. Beaver foraging was apparent in nearly 90% of stands within 50 m of the river channel but only 21% of stands farther away, creating a sunny corridor along the river channel that may increase the invasive potential of Russian olive and tamarisk. Growth rates of both Russian olive and tamarisk were substantially higher where beavers had reduced the cottonwood canopy cover. Managers wishing to reintroduce beavers should consider the potential effect on invasive exotic plants.

Key words: *exotic invasion, beavers, riparian, cottonwood, Russian olive, tamarisk,* Elaeagnus angustifolia, Tamarix, *corridors, natural enemies hypothesis.*

Exotic species may become invasive in native communities because they lack natural enemies while the native community dominants do not (Harris 1988, Keane and Crawley 2002). Herbivory of plant community dominants benefits invading plants indirectly by reducing their competitive superiority (Keane and Crawley 2002). Herbivore-caused disturbances have been implicated in the invasion of several nonnative species (Mack 1981, Braithwaite et al. 1989, McClaran and Anable 1992).

North American beavers (*Castor canadensis*) are an important force structuring riparian systems throughout temperate and boreal North America (Naiman et al. 1988, Donkor and Fryxell 1999). On smaller streams they construct dams and build lodges in the resulting impoundments. On larger rivers beavers usually dig dens in banks near the water line and never construct dams. Beavers consume many species of plants, often preferring willows, aspen, poplars, and cottonwoods (*Salix* spp. and *Populus* spp.; Hall 1960, McGinley and Whitham 1985, Johnston and Naiman 1990). They sever stems of trees and shrubs at the base and eat the bark and cambial tissue. Beavers can alter structure and composition of riparian plant communities by reducing the dominance of

their preferred trees and shrubs (Johnston and Naiman 1990). However, little is known about the effects of beavers on the growth and dispersal of exotic plants.

Russian olive (*Elaeagnus angustifolia*) and tamarisk (*Tamarix* spp.) are large shrubs or small trees introduced from Eurasia. Both species invade wetland and riparian habitats of western North America (Robinson 1965, Olson and Knopf 1986). Mature Russian olive trees bear numerous clusters of small, edible, berry-like fruits in late summer. Fruits are consumed and dispersed by birds and mammals such as starlings (*Sturnus vulgaris*) and racoons (*Procyon lotor;* Kindschy 1998, Lesica and Miles personal observation). In addition, ripe fruits will float for up to 48 hours (Lesica and Miles unpublished data), allowing dispersal by water. Seeds germinate under a wide variety of moisture conditions at different times of the growing season (Shafroth et al. 1995). Tamarisk produces large numbers of small, wind-borne seeds throughout the growing season (Brock 1994). Seedlings establish on bare, fresh alluvial deposits or in other moist, disturbed soil (Stromberg 1997, Taylor et al. 1999). Both species have the potential to greatly alter the composition, structure, and functioning of riparian

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communities in the western U.S. (Everitt 1980, Bush and Smith 1995, Lesica and Miles 2001a).

We previously found that beavers facilitate replacement of cottonwood by Russian olive along the Marias River in north central Montana (Lesica and Miles 1999). Here we expand our study of exotic woody plants to 3 rivers in southeastern Montana and explore how beavers may be affecting both Russian olive and tamarisk invasions. In particular, we seek to determine (1) how commonly beavers use tamarisk and Russian olive and (2) how beaver use of cottonwood affects the performance of these co-occurring exotics.

METHODS

Study Areas

We conducted our study on portions of 4 major rivers on the Great Plains of eastern Montana (Fig. 1). Climate of the region is semiarid and continental. Mean annual precipitation was ca. 32 cm in 1950–1980 with 70% to 80% falling in April through September. Mean January minimum and July maximum temperatures ranged from –15°C to –17°C and 30°C to 32°C, respectively (NOAA 1982). Natural vegetation of highest riparian terraces is dominated by silver sagebrush (*Artemisia cana*), western wheatgrass (*Agropyron smithii*), prairie sandreed (*Calamovilfa longifolia*), and green needlegrass (*Stipa viridula*); 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 (*Populus deltoides*, hereafter referred to as cottonwood), sandbar willow (*Salix exigua*), buffaloberry (*Shepherdia argentea*), and hydrophytic grasses and sedges. Cottonwood forests may be hundreds of meters wide in meandering reaches of the rivers.

We sampled stands on the lower Marias River between Tiber Dam and Loma. The lower river valley is a few hundred meters to over 1 km wide and frequently bounded by steep breaks eroded from soft sedimentary formations. Surface elevations range from 861 m to 779 m. We sampled stands on the lower Yellowstone River between Billings and Terry. The upper portion of the study reach generally has a braided channel, while the lower portion has a single channel confined between high terraces or low bluffs. Surface elevations

range from 939 m to 662 m. The entire Montana reach of the Bighorn River below Yellowtail Dam was included in our study. The river flows with relatively few meanders and little braiding against bluffs on 1 side or the other of a wide valley. Surface elevations at Yellowtail Dam and Custer are 916 m and 860 m, respectively. Our study sites on the Powder River were between the Wyoming border and Powderville. The river meanders through a wide valley with surface elevations of 975 m to 870 m.

Field Methods

We conducted our study over a 3-year period: Marias River in 1997, Yellowstone River in 1998, Bighorn and Powder Rivers in 1999. We mapped potential study sites from a canoe. We located 34 sites on the Marias and Yellowstone Rivers with large (≥20 plants · ha⁻¹) stands of Russian olive and 93 sites on the Bighorn and Powder Rivers with large (≥1 ha with ≥2 distinct size classes) stands of tamarisk. We blindly selected a subset from this preliminary inventory for study (see Lesica and Miles 2001a, 2001b for more detail on site selection). At each site we subjectively located 1 or 2 sample plots representing stands with sapling or larger cottonwood (>2.5-cm diameter at ground level) and representative of distinct river terrace habitats supporting Russian olive or tamarisk: 9 plots on the Bighorn River, 21 on the Marias River, 8 on the Powder River, and 26 on the Yellowstone River. Sample plots were 500 m² and circular or rectangular, depending on the shape of the stands being sampled.

For each sample plot we estimated mean distance from plot center to edge of the nearest river channel. Estimates of this variable for 6 plots on the Yellowstone River were inadvertently lost during fieldwork. In each sample plot we estimated tall-cottonwood (>10 m high) canopy cover with a spherical densiometer at plot center in circular plots or at centers of the 2 halves of rectangular plots. We recorded number of cottonwood trees >2.5 cm basal diameter (bd) into 3 size classes: sapling (2.5–13 cm bd), pole (13–23 cm bd), and mature (>23 cm bd). Russian olive trees >90 cm tall were divided into 3 size classes: sapling (<8 cm bd), pole (8–13 cm bd), and mature (>13 cm bd). For tamarisk plants we recorded plants >100 cm tall, measured the tallest stem with a gauging pole, and counted number of live stems.
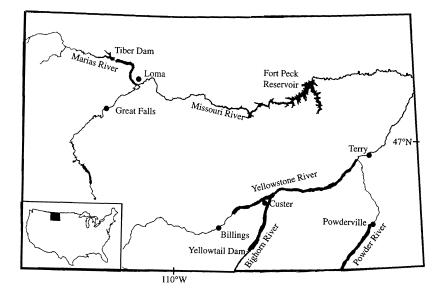
Fig. 1. Location of study reaches (thickened lines) along 4 rivers on the Great Plains of eastern Montana.

We obtained age estimates for 3 representative Russian olive and tamarisk plants in dominant size classes and at least 1 plant in subordinate classes. In eastern Montana, tamarisk has a shrub growth form. New branches and roots arise from older branches that have been buried by sediment (Everitt 1980). We excavated tamarisk plants and attempted to obtain a cross section from the point just below the union of the lowest stems. However, some tamarisk age estimates may be inaccurate because it was not always possible to determine exactly the level of initial establishment. We obtained age estimates for Russian olive from cross sections or increment cores taken just above ground level. Many Russian olive branch at ground level, and root flare occurs just below, so we often took increment cores or cross sections from the base of the largest leader. The largest leader was 1 year younger than the plant in 13 of 16 juveniles where both were measured; thus, we added 1 year to the estimated age of Russian olive when cores were taken from the largest leader. We measured basal diameter of sample cottonwood and Russian olive to the nearest 1 cm with a diameter tape. Annual rings were counted using a 10X microscope.

In each plot we recorded the number of cottonwood, Russian olive, and tamarisk plants damaged by beavers. We recognized beaver damage by tapered severing with tooth marks on limbs or boles.

Vascular plant nomenclature follows the Great Plains Flora Association (1986). We follow Welsh et al. (1987) in referring to our tamarisk plants as *T. ramosissima*. These plants are difficult to distinguish from *T. chinensis* (Brock 1994) and have also been incorrectly called *T. pentandra* (Baum 1967).

Data Analysis

Mean annual growth rate was estimated as basal diameter divided by age for Russian olive and as size index divided by age for tamarisk. Tamarisk size index is height of the tallest live stem multiplied by the number of live stems, integrating the influence of height and stem number on shrubby tamarisk plants. We believe this is a reasonable index of biomass because linear regression models of stem length effectively accounted for variation in weight of tamarisk stems ($R^2 = 0.87$, $P < 0.001$, $n = 24$). Only Russian olive and tamarisk plants with unambiguous age determinations were used for growth-rate estimates. We used analysis of variance (ANOVA) to assess the effect of a tall-cottonwood canopy on the untransformed values of growth rates for Russian olive and tamarisk. Growth rates for Russian olive were higher for older trees, so we analyzed juvenile (5–10 years old) and mature (>10 years old) trees

separately. Russian olive growth did not vary among rivers ($F_{2,169} = 1.4$, $P = 0.25$), but because it had a tendency to decrease farther from the river ($R^2 = 0.07$, $P < 0.05$), we used distance to channel as a covariate in the ANOVA models to account for this correlation. Tamarisk growth rates did not vary with distance from the river ($R^2 = 0.001$, $P = 0.77$) but were different among rivers ($F_{2,117} = 6.6$, $P = 0.002$), so river was included as a factor in the ANOVA model. We used the non-parametric Spearman's rank correlation coefficient (ρ) to assess the association between proportion of cottonwood damaged by beaver and plot distance from the river channel, because a large number of plots had either 0% or 100% beaver damage.
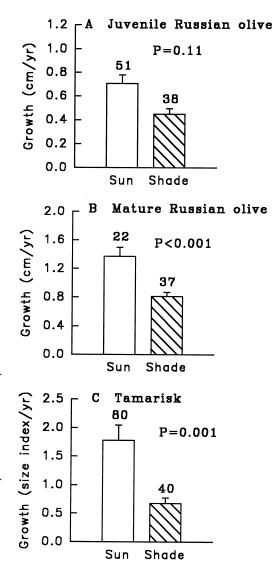
RESULTS

Cottonwood occurred with either Russian olive or tamarisk or both in 64 study plots on the 4 rivers. Russian olive did not occur in study plots on the Powder River, and tamarisk did not occur on the Marias River. Density of sapling and larger cottonwood varied from 20 to 2420 plants · ha^{-1} with a mean of 511 plants · ha^{-1} ($s_{\bar{x}} = 64$ plants · ha^{-1}). Density of Russian olive varied from 20 to 1220 plants · ha^{-1} with a mean of 153 plants · ha^{-1} ($s_{\bar{x}} = 28$ plants · ha^{-1}). Russian olive trees varied from 4 to 36 years old with a mean of 11 years. Density of tamarisk varied from 40 to 2200 plants · ha^{-1} with a mean of 815 plants · ha^{-1} ($s_{\bar{x}} = 163$ plants · ha^{-1}). Tamarisk plants were 3 to 37 years old with a mean of 17 years. Density did not vary significantly among the rivers for cottonwood ($F_{3,60} = 1.1$, $P = 0.34$), Russian olive ($F_{2,49} = 1.9$, $P = 0.17$), or tamarisk ($F_{2,16} = 1.6$, $P = 0.23$). We failed to find a difference in density of Russian olive ($t = 0.69$, $P = 0.50$) or tamarisk ($t = 0.16$, $P = 0.87$) in open areas compared with those beneath a cottonwood canopy, probably due to large variation in density among stands.

The presence of a cottonwood canopy was associated with a lower growth rate of Russian olive and tamarisk (Fig. 2). Mean annual growth rate (diameter/age) of juvenile Russian olive was reduced by 36% under a cottonwood canopy compared with the open ($F_{1,86} = 2.5$, $P = 0.11$), and growth rate of mature plants was reduced by 41% under cottonwood ($F_{1,56} = 21.1$, $P < 0.001$). Mean annual growth rate of

Fig. 2. Basal diameter growth rate of (A) juvenile (5–10 years) and (B) mature (>10 years) Russian olive, and (C) size (maximum stem height × stem number) growth rate of tamarisk with and without a cottonwood canopy >10 m high. Sample sizes given above the bars.

tamarisk plants under a cottonwood canopy was reduced by 62% compared with those in the open ($F_{1,116} = 7.2$, $P = 0.009$).

Beaver damage to cottonwood was common and severe. In stands along the Marias, Powder, or Yellowstone Rivers where beaver use was recorded, beavers damaged more than 80% of cottonwood trees on average (Fig. 4). Beaver damage to cottonwood was less severe along
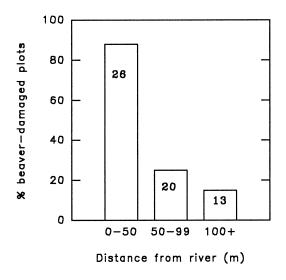
Fig. 3. Percent of study plots with beaver-damaged cottonwood at different distances from river channels. Sample sizes given inside bars.

Fig. 4. Mean proportion ($\pm s_{\bar{x}}$) of cottonwood, Russian olive, and tamarisk plants damaged by beaver in study plots where they had been present. Sample sizes given above bars.

the Bighorn River. Overall beaver damage was present in nearly 90% of study plots within 50 m of river channels, but only 21% of plots farther away from channels showed damage (Fig. 3; $\chi^2 = 8.54$, $P = 0.003$). There was strong negative correlation between plot distance from the river and proportion of cottonwood trees damaged by beaver ($\rho = 0.66$, $P < 0.001$).

Beaver had little or no direct impact on Russian olive and tamarisk. There were no beaver-damaged tamarisk in any of the 10 plots where beaver use was recorded on the Bighorn, Powder, and Yellowstone Rivers (Fig. 4). Tamarisk did not occur in Marias River study plots. Russian olive was not damaged by beavers in Bighorn and Yellowstone River study plots (Fig. 4). A mean of 15% of Russian olive showed beaver damage compared to 89% for cottonwood in plots where both occurred on the Marias River (paired-sample $t = 8.81$, $P < 0.001$). Most beaver-damaged cottonwoods were cut off at the base, while damage to Russian olive was usually confined to 1 or 2 basal limbs.

DISCUSSION

Exotics may become invasive because they lack a full complement of pests, predators, and pathogens that negatively affect native s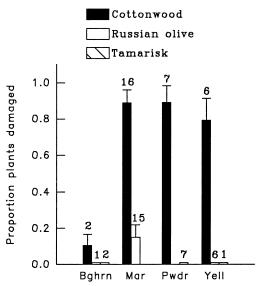pecies (Harris 1988, Keane and Crawley 2002). This may be the case with Russian olive and tamarisk in North America. Cottonwood is potentially a stronger competitor than either Russian olive or tamarisk because it grows taller (Sher et al. 2000, Lesica and Miles 2001a, 2001b), out-competing them for light, presumably the limiting resource in these mesic environments. Cottonwood and other trees in the genus *Populus* are highly preferred food of beavers (Hall 1960, McGinley and Witham 1985, Johnston and Naiman 1990). Presence of beavers strongly alters the competitive hierarchy between cottonwood and the introduced species. At our study sites with evidence of beaver damage, an average of 80% of cottonwoods had been felled. In contrast, Russian olives were rarely damaged by beavers, and we never observed beaver-damaged tamarisk.

Beavers create areas of lower competitive stress by felling the dominant cottonwoods. Most beaver damage to cottonwood occurred within 50 m of river channels, and most cottonwood stands within this distance had been damaged. Beavers forage near river banks for 2 possible reasons: they are more vulnerable to coyotes and other predators farther from the safety of water, and transporting food material

greater distances requires more energy (Jenkins 1980, Belovsky 1984). Beaver activity helps create and maintain corridors of open, sunny habitat along river channels that would otherwise be dominated by cottonwood.

Absence of a cottonwood canopy in low-terrace, streamside habitats allowed higher growth rates for both Russian olive and tamarisk. Although a tall-cottonwood canopy significantly affects growth of the exotic species, it may not always reduce recruitment (Lesica and Miles 2001a) or density. Nonetheless, plants of both introduced species under a cottonwood canopy are smaller and presumably produce fewer fruits than plants of the same age growing in full sun. Slower growth and associated reduced fecundity could retard population growth rates and invasion potential (Williamson 1989, Rejmanek 1996).

Rivers act as dispersal corridors for many plants (Malanson 1993, Jansson et al. 2000), including exotics (Thebaud and Debussche 1991, de Waal et al. 1994, Parendes and Jones 2000). Non-forested corridors created by beavers along rivers may facilitate dispersal of Russian olive and tamarisk. Russian olive fruits have spongy flesh surrounding the large seed. They float for at least 48 hours once the seed is mature and the flesh has dried (Lesica and Miles unpublished data). Russian olive fruits are readily eaten by racoons that use the riparian zone as foraging corridors (Jones et al. 1983) and disperse the seeds in their feces (Lesica and Miles personal observation). Unfortunately, viability of these seeds is not known. Frugivorous birds also disperse Russian olive seeds (Olson 1974, Kindschy 1998), and many of these species preferentially use riparian corridors for foraging (Finch and Ruggiero 1993). By removing cottonwoods near the river, beavers could promote earlier and greater Russian olive fruiting and allow more fruits to reach the water or be moved along the riparian corridor by dispersing animals. Beavers may also enhance the dispersal of tamarisk wind-borne seeds along the river corridor by removing trees and widening the zone of increased wind turbulence.

Continued spread of both Russian olive and tamarisk is considered a threat to the integrity of native communities. Researchers have speculated that Russian olive can hinder recruitment of native cottonwoods (*Populus*) and willows (*Salix;* Currier 1982, Lesica and Miles 2001a). Decline of these dominant native riparian woody plants could cause loss of habitat for species such as cavity-nesting and insectivorous birds (Knopf and Olson 1984, Olson and Knopf 1986). Tamarisk infestations may alter riparian function in a number of ways. Dense stands of tamarisk are reported to transpire large quantities of water, perhaps leading to lowered stream flows (Brotherson and Field 1987). Tamarisk invasion may have a detrimental effect on small mammal populations (Ellis et al. 1997). In addition, tamarisk stands have altered avian communities, with insectivores and frugivores being more common in native vegetation (Cohan et al. 1978).

Although both species of beavers have been extirpated from much of their original range in historic times, this trend is now being reversed, as they are reintroduced in parts of North America (Albert and Trimble 2000) and northern Europe (*Castor fiber;* Danilov and Kan'shiev 1983, Hartman 1994, Macdonald et al. 2000). In general, these reintroductions enhance natural functioning of riparian areas (Naiman et al. 1988, Naiman and Rogers 1997) and may even help control exotic plants (Albert and Trimble 2000). Many native plant species benefit from streamside beaver activity (Naiman et al. 1988). For example, herbaceous species, especially grasses and sedges, are more abundant in the zone of reduced shade created by beaver (Lesica and Miles unpublished data). We certainly do not recommend removing beavers from natural systems. However, if tamarisk, Russian olive, or other invasive riparian exotics occur in drainages, the presence of beavers may exacerbate the problem and make control more difficult. It may be best to first control undesirable plants before proceeding with beaver reintroduction.

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