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NATURAL HISTORY AND INVASION OF RUSSIAN OLIVE ALONG EASTERN MONTANA RIVERS

Peter Lesica¹ and Scott Miles¹

ABSTRACT.—Russian olive (*Elaeagnus angustifolia*) is an exotic tree considered invasive in the western U.S. There is concern it will replace native riparian forests, resulting in a loss of biological diversity. We studied the dynamics of Russian olive invasion on the Marias River in north central Montana and the lower Yellowstone River in southeastern Montana to determine where and in what habitats it occurs, how it is interacting with plains cottonwood (*Populus deltoides*) and green ash (*Fraxinus pennsylvanica*), the dominant native riparian trees, and how these interactions will alter future riparian forests. We measured size, density, and age of Russian olive, cottonwood, and green ash as well as vegetative composition and overstory canopy cover in sample plots in alluvial bar and terrace habitats at randomly chosen sites.

Russian olive occurred in multiple-age stands on terraces along both rivers but was rarely found establishing in recently flood-deposited alluvium. Diameter growth rates decreased with increasing overstory canopy cover but did not vary significantly with soil moisture as reflected by ground-layer vegetation. Russian olive grew at nearly 3 times the rate of the native late-successional green ash at sites where both occurred together. Russian olive attained reproductive maturity at ca 10 years of age on both rivers, and, on average, there was less than 1 new plant recruited per mature tree per year. Beaver felled a high proportion of cottonwood within 50 m of both river channels, but Russian olive was little damaged.

Russian olive will establish with increasing frequency in riparian forests as well as wet meadows and along ditches and overflow channels in eastern Montana. Native riparian forests will be replaced by Russian olive as old cottonwoods die on upper terraces or are removed by beaver near active channels. Cottonwood establishment and dominance will not be precluded on rivers where flooding regularly reinitiates primary succession beyond the zone of beaver activity. However, Russian olive may preclude cottonwood recruitment by shading seedlings along streams where flooding does not occur or merely deposits alluvium on top of existing vegetation rather than creating new channels or broad point bars. Because of its long maturation time and low recruitment rate, Russian olive invasion in Montana will proceed slowly compared with many exotics.

Key words: Russian olive, *Elaeagnus angustifolia*, exotic, cottonwood, riparian habitat, Montana, beaver.

Riparian areas provide important wildlife habitat in the semiarid landscapes of western North America (reviewed in Finch and Ruggerio 1993, Naiman et al. 1993). Numerous species of plants and animals are restricted to these habitats, and productivity of riparian systems is usually much higher than water-limited uplands (Brinson et al. 1981). Exotic species invade these dynamic systems and alter processes and species composition (deWaal et al. 1994, Stohlgren et al. 1998), often causing a loss of biological diversity (Drake et al. 1989).

Russian olive (*Elaeagnus angustifolia*) is native to southern Europe and western Asia (Little 1961) and was introduced into North America during Colonial times, probably for ornamental purposes (Elias 1980). Since ca 1900 it has been planted for windbreak and wildlife enhancement purposes and has become

extensively naturalized throughout the western United States, especially in riparian areas (Christiansen 1963, Olson and Knopf 1986a, 1986b). In Montana an average of 40,000 Russian olive nursery stock are distributed by the state each year (Montana Department of Natural Resources and Conservation nursery data, 1997). Russian olive has been planted as windbreaks in Montana since at least 1953 (Montana Department of Natural Resources and Conservation nursery data, 1997), and naturalized trees occur along most major rivers in the Great Plains portion of the state (Olson and Knopf 1986a).

Russian olive can enhance habitat for some wildlife species (Knopf and Olson 1984). On the other hand, there is speculation that Russian olive may hinder recruitment of native cottonwoods (*Populus*) and willows (*Salix*; Currier

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1982). A decline of these dominant native riparian woody plants could cause the loss of habitat for species such as cavity-nesting and insectivorous birds (Knopf and Olson 1984, Olson and Knopf 1986a).

The purpose of our study was to document the dynamics of Russian olive invasion along the regulated lower Marias and unregulated lower Yellowstone rivers in eastern Montana. Both rivers have peak discharges dominated by late spring/early summer snowmelt. In particular we ask: (1) What habitats does Russian olive occupy? (2) How are growth, reproduction, and recruitment affected by habitat and how do these vital rates influence its invasiveness? (3) How does beaver herbivory affect the interaction between plains cottonwood (*Populus deltoides*; hereafter referred to as cottonwood) and Russian olive? We then use this information to speculate on how Russian olive will affect riparian vegetation in the future and the implications for management.

STUDY AREAS

The Marias River has its headwaters along the eastern front of the Rocky Mountains 60–150 km south of the Canadian border. Tiber Dam on the Marias was completed in 1956 ca 135 river km above its confluence with the Missouri River just below the town of Loma. We conducted our study between Tiber Dam and Loma (Fig. 1). The lower Marias cuts through sedimentary plains composed primarily of Cretaceous shales and sandstones (Alt and Hyndman 1986) glaciated during the Illinoian Ice Age (Perry 1962). The lower river valley is between a few hundred meters and >1 km wide and frequently bounded by steep breaks eroded from the soft sedimentary formations. Surface elevations of the Marias River just below Tiber Dam and at Loma are 861 and 779 m, respectively.

The Yellowstone River has its headwaters in the mountains of southwestern Montana and northwestern Wyoming. In Montana it flows north and then east from Yellowstone National Park to the confluence with the Missouri River just east of the Montana–North Dakota border. It is unregulated its entire length. We conducted our study on 2 reaches of the lower Yellowstone River: (1) from Pompeys Pillar to Hysham and (2) from Sheffield to Terry (Fig. 1). The river flows through unglaciated, dissected

plains underlain by late Cretaceous sandstone of the Fort Union formation (Alt and Hyndman 1986). The upper reach generally has a braided channel and relatively level floodplain. In much of the lower reach the river has a single channel confined between high terraces or low bluffs. Surface elevations of the Yellowstone River are 939 m at Billings, 711 m at Miles City, and 662 m at Terry.

Climate along both rivers is similar: semi-arid and continental. Mean annual precipitation in 1950–1980 for the Marias (at Loma) and Yellowstone (at Hysham) was 32 cm with 70–75% falling in April through August. Mean annual temperature in 1950–1980 was 6.8°C and 8.0°C for Loma and Hysham, respectively (NOAA 1982).

Upland vegetation in the study areas is shrub-steppe or mixed-grass prairie dominated by sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and/or perennial grasses including needle-and-thread (*Stipa comata*), western wheatgrass (*Agropyron smithii*), and blue grama (*Bouteloua gracilis*). Vegetation of uppermost river terraces is dominated by silver sagebrush (*Artemisia cana*), western wheatgrass, and green needlegrass (*Stipa viridula*); however, extensive areas of upper terrace along the Yellowstone River have been converted for agricultural crops. Terraces closer to the river channel support riparian vegetation dominated by cottonwood (*Populus deltoides*, some *P. angustifolia*), willow (*Salix* spp.), buffaloberry (*Shepherdia argentea*), and hydrophytic grasses, sedges, and bulrushes. Vascular plant nomenclature follows Great Plains Flora Association (1986). Cottonwood forests may be hundreds of meters wide in meandering reaches of the rivers.

RUSSIAN OLIVE

Russian olive is a small tree; naturalized plants may reach 10 m tall in Montana. It occurs on soils with low to moderate soluble salt concentrations (Carman and Brotherson 1982). Our observations indicate that Russian olive frequently branches at ground level, only 1–2 dm above root flare in moist, unshaded sites. However, it branches well above ground level more often in drier, shaded habitats. Twigs have spines, and branches elongate each year by growth from a lateral bud near the terminus of the previous year's growth. Russian olive is capable of sprouting from the base

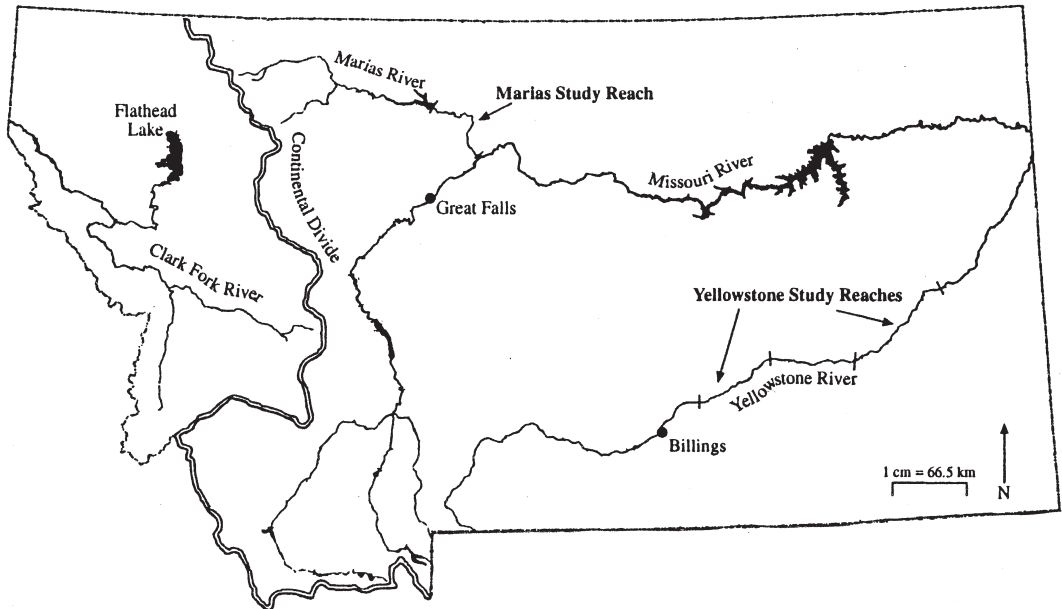


Fig. 1. Location of study reaches on the Marias and Yellowstone rivers in Montana.

when damaged. Mature trees bear nectar-producing flowers (Hayes 1976) that mature into numerous clusters of small, edible, berry-like fruits in late summer. Seeds germinate under a wide variety of moisture conditions at different times of the growing season (Shafroth et al. 1995). Russian olive fixes nitrogen in its roots through a symbiotic relationship with the bacteria *Frankia* spp. (Huss-Danell 1997).

METHODS

Field Methods

We conducted our study on the Marias and Yellowstone rivers in spring and summer of 1997 and 1998, respectively. During spring canoe trips we mapped all areas where we observed Russian olive density of at least 20 plants · ha⁻¹ and randomly selected 19 sites on the Marias and 15 sites on the Yellowstone for sampling during mid-August and early September. At each site we subjectively located sample plots to represent a recently deposited alluvial bar (when present) and all the distinct habitats that supported Russian olive. Each site had 2–4 sample plots, for a total of 38 plots on the Marias and 42 plots on the Yellowstone. 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 to the edge of the nearest river channel and recorded the distance above the September river level with a hand-held level and gauging pole. Estimates for 6 plots on the Yellowstone were inadvertently lost during fieldwork.

In each sample plot we estimated canopy cover (Daubenmire 1959) of all common ($\geq 1\%$ cover) vascular plant species to the nearest 5% and estimated tall-tree canopy cover with a spherical densiometer at the center of circular plots and at 2 equidistant points in rectangular plots. Estimates of seedling density on alluvial bars were made from ten 1- or 2-m² circular microplot samples spaced evenly throughout the plot. We were not always able to distinguish between 2 sedges, *Carex aquatilis* and *C. lanuginosa*, and so they were combined in the analyses.

In each sample plot we recorded the number of Russian olive trees in each of 4 size classes: seedling (<90 cm tall), sapling (>90 cm tall and <8 cm basal diameter [bd]), pole (>183 cm tall and 8–13 cm bd), and mature (>13 cm bd). We obtained age estimates for 3 plants in the 1–2 dominant (with the greatest basal area) size classes and at least 1 plant in subordinate size classes for cottonwood, Russian

olive, and green ash (*Fraxinus pennsylvanica*) from cross sections or increment cores taken just above ground level (basal diameter). We counted the number of annual rings using a 10× microscope. Age estimates of cottonwood taken from increment cores are likely to be less than the actual age because ground level is not always the level of the establishment surface (Bradley and Smith 1986, Scott et al. 1997). In addition, some cottonwood trees had rotten centers, resulting in underestimates of age. We used the oldest measurement for cottonwood stand age, but this should be considered a minimum estimate. 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 base in 5 of 6 juvenile plants 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 to the nearest 1 cm with a diameter tape and also recorded whether the sampled Russian olive trees had fruit.

We recorded the number of cottonwood and Russian olive trees in each plot damaged by beavers. We estimated ungulate browse use as the proportion of at least 25 two-year-old Russian olive or cottonwood twigs browsed. Twigs with abruptly blunt ends and new shoots arising from lateral buds were considered browsed (Rutherford 1979). Only twigs easily available to native or domestic ungulates (1–5 ft high) on vigorous plants were chosen haphazardly on a random walk through the plot.

Data Analysis

We ordinated plot understory species by percent cover with reciprocal averaging (RA). RA was chosen because it is an effective method when the data set is structured by a single predominant gradient (Gauch 1982, McCune and Mefford 1995). Species scores indicated that the 1st axis represented a moisture continuum and was a metric of stand successional age (see Results), a continuum that structures many Great Plains floodplain vegetation mosaics (Johnson et al. 1976, Boggs 1984). We used RA axis 1 plot scores to quantify a successional continuum because vegetation changes as represented by a multivariate gradient often integrate important correlated

environmental variables (Whitaker 1975:120, Gauch 1982).

Average growth rate was estimated as basal diameter divided by age. We compared the growth rate of each recorded green ash tree with the Russian olive from the same plot with the most similar age within 10 years using a paired-sample *t* test. For all other growth rate calculations, only Russian olive plants with unambiguous age determinations and 5–12 years old were used.

Recruitment rate is a measure of how quickly the density of Russian olive trees increases in a stand. We estimated recruitment rate as the number of seedling plus sapling plus pole (if poles averaged <10 years old) plants divided by the number of poles (if they averaged ≥10 years old) plus mature plants multiplied by their mean age minus 10 (number of years to maturity). In other words, recruitment rate is the number of recruits per mature tree per year since the stand was 10 years old. Plots without mature Russian olive were excluded from these analyses. This measure assumes no immigration of recruits and is only an approximate metric of how quickly Russian olive can increase at a site. Seedling and sapling size classes were considered juvenile because only 15% ($N = 114$) bore fruit, while 86% ($N = 128$) of pole and mature classes bore fruit.

We used regression analysis to test for significant relationships between Russian olive growth and recruitment rates and age, tall-tree canopy cover, height above the river, and vegetation. We used analysis of variance (ANOVA) to test for a difference in Russian olive growth rate between the 2 rivers with age of the trees as a covariate in the model. A *t* test was used to test for a difference in Russian olive recruitment rate between the 2 rivers. Two-way ANOVA was employed to assess differences in browse use between cottonwood and Russian olive between the 2 rivers.

RESULTS

Vegetation of Study Sites

Vegetation on alluvial bars was sparse. Common plants included the annuals *Xanthium strumarium* on the Marias ($n = 6$ plots) and *Eragrostis hypnoides*, *Panicum capillare*, and *Chenopodium botrys* on the Yellowstone ($n = 14$). Cottonwood and *Salix exigua* seedlings were common on both rivers.

TABLE 1. Understory plant species with highest and lowest scores on RA axis 1. Wetland indicator status estimates the probability of a species occurring in wetlands; obl = >99%, facw = 67–99%, fac = 34–66%, facu = 1–33% (Reed 1988). Species without a status generally do not occur in wetlands.

Species	RA score	Wetland indicator status
High scores (wet sites)		
<i>Scirpus maritimus</i>	447	obl
<i>Equisetum arvense/fluviatile</i>	346	fac/obl
<i>Mentha arvensis</i>	290	facw
<i>Phalaris arundinacea</i>	285	facw+
<i>Salix exigua</i>	255	facw+
<i>Carex aquatilis/lanuginosa</i>	238	obl
<i>Solidago graminifolia</i>	235	facw
<i>Muhlenbergia asperifolia</i>	195	facw
<i>Spartina pectinata</i>	192	facw
<i>Salix lutea</i>	174	facw+
Low scores (moist sites)		
<i>Medicago lupulina</i>	-170	facu
<i>Rhus trilobata</i>	-172	—
<i>Symphoricarpos occidentalis</i>	-201	—
<i>Poa pratensis</i>	-229	facu
<i>Agropyron smithii</i>	-269	facu
<i>Thermopsis rhombifolia</i>	-281	—
<i>Stipa viridula</i>	-296	—
<i>Elymus canadensis</i>	-316	facu
<i>Agropyron cristatum</i>	-319	—
<i>Calamovilfa longifolia</i>	-377	—

Terrace vegetation associated with Russian olive was diverse. The 1st RA axis accounted for 39% of variation among plots and clearly represented a moisture/successional gradient spanning very wet low terraces to very dry upper terraces on both rivers. All 10 species with the highest RA scores are obligate or facultative wetland plants, while 4 of the 10 lowest scoring species are facultative upland plants, and the remainder are considered upland species (Table 1; Reed 1988). There was also a strong correlation between cottonwood stand age (oldest tree) and RA plot scores ($r = 0.59$, $P < 0.001$).

Russian Olive Habitats

Russian olive did not occur in alluvial bar sample plots on the Marias River and was found in only 2 alluvial bar plots (14%) on the Yellowstone where density was < 4 plants \cdot 100 m^{-2} . On young, moist terraces (high RA scores), Russian olive occurred with and without a cottonwood canopy; however, it never occurred outside a cottonwood canopy on the dry, highest terraces. Density of Russian olive in terrace stands varied from 20 to 760 plants \cdot ha^{-1} with a mean of 186 plants \cdot ha^{-1} on the Marias

River. On the Yellowstone River, Russian olive varied from 20 to 5120 plants \cdot ha^{-1} with a mean of 676 plants \cdot ha^{-1} .

Russian olive in all size classes occurred along both rivers, and most stands were multiple-aged. The oldest Russian olives recorded were 36 and 40 years old on the Marias and Yellowstone rivers, respectively. Mean age of Russian olive stands (i.e., age of oldest tree in plot) was 15.3 years ($\bar{x} = 1.2$) on the Marias and 18.6 years ($\bar{x} = 1.4$) on the Yellowstone. The oldest Russian olive tree was as old as or older than the oldest cottonwood in 39% and 14% of the stands on the Marias and Yellowstone rivers, respectively. In many cases these were stands where cottonwoods appeared to have established in fresh alluvium deposited on existing terraces with established Russian olives.

Growth

Growth rate of Russian olive (diameter \cdot age $^{-1}$) increased with age over all age classes ($r^2 = 0.10$, $P < 0.001$, $n = 153$). This relationship was significant for juvenile trees (5–10 years; $r^2 = 0.11$, $P = 0.002$, $n = 91$) but not for mature trees (> 10 years; $r^2 = 0.02$, $P =$

0.31, $n = 62$). Growth varied between 0.1 and 2.7 $\text{cm} \cdot \text{yr}^{-1}$, with a mean of 0.80 $\text{cm} \cdot \text{yr}^{-1}$ ($\bar{x} = 0.04$) and was not different between the 2 rivers ($F_{1,150} = 15.3$, $P = 0.61$) when corrected for age. Growth rate was negatively associated with height above the September river level for both the Marias ($r^2 = 0.20$, $P = 0.028$) and Yellowstone ($r^2 = 0.18$, $P = 0.012$) rivers.

There was no relationship between growth rate of Russian olive and understory vegetation as represented by the 1st RA axis ($r^2 = 0.01$, $P = 0.32$, $n = 153$). There was a significant negative relationship between Russian olive growth rate and tall-tree (i.e., cottonwood) canopy cover ($r^2 = 0.06$, $P = 0.002$, $n = 153$), which explained 21% of the variation when age was included as a covariate in the regression model ($r^2 = 0.21$, $P < 0.001$).

Green ash occurred in 6 sample plots on the Yellowstone River in the vicinity of Miles City. Mean density of green ash and Russian olive juveniles (seedling + sapling) was 33 and 13 plants $\cdot \text{plot}^{-1}$ respectively, but this difference was not significant ($t = 0.74$, $P = 0.49$). Sapling or larger green ash varied from 7 to 28 years old. Mean diameter growth rate of green ash was 0.43 $\text{cm} \cdot \text{year}^{-1}$, while growth rate of paired Russian olive was 1.10 $\text{cm} \cdot \text{year}^{-1}$ (paired sample $t = 7.0$, $P < 0.001$), nearly 3 times as great. Mean ages of green ash and the paired Russian olive were 16.5 and 16.6 years respectively.

Reproduction

None of the Russian olive trees sampled on the Marias River under age 5 produced fruit, while all trees over age 14 fruited (Fig. 2). On the Yellowstone River only 1 of 38 plants ≤ 6 years old fruited in 1998. Fruiting generally began at 7–10 years, and 89% of Russian olive > 10 years old produced fruit (Fig. 2). These results suggest the average age of 1st reproduction for Russian olive on both rivers is ca 10 years.

Recruitment

Russian olive recruitment rate per mature tree in 46 stands varied from 0 to 4.07 recruits $\cdot \text{yr}^{-1}$, with a mean of 0.69 recruits $\cdot \text{yr}^{-1}$ ($\bar{x} = 0.15$). There was no difference in recruitment rate between the Marias and Yellowstone rivers ($t = 0.51$, $P = 0.61$). There was no significant

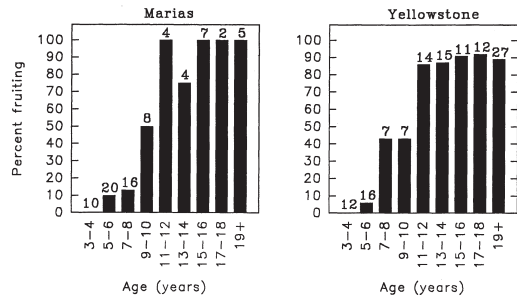


Fig. 2. Proportion of Russian olive trees producing fruit in 2-year age classes on the Marias and Yellowstone rivers.

relationship between recruitment rate and tall-tree canopy cover ($r^2 = 0.006$, $P = 0.61$). There was also no significant relationship between Russian olive recruitment rate and associated understory vegetation as represented by RA axis 1 plot scores ($r^2 = 0.001$, $P = 0.87$), and there was no relationship between recruitment rate and elevation above September river levels for either the Marias ($r^2 = 0.06$, $P = 0.28$) or Yellowstone ($r^2 < 0.01$, $P = 0.86$).

Herbivory

Beaver damage occurred in 59% of the Marias River terrace stands where an average of 57.1% ($\bar{x} = 9.4$) of the cottonwood were damaged by beaver, while only 14.6% ($\bar{x} = 5.2$) of the Russian olive were damaged. Only 18% of sample plots on the Yellowstone showed evidence of beaver, with 78% of cottonwood trees damaged, while none of the Russian olive in these plots were injured. Most beaver-damaged cottonwood were felled at the base, while damage to Russian olive was usually confined to 1 or 2 basal limbs.

Ungulate browse use of 2nd-year branch ends was 39% ($\bar{x} = 5\%$) and 56% ($\bar{x} = 5\%$) for Russian olive and cottonwood, respectively, on the Marias River and 57% ($\bar{x} = 6\%$) and 48% ($\bar{x} = 6\%$) on the Yellowstone. There were no significant differences in overall browse use between the 2 rivers ($F_{1,54} = 1.19$, $P = 0.28$) or between the 2 species when both rivers were taken together ($F_{1,54} = 0.57$, $P = 0.45$). There was a significant interaction between tree species and river ($F_{1,54} = 6.02$, $P = 0.02$), indicating different ungulate preferences between the 2 rivers.

DISCUSSION

Vegetation of large riparian systems is dynamic. Cottonwood and willow usually establish from wind-borne seed on fresh, moist alluvium deposited by floods or channel meandering (Braatne et al. 1996, Scott et al. 1996). Both native species are intolerant of shade and rarely reproduce in their own shade or that of other species (Johnson et al. 1976, Rood and Mahoney 1990). On the Marias and Yellowstone rivers, terraces with an understory of willow and a ground layer of hydrophytic plants (high RA scores) were dominated by relatively young cottonwoods. As stands became older, periodic deposition raised ground level higher above the water table. These older stands supported an understory dominated by less hydric shrubs and grasses (Johnson et al. 1976, Boggs 1984). After 100–200 years cottonwoods die and are replaced by sagebrush or shade-tolerant green ash if it is present (Johnson et al. 1976, Boggs 1984, Hansen et al. 1995). Our results suggest that Russian olive may affect this successional riparian sequence in several ways.

Russian olive was common along both rivers, and older stands generally had plants of many ages, suggesting that recruitment occurs under established trees and does not require uncommon flood events. Russian olive has large seeds that help allow establishment in the shade of a cottonwood canopy and in the open on lower terraces and other relatively wet sites, such as banks of overflow channels (Shafroth et al. 1995). Recruitment and growth were not significantly affected by stand age as reflected by understory vegetation; however, growth, but not recruitment, was greater on lower sites closer to alluvial ground water.

Although Russian olive is capable of germinating on bare, moist alluvium with cottonwoods (Shafroth et al. 1995), we rarely observed this in the study areas, and Russian olive was younger than cottonwood in most stands. Both species grow quickly, but Russian olive does not become as tall as cottonwood. On very active river reaches where cottonwood establishment occurs on new point bars or in flood channels, cottonwood will persist in the presence of Russian olive. However, on many streams and entrenched rivers, cottonwood recruitment occurs primarily in alluvium deposited on existing vegetation by overbank

flows. Here Russian olive could eventually preclude establishment of cottonwood's shade-intolerant seedlings (Read 1958, Shafroth et al. 1995).

Cottonwood establishment and dominance will not be precluded by Russian olive on the upper reaches of the free-flowing Yellowstone River where flooding and new channel development continuously create new habitat for cottonwood establishment well beyond the zone of beaver activity. However, cottonwood may eventually be replaced by Russian olive on the Marias River where flow regulation by Tiber Dam has changed seasonal flow patterns and attenuated flood flows (Rood and Mahoney 1995). Here riparian cottonwood forests will eventually be replaced by Russian olive as old cottonwoods die on upper terraces and young cottonwoods on low terraces are removed by beaver or shaded by less palatable species (Lesica and Miles 1999). Absence of flooding decreases alluvial deposition and cottonwood recruitment on all but the lowest terraces close to the river channel. Beaver damage to cottonwood was usually severe on these lower terraces, but Russian olives were little affected (Lesica and Miles 1999). Beaver damage occurred primarily close to the active channels on both rivers probably for 2 reasons: beaver are more vulnerable to predators such as coyotes farther from the safety of water, and transporting food material greater distances requires more energy (Jenkins 1980, Belovsky 1984, Easter-Pilcher 1987). Indeed, on both rivers we observed that Russian olive often lined the riverbank, with cottonwood becoming more common farther away from the channel, suggesting that beaver can prevent cottonwood from developing a mature canopy close to the river while having little effect on the continued invasion of Russian olive.

Cottonwood recruitment and growth can be adversely affected by livestock browsing (Kauffman and Krueger 1984, Green and Kauffman 1995). Selective browsing could also favor one woody species over another; however, we found no evidence of a preference for cottonwood over Russian olive in our study reaches. We did not distinguish between wildlife and livestock browsing, and we measured frequency but not quantity of browse damage. However, our impression was that a higher proportion of cottonwood than Russian olive twig

length was removed. This aspect of Russian olive–cottonwood dynamics needs further study.

Russian olive did not appear to expand the aerial extent of riparian vegetation in our study areas, but it may allow tree-dominated habitats to persist indefinitely in areas where cottonwoods have died or been killed by beaver. Knopf and Olson (1984) predicted that Russian olive could increase the width of riparian corridors in some areas by establishing adjacent to, but outside of, native woody riparian vegetation. However, we found that Russian olive did not establish on drier high terraces without a cottonwood overstory. The presence of Russian olive recruitment on upper terraces only in riparian forests may be due to facilitation by cottonwood. The overstory canopy could be making the local microclimate cooler and more humid than in the adjacent steppe (Callaway 1992), and/or cottonwood may be acting as a hydraulic pump, bringing water from the water table to the upper rooting zone (Caldwell et al. 1998). However, once Russian olive is present on these high terraces, it appears to persist after overstory cottonwoods have died. In the absence of Russian olive, many such sites would be dominated by sagebrush steppe (Boggs 1984).

In the riparian systems of eastern Montana, Russian olive can fill the niche of late-successional canopy dominant. It is ecologically similar to green ash and could replace it where both occur. Russian olive is shade tolerant (Campbell and Dick-Peddie 1964), capable of reproducing beneath a cottonwood canopy or in other shaded sites. Older stands of Russian olive generally have plants of many ages, indicating that infrequent disturbance events are not required for recruitment. As cottonwoods decline with age and eventually disappear, Russian olive can continue to reproduce and may become the canopy dominant (Lesica and Miles 1999). Green ash is also capable of reproducing in the shade of cottonwood and is the native late-successional dominant along major rivers in much of the Northern Great Plains and parts of eastern Montana (Johnson et al. 1976, Hansen et al. 1995). However, Russian olive is becoming more common in Montana, and our data indicate that it grows 3 times faster in girth than green ash.

Russian olive has a low recruitment rate in eastern Montana and requires ca 10 years to reach reproductive maturity; thus, invasion

should proceed slowly compared to many aggressive herbaceous or shrubby weeds. The average recruitment rate (mean number of recruits per mature tree per year) was 0.69. In our simplified model of invasion dynamics, we assume that a stand of Russian olive is initiated by a single plant with no density-dependent change in recruitment rate, no age-dependent changes in fecundity, and no subsequent immigration. An average stand will have 1 reproductive tree after 1 generation (10 years) and a 2nd one after another generation (20 yrs). An additional 0.69 mature trees will be recruited into this stand each year for the next 10 years, bringing the total to 8 mature trees after 3 generations (30 years). After this point the number of mature trees begins to increase geometrically as increasingly more mature trees are recruited in each consecutive year (Fig. 3).

Our model is based on a mean annual recruitment rate, and few stands will develop exactly as predicted in Figure 3. Recruitment will be temporally sporadic, and the rate will be higher in some sites but lower in others. Nonetheless, our model has heuristic value in illustrating how low recruitment rate and late maturation age interact to damp the speed of invasion. It also can provide guidelines for the frequency of eradication treatments (see below). This model is consistent with our stand data, indicating that Russian olive has been present for at least 36–40 years on both rivers, but density in many stands is low. In Montana, Russian olive is near the northern limit of its naturalized range in North America. It may be more invasive in warmer parts of semiarid western North America

MANAGEMENT IMPLICATIONS

Russian olive will continue to increase along Montana rivers and streams, at least partly due to relative immunity from beaver use and its tree-size stature and shade tolerance. Cottonwood successfully establishes on alluvial bars and in flood channels and will continue to be the dominant tree along many reaches of free-flowing rivers. However, we believe that Russian olive may replace cottonwood along reaches of rivers and streams where overbank alluvial deposition provides the only establishment surfaces for cottonwood seedlings. Russian olive can become dominant along riverbanks, ditches,

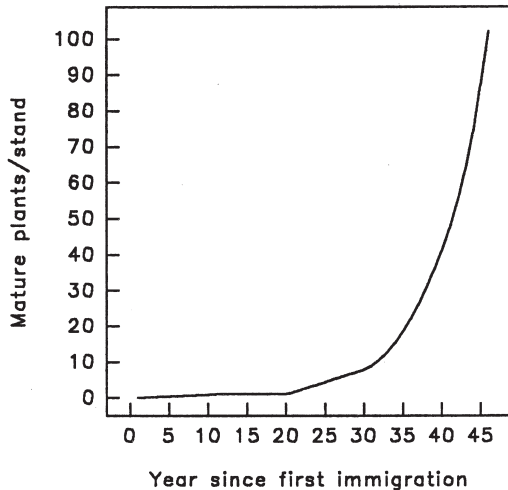


Fig. 3. Average number of mature Russian olive trees over time since colonization based on a model employing empirically derived values for mean recruitment rate and maturation age and assuming a single immigration and no density-dependent effects.

and overflow channels as well as in late-successional, declining cottonwood forests. Moist, little-shaded channels and ditches where flooding rarely occurs provide habitat conducive to invasion. Russian olive may also increase its prevalence in the understory of many younger riparian forests, possibly displacing native shrubs and small trees such as green ash.

Russian olive does not establish well in dry, upland habitats, and invasion of riparian communities often depends on proximity to established, mature trees. Invasion in our study areas and presumably along most Montana rivers is relatively recent and ongoing, receiving important impetus from domestic plantings (Lesica and Miles 1999). Russian olive should not be planted close to riparian or overflow areas or irrigation ditches if invasions are to be avoided.

Where a dynamic disturbance regime maintains most of the active floodplain in early-successional vegetation (i.e., young to middle-age cottonwoods and willows), only a small proportion of the riparian zone will remain undisturbed long enough to become fully stocked with Russian olive. Russian olive is more likely to become dominant in reaches where the riparian zone is less dynamic or where the stream is more entrenched or has been artificially channelized. These include regulated or entrenched rivers, smaller streams, and irrigation

ditches. Consequently, these are the places where control measures will have a more long-term benefit. Most, but not all, Russian olive invasions in eastern Montana occur over a period of several decades. Eradication of mature trees every 10 years or of all plants every 30 years may be effective strategies for controlling Russian olive.

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