

Plains Cottonwood's Last Stand: Can It Survive Invasion of Russian Olive onto the Milk River, Montana Floodplain?

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ABSTRACT / Russian olive (*Elaeagnus angustifolia* L.) was introduced in 1950 onto one site on the Milk River floodplain, northern Montana, 10 km downstream from the Canada/United States border. To analyze dispersal of Russian olive from the point source between 1950 and 1999, we compared distribution, numbers, size structure, and mortality of Russian olive and plains cottonwood (*Populus deltoides* Marsh.) on an unregulated reach of the Milk River floodplain in southeastern Alberta and north-central Montana. Within 50 years, Russian olive in this reach has

moved upriver into Alberta and downriver to the Fresno Reservoir. It is now present on 69 of the 74 meander lobes sampled, comprising 34%, 62%, and 61% of all Russian olive and plains cottonwood seedlings, saplings, and trees, respectively. On some meander lobes, Russian olive has colonized similar elevations on the floodplain as plains cottonwood and is oriented in rows paralleling the river channel, suggesting that recruitment may be related to river processes. Breakup ice had killed 400 Russian olive saplings and trees and damaged >1000 others on 30 of the meander lobes in 1996. Nevertheless, Russian olive now outnumbers cottonwood on many sites on the Milk River floodplain because its seeds can be dispersed by wildlife (particularly birds) and probably by flood water and ice rafts; seeds are viable for up to 3 years and germination can take place on bare and well-vegetated soils; and saplings and trees are less palatable to livestock and beaver than plains cottonwood. Without control, Russian olive could be locally dominant on the Milk River floodplain in all age classes within 10 years and replace plains cottonwood within this century.

The eventual replacement of native plains cottonwood (*Populus deltoides* Marsh.) forests by Russian olive (*Elaeagnus angustifolia* L.) may be a serious threat to biodiversity on floodplains in western North America (Christiansen 1963, Hansen and others 1995, Olson and Knopf 1986a, Haber 1999, Lesica and Miles 1999). Russian olive was introduced to the Great Plains from southern Europe and western Asia in the late 1800s for windbreaks, ornamental hedges, and wildlife habitat on treeless prairie sites. Russian olive regenerates successfully when planted near water (Shafroth and others 1995); it has become naturalized on river floodplains, lakeshores, irrigation ditches, and other wet sites in 17 of the western states and is increasing in 19 others (Olson and Knopf 1986a,b, Haber 1999, Lesica and Miles 1999). Once established, Russian olive is difficult to control and expensive to eradicate (Olson and Knopf 1986b, Hansen and others 1995). Cutting, spraying with herbicides, girdling, pulling and mowing seed-

lings, and bulldozing larger plants have been used to control it, but these treatments have been largely unsuccessful for eradication (Olson and Knopf 1986a,b, Shafroth and others 1995). Nevertheless, some agencies in the United States and Canada are still providing Russian olive stock at low cost, and even free of charge, to landowners (Olson and Knopf 1986b). Native riparian ecosystems are already in jeopardy on the Great Plains as a result of dams and channel diversions, heavy livestock grazing, and land clearing (Boldt and others 1978, Rood and Mahoney 1990, Bradley and others 1991, Naiman and others 1993, Auble and Scott 1998), and may not be able to withstand invasion from introduced trees such as Russian olive (Currier 1982).

Plains cottonwood is the dominant and often the only tree species on river floodplains in Montana and the rest of the northern Great Plains (Bradley and others 1991, Hansen and others 1995, Rood and Mahoney 1995). Plains cottonwood has relatively specific recruitment requirements (Shafroth and others 1995). Recruitment by seed is not successful every year: rates for rivers in the northern Great Plains average 1 year in 5–10 years (Bradley and Smith 1986, Auble and Scott 1998). Plains cottonwood also propagates through stem

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and stump sprouting (Rood and others 1994). Flow regulation resulting in reduced flood peaks and point bar accretion rates, in addition to land clearing, live-stock grazing, beaver cutting, ice damage, and fire, have curtailed cottonwood recruitment on many prairie rivers (Rood and Mahoney 1990, Bradley and others 1991, Rood and Mahoney 1995, Scott and others 1997, Lesica and Miles 1999, Smith and Pearce 2000). Flow regulation may be providing ideal site conditions for Russian olive establishment and eventual dominance on floodplains in the Great Plains as seeds germinate on both bare and vegetated surfaces, an advantage in regulated river systems (Shafroth and others 1996, Lesica and Miles 1999). Seeds are distributed by birds and small mammals throughout the year and are viable for up to 3 years, germinating when moisture conditions are favorable (Shafroth and others 1995). Seed dispersal by water and ice transport in river systems is probable, but this dispersal mechanism has not yet been documented. Like plains cottonwood, Russian olive can produce sprouts on broken trunks. Given these advantages, Russian olive may be able to outnumber, and eventually replace, native plains cottonwood on prairie river floodplains.

Parker and others (1999) suggest that, on a geographic scale, the overall impact of an introduced species on native species can be determined by its distribution range and its population abundance. Only a few studies have mapped the distribution of Russian olive on floodplains in the United States (e.g. Christiansen 1963, Knopf and Olson 1984, Olson and Knopf 1986a, Hansen and others 1995) and analyzed its impact on native vegetation (Lesica and Miles 1999); there have been no studies like this in Canada (Haber 1999). This lack of research is surprising and disturbing given the environmental and economic problems caused by other invasive introduced trees [e.g., salt-cedar (*Tamarix* spp.)] in western rivers (Robinson 1965, Harris 1966, Graf 1982).

The naturalization of Russian olive in riparian systems in Montana and adjacent Alberta, where it could replace native trees such as plains cottonwood, should be a management concern (Hansen and others 1995, Lesica and Miles 1999, T. Hood, personal communication, 1999, G. Wagner, personal communication, 2000). Spatially discontinuous plains cottonwood stands dominate the Milk River floodplain throughout much of its length in southeastern Alberta and north-central Montana. In 1950, Russian olive was introduced to the floodplain at the lower Aageson Ranch, 10 km downstream from the Alberta/Montana border, to protect ranch buildings from wind and to slow the rate of bank erosion (D. Aageson, personal communication,

1999) (Figure 1). This introduction provided a unique opportunity to examine the pattern and rate of Russian olive invasion from the point source over the past 50 years. We compared the distribution and numbers of Russian olive and plains cottonwood seedlings, saplings, and trees along an unregulated 100 km reach of the Milk River, upstream and downstream of the ranch point source between the Pinhorn Ranch (Alberta) and Fresno Reservoir (Montana) (Figure 1). We estimated the numbers of Russian olive on Fresno Reservoir and on a 60-km regulated reach of the Milk River below Fresno Dam. We also assessed the extent of damage to both Russian olive and plains cottonwood following ice drives and jams, beaver cutting, and livestock grazing. We then examined the distribution and abundance of Russian olive on other eastward-flowing rivers in Montana and one in North Dakota to determine if its patterns on the Milk River were anomalous, or typical of other river floodplains in the northern Great Plains.

Methods

Study Area

The Milk River rises in the foothills of the eastern slope of the Rocky Mountains in Montana, then flows northeast crossing into Alberta and continuing eastward for 185 km before reentering Montana at Eastern Crossing (Figure 1). Typical of northern prairie rivers, the Milk River is frozen for 4–5 months each winter and discharge is variable, with very low flows beneath the ice ($2 \text{ m}^3/\text{sec}^{-1}$) between November and March. In spring, high flows (to $220 \text{ m}^3/\text{sec}^{-1}$) result from snowmelt and high rainfall (Bradley and Smith 1984, Environment Canada 1997, US Geological Survey 1999). Maximum instantaneous river stages between January and April are generated by ice breakup, drives, and jams (Smith and Pearce 2000). The record ice breakup flood ($340 \text{ m}^3/\text{sec}^{-1}$) between 1911 and 1999 took place on 13 March 1996. The Fresno Dam, constructed 20 km northwest of Havre in 1939, has reduced flood peaks and meander migration downstream (Bradley and Smith 1984).

The Milk River meanders through most of the study area except for a braided reach that begins 20 km down river of the International Border and extends to within 10 km of the Fresno Reservoir. The river flows through semiarid Mixed Grass Prairie, parts of which have been cultivated. Vegetation occupying the floodplain has been described by Wallis (1976) and Bradley (1982). The floodplain is characterized by spatially discontinuous riparian woodlands dominated by plains cottonwood in association with sandbar willow (*Salix exigua*

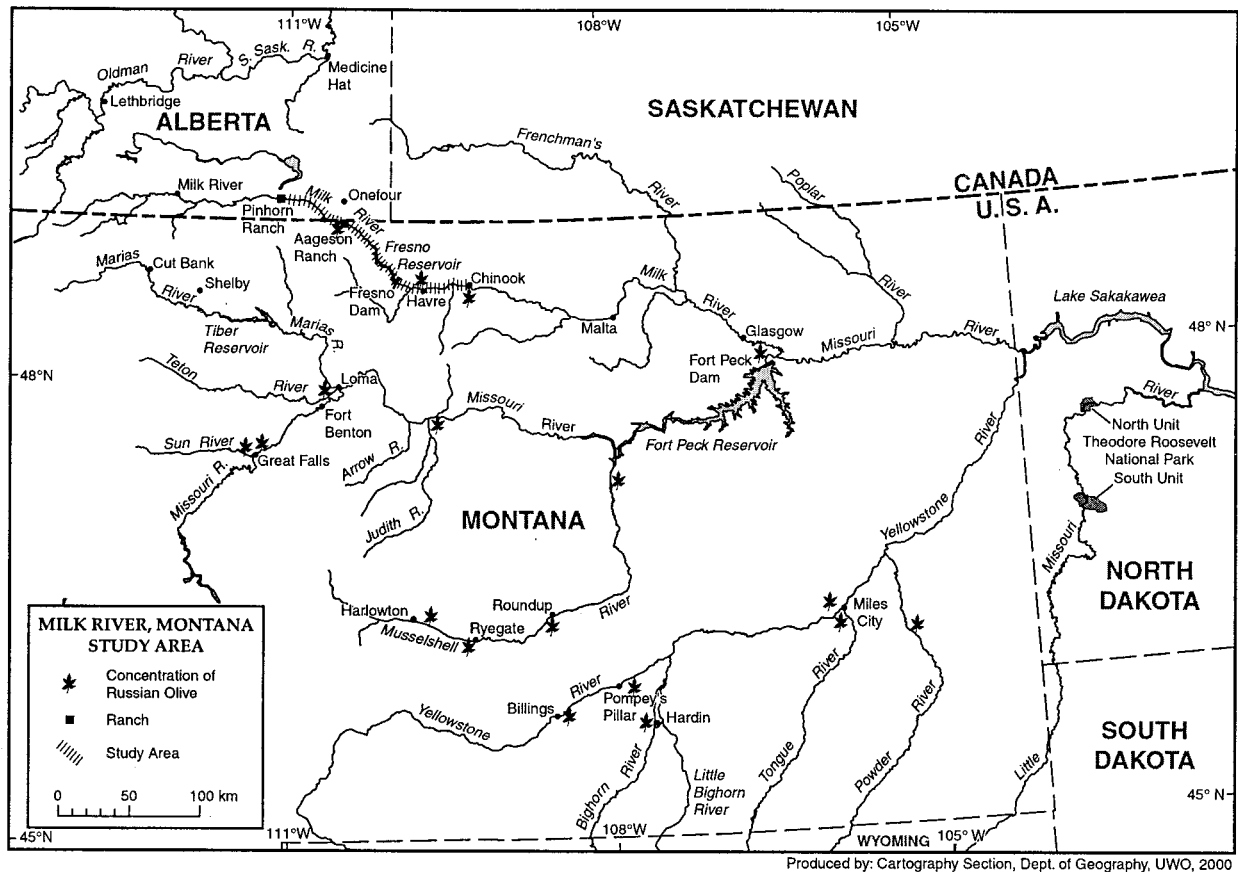


Figure 1. Location of study area on the Milk River, north-central Montana and south-eastern Alberta. Named rivers in the central and eastern part of Montana show where concentrations of Russian olive were observed on floodplains in 1999.

Nutt.), peach-leaf willow (*S. amygdaloides* Anderss.), and thorny buffaloberry (*Shepherdia argentea* Nutt.) (Figure 2). Plains cottonwood and the willows are pioneer plants that colonize bare, moist point bars and other channel lateral accretion sites. Approximately 500 Russian olive seedlings and saplings were introduced directly to the floodplain in 1950 at the lower Aageson Ranch in Montana; secondary growth since then has formed thickets so dense that other riparian species have been excluded (Figure 3). Russian olive was not planted on any Milk River floodplain ranches in Alberta (T. Hood, personal communication, 2000). Downstream of the Aageson Ranch and for about 30 km, plains cottonwood and Russian olive are scattered on the floodplain. On these sites, plains cottonwood, Wood's rose (*Rosa woodsii* Lindl.), peach-leaf and sandbar willow, thorny buffaloberry, smooth brome (*Bromus inermis* Leyss), and Canada thistle (*Cirsium arvensis* L.) are commonly associated with Russian olive. Many Russian olive and plains cottonwood saplings and small trees have been repeatedly scarred and broken by river

ice jams (Smith and Pearce 2000). Silver sagebrush (*Artemisia cana* Pursh), western wheatgrass (*Agropyron smithii* Rydb.), and needle-and-thread (*Stipa comata* Trin & Rupr.) occupy the most elevated and driest sites on alluvial fans between the floodplain and valley slopes.

Field Measurements

Field sampling was carried out in June 1999. Much of the study area between the Pinhorn Ranch and Fresno Reservoir is inaccessible to vehicles, and because of the shale badlands associated with the valley sides, none of the roads to the floodplain in this reach are passable when wet. We divided the Milk River floodplain into four study segments: (1) from Pinhorn Ranch to the Alberta/Montana border (40 km); (2) from the Alberta/Montana border to and including the backwater of Fresno Reservoir (50 km); (3) the lower delta plain (10 km) and shoreline (40 km) of Fresno Reservoir; and (4) from the Fresno Dam to Chinook (60 km) (Figure 4). Because of access difficulties, different methods were used for sampling each segment; the



Figure 2. Aerial view of Milk River bottomlands, meandering reach near Pinhorn Ranch, Alberta. Note spatially discontinuous plains cottonwood forests growing on the upper meander lobes and colonizing cottonwood and willow on the point bars. There were no Russian olive in this stretch of the river.

most detailed measurements were carried out in segment 2.

Segment 1: Pinhorn Ranch, Alberta to international boundary. From a road and boat access point at the Pinhorn Ranch (Alberta), 40 km upriver from the international boundary, we sampled six meander lobes (about 6 river km) downstream of the ranch. We estimated numbers of Russian olive trees and saplings between the Pinhorn and the Alberta/Montana border from color aerial photographs (flown June 1997 at 1:5000) provided by Alberta Environment. These estimates were validated by comparing to surveys on the Milk River carried out by the Alberta government on the Milk River in 1999 (T. Hood, personal communication, 1999).

Segment 2: International boundary to lower delta plain, Montana. We completed the most detailed measurements in segment 2 because the Milk River floodplain between the Alberta/Montana border and Fresno Reservoir was accessible from four unimproved roads and four-wheel drive trails from which we could launch a boat. We boated upriver from the Lower Aageson Ranch in Montana to a starting point at the international boundary. Using binoculars, we counted all Rus-

sian olive trees and saplings on two meander lobes directly upriver from the border into Alberta (seedlings could not be seen). From the border, we boated downriver and sampled every meander lobe (74 in total) to and including the backwater reach of Fresno Reservoir, a distance of 50 km (Figure 4). Lobes 1–30 were in the meandering reach, 31–65 in the braiding reach, and 66–74 in the backwater. We walked a zigzag pattern over each lobe surface to count all Russian olive and plains cottonwood in the following size classes: seedlings <1 m tall, saplings 1–1.5 m tall, and trees >1.5 m tall. We estimated elevations of Russian olive and plains cottonwood seedlings, saplings, and trees above base summer flow. We also counted the numbers of dead saplings and trees and the extent of structural damage from river ice, beaver cutting, and livestock grazing. Ice damage was determined by the presence of scars, broken stems and branches, and toppled trunks (see Smith and Pearce 2000 for details). Beaver harvesting was determined by the presence of gnawed and broken stems but no scars. Livestock grazing was determined by the visible evidence of animals, trampling and pugging of the soils, deposits of fecal pads, and ragged edges on



Figure 3. Aerial view of Milk River bottomlands and original plantings (1950) of Russian olive (light-toned trees at 1) at Aageson Ranch. Russian olives at 2 have seeded naturally and are growing on the point bar at elevations usually occupied by colonizing plains cottonwood and willows. Note distribution parallel to channel (river flow is indicated by arrow).

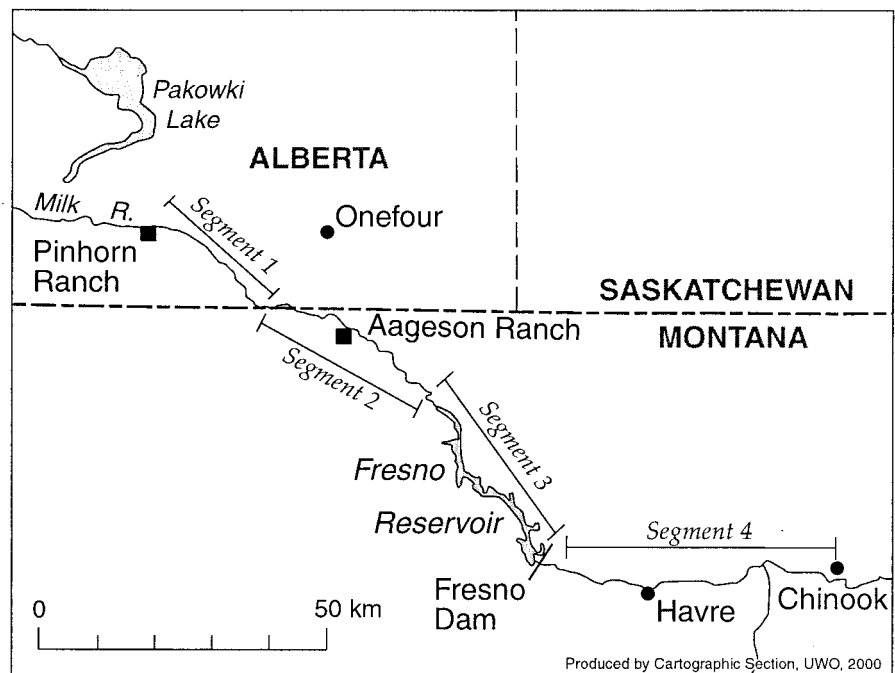


Figure 4. Enlarged view of study area showing locations of four sampling segments. The Milk River channel meanders between the Pinhorn Ranch and 1 km downriver of the Aageson Ranch, then braids to the start of segment 3, and meanders again down river of Fresno Dam in segment 4.

chewed stems and branches rather than the clean cuts more characteristic of beaver.

The measurements for all 74 meander lobes between the Canada USA border and Fresno Reservoir were separated into eight variables for statistical analysis: 1–4—Russian olive seedlings, saplings, live trees, dead trees; 5–8—plains cottonwood seedlings, saplings, live trees, dead trees. The Kolmogorov-Smirnov test for normality was used to examine the distribution of the eight variables (all variables deviated significantly from a normal distribution, $P < 0.01$). We used a two-sample Kolmogorov-Smirnov (KS) statistic, scaled for discrete data (see Smith and others 1998), to measure the maximum absolute differences in cumulative abundance profiles between Russian olive and plains cottonwood, in the three size classes and the dead class, on all 74 meander lobes. Because different channel forms could contribute to differences in abundance, the KS statistic was also used to compare frequency distributions within the meandering (31 lobes), braiding (34 lobes), and backwater (9 lobes) reaches.

Segment 3: Lower delta plain and Fresno Reservoir, Montana. There was no road or boat access between the 10 km lower delta plain and Fresno Reservoir, so we walked along adjacent bluffs and used binoculars to search the floodplain for Russian olive and plains cottonwood all the way to the reservoir. We also counted Russian olive and plains cottonwood along the shoreline of the Fresno Reservoir (approximately 40 km shoreline length) from the boat and at eight road access points.

Segment 4: Fresno Dam to Chinook, Montana. Between Fresno Dam and Chinook (60 km, Figure 4), mature plains cottonwood forests dominate the floodplain; however, cottonwood recruitment has been limited following construction of the Fresno Dam in 1939 (Bradley and Smith 1984, 1986). In this reach, we counted only the numbers of Russian olive by size class at four road access points to the Milk River floodplain. We used these counts to estimate average number of plants/km (valley length).

Reconnaissance

We compared the distribution patterns of Russian olive on the Milk River floodplain to 12 other eastern-flowing rivers in the Great Plains region of Montana (Marias, Teton, Sun, Missouri, Arrow, Judith, Musselshell, Yellowstone, Bighorn, Little Bighorn, Tongue, Powder) and one river (Little Missouri) in western North Dakota (Figure 1). Of these, the Teton, Arrow, Judith, Yellowstone, Powder, and Little Missouri are unregulated. We accessed the floodplains of these rivers from adjacent highways and bridge crossings, re-

corded the presence or absence of Russian olive, and, if Russian olive was present, noted whether the infestation was severe or only scattered.

Results

Segment 1: Pinhorn Ranch, Alberta to International Boundary

Plains cottonwood forests dominated the Milk River floodplain for 40 km between the Pinhorn Ranch and the Alberta/Montana border (Figure 1). All stages of cottonwood succession were represented on most meander lobes. Livestock use was light in this reach (i.e., grazed infrequently and only in winter; B. Adams, personal communication, 1999) because of limited access to the floodplain. No Russian olive were observed along a 6-km reach of the Milk River at the Pinhorn Ranch, but 48 Russian olive plants (seedlings, saplings, and trees) could not be separated reliably on the photographs were identified on the 1997 color aerial photographs downriver of the ranch to the border; most (30) of these plants were counted within 2 km of the border. Twenty-three trees in this reach were removed in late September 1999 during an eradication program organized by the Alberta government (T. Hood, personal communication, 1999).

Segment 2: International Boundary to Lower Delta Plain, Montana

Live plants. Between the International Boundary and backwater reach of Fresno Reservoir (50 km), where we completed the most detailed measurements, we counted 17,555 live Russian olive and plains cottonwood seedlings, saplings, and trees on 74 meander lobes on the Milk River floodplain (Table 1, Figure 5).

Of the 17,555 plants, 46% (8000) were Russian olive (approximately 160 plants/km valley length), which comprised 34%, 62%, and 61% of all Russian olive and plains cottonwood seedlings, saplings, and trees, respectively, on the floodplain. Russian olive occupied most meander lobes on the floodplain (69 lobes, or 93%). Highest numbers were measured at and just down river of the Ageson Ranch source in the meandering reach (2900 plants, Figures 3 and 5) and in the backwater of Fresno Reservoir (>3000 plants) (Table 1, Figure 5). Two other concentrations were sampled at the beginning of the braiding reach and midway between the ranch and backwater of the reservoir. Of the 8000 Russian olive plants counted, 42% were seedlings, 37% were saplings, and 21% were trees (Table 1). Russian olive in the seedling and tree size classes were found together on 45 (of 74) meander lobes and had

Table 1. Plains cottonwood and Russian olive, segment 2, Milk River, Montana (see Figure 4 for locations of reaches)

	Plains cottonwood (<i>N</i>)	Russian olive (<i>N</i>)
Meandering reach		
Seedlings	4091	1078
Saplings	696	1505
Trees	911	1318
Dead	37	132
Braiding reach		
Seedlings	711	217
Saplings	582	556
Trees	71	56
Dead	37	170
Backwater reach		
Seedlings	1814	2038
Saplings	533	871
Trees	146	361
Dead	13	177
Total all reaches		
Seedlings	6616	3333
Saplings	1811	2932
Trees	1128	1735
Dead	87	479

similar cumulative frequency distributions in all river reaches ($D = 0.0676$, $P > 0.10$). The abundance pattern of saplings was significantly different from seedlings ($D = 0.3784$, $P < 0.001$) and trees ($D = 0.4054$, $P < 0.001$) as saplings were counted on most (68 of 74) meander lobes.

The highest numbers of Russian olive seedlings were counted at and near the ranch, on a few sites in the braiding reach and within the backwater zone (Table 1, Figure 5). Seedlings had colonized point bars and other lateral accretion sites 0.5–1.5 m above base summer flow between the river channel and mature plains cottonwood stands on the most elevated floodplain sites. (This is the same elevation range colonized by cottonwood and willow seedlings.) Russian olive seeds and seedlings were found on both bare and vegetated surfaces. Saplings and trees occupied sites 1.5–2.5 m above base summer flow. Seedlings, saplings, and trees were often oriented in rows paralleling the river channel, suggesting seed dispersal by fluvial processes (Figure 3). Russian olive were not observed growing underneath canopies of mature plains cottonwood, as has been observed on other rivers in Montana (Hansen and others 1995, Lesica and Miles 1999, and personal observation); however, in the backwater reach, we did sample some saplings under dense peach-leaf willow canopies.

Approximately 500 seedlings and saplings had been planted at the Ageson Ranch in 1950 (D. Ageson,

personal communication, 1999). Surviving plants were now large trees with trunk diameters of 30–50 cm. Large trees were also sampled in parts of the backwater reach.

More than 1000 ice-damaged Russian olive were counted on 30 meander lobes, but many plants, particularly in the sapling size class, had sprouted from damaged trunks. Ice damage was most severe at Ageson Ranch (in the meandering reach) and in the braiding reach (418 plants on 20 lobes in this reach) (Table 2, Figure 6). Browsing by livestock and wildlife was not evident in any size class. Beaver harvesting was minimal, affecting only 27 Russian olive on 3 of the 74 sample sites (Table 2). However, many of the rigid upper branches of trees at all sample sites were broken as a result of fall and winter perching and fruit-gleaning activities of the introduced ring-necked pheasant (*Phasianus colchicus*) and possibly gray partridge (*Perdix perdix* L.) (M. Forsyth and S. Huhtala, personal communication, 1999, and personal observation).

Plains cottonwood occupied only 47 of the 74 meander lobes (64%) between the Canada/USA border and Fresno Reservoir. We counted 9555 plants in the segment 2 study reach (approximately 190 plants/km). The numbers of cottonwood were higher than Russian olive only in the seedling size class (6616 compared to 2932). Cottonwood numbers were highest in the meandering reach (60% of all cottonwood counted were in this zone), in two areas in the braiding reach approximately midway between the Ageson Ranch and the backwater reach, and on one meander lobe in the backwater reach (Table 1, Figure 5). Seedlings, saplings, and trees had similar abundance profiles ($D = 0.1622$, 0.1351 , and 0.1081 for seedlings/saplings, seedlings/trees, and saplings/trees respectively, all $P > 0.10$), but there were fewer trees in the braiding reach because of repeated ice damage (Smith and Pearce 2000). Seedlings had colonized moist, bare, lateral accretion surfaces 0.5–1.5 m above base summer flow; saplings and trees occupied sites between 1.5 and 2.5 m.

Based on the count data (and assuming a constant seed-in rate), there appeared to have been a substantial loss (73%) of cottonwoods in segment 2 between the seedling and sapling growth stages, from 6616 seedlings to only 1811 saplings, compared to Russian olive (12% loss, from 3333 seedlings to 2932 saplings), that we attributed to livestock grazing and beaver harvesting. Forty-four of the meander lobes (60%) had been grazed by cattle and other livestock in 1999. Cattle use was concentrated on meander lobes close to the ranch and within the braiding reach. Nevertheless, the abun-

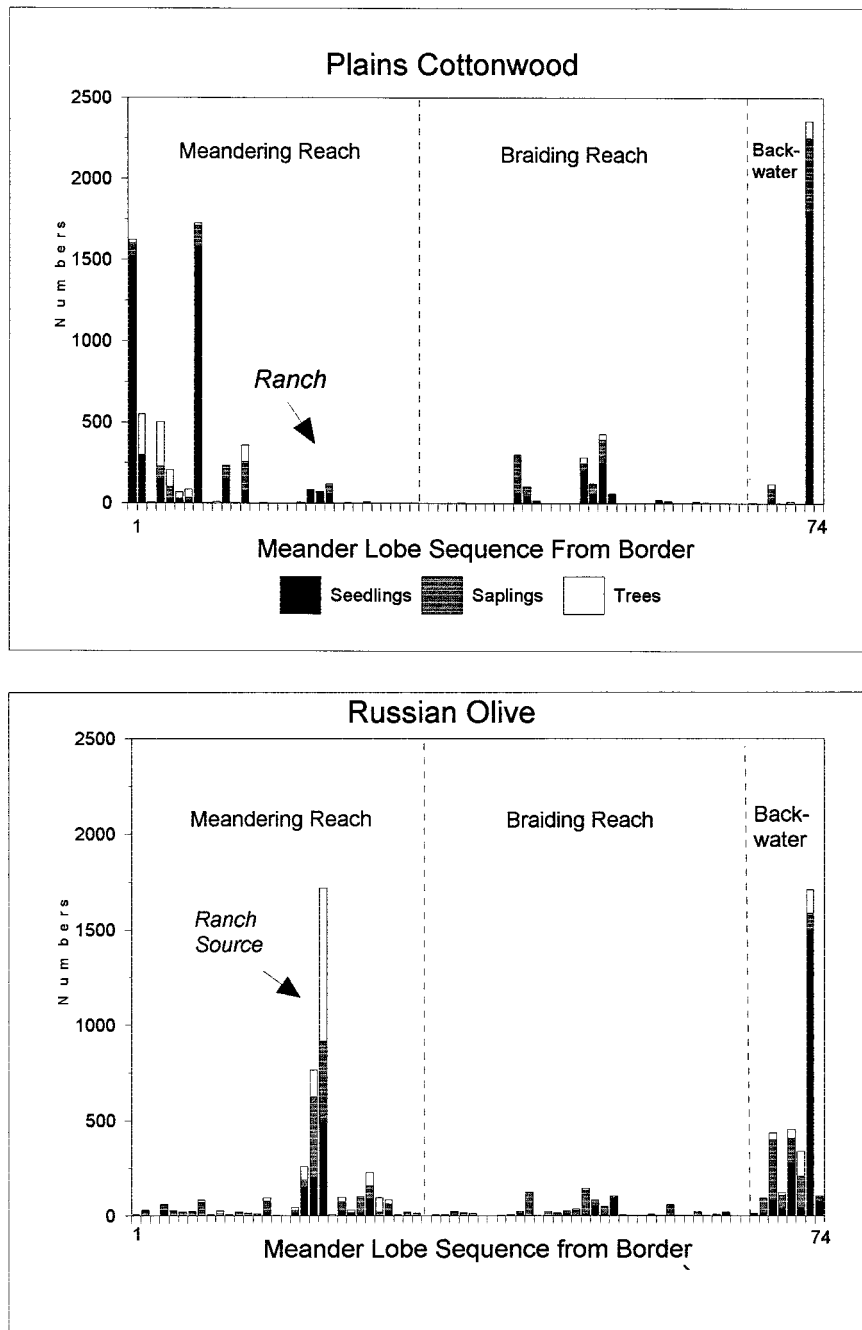


Figure 5. Numbers in 1999 of live seedlings, saplings, and trees, plains cottonwood and Russian olive, on 74 meander lobes on the Milk River from the Alberta/Montana border to backwater of Fresno Reservoir (segment 2 on Figure 4). Note high numbers of Russian olive at Aageson Ranch planted as a shelterbelt in 1950.

dance profiles of plains cottonwood and Russian olive seedlings in all reaches of segment 2 showed similar patterns ($P > 0.10$, Table 3).

Trees and saplings of both species had dissimilar abundance profiles ($P < 0.001$ and < 0.05 respectively, Table 3) when all river reaches were analyzed together. Russian olive saplings had significantly different abundance patterns from plains cottonwood in the meandering and braiding reaches ($P < 0.001$), but not

in the backwater reach ($P < 0.10$). The abundance profiles of trees were dissimilar only in the braiding reach. These differences may relate to differential harvesting by beaver. Many (413) cottonwoods had been harvested by beaver (on 11 of the 47 meander lobes occupied by cottonwood; Table 2, Figure 6). On one lobe in the meandering reach upstream of Aageson Ranch, 70% of all cottonwood saplings had stems and branches cut by beaver. In contrast, only 27 Russian

Table 2. Plains cottonwood and Russian olive damaged by ice and beaver (*Castor canadensis*), segment 2, Milk River, Montana (see Figure 4 for locations of reaches)

Damage type/reach	Plains cottonwood (N)	Russian olive (N)
Ice		
Meandering reach	116	335
Braiding reach	650	418
Backwater reach	153	311
Total	919	1064
Beaver		
Meandering reach	258	1
Braiding Reach	97	0
Backwater Reach	58	26
Total	413	27

olive had been damaged by beaver, most of them in the backwater reach.

Dead saplings and trees. In total, there were 566 dead saplings and trees on the Milk River floodplain between the Alberta/Montana border and backwater reach of Fresno Reservoir, of which 85% were Russian olive (Table 1, Figure 7). However, dead Russian olive and plains cottonwood had similar abundance profiles in all river reaches ($P > 0.10$, Table 3). Ice was the main cause of death of both Russian olive and cottonwood saplings and trees. We counted dead Russian olive in all reaches. Most of the dead plants had been killed during ice drives; on one meander lobe in the braiding reach, 128 of 158 small trees and saplings (83%) were destroyed during the 1996 ice drive and jams (Figure 7). (Smith and Pearce 2000). Only 87 dead cottonwood trees were counted in 1999, many (43%) of them in the meandering reach that had been cut by beaver and had not survived by sprouting. Diseases were not identified, although the death of 50 olive trees on one meander lobe in the backwater reach, which showed no signs of damage from ice or beaver, may have resulted from fungal infection.

Segment 3: Lower Delta Plain and Fresno Reservoir, Montana

Russian olive and plains cottonwood trees and saplings ended abruptly beyond the backwater reach, although there may have been seedlings of both species that were not visible from adjacent bluffs. The river here flowed 10 km through a narrow, deep channel flanked by saturated mudflats where only peach-leaf and sandbar willow grew on the channel levees. Along the reservoir shoreline (40 km) we counted 175 Russian olive (97 saplings and 78 trees, fewer than 5 plants/km)

and 1319 plains cottonwood (402 saplings, 917 trees, approximately 33 plants/km); seedling counts were unreliable from the boat. The Russian olive were generally clustered at cottage and picnic sites at the southeast end of the reservoir.

Segment 4: Fresno Dam to Chinook, Montana

Mature to old-age plains cottonwood forests dominated the 60-km floodplain between Fresno Dam and Chinook, but recruitment has been curtailed because of flow regulation (Bradley and Smith 1986). From four road access sites between the Fresno Dam and the town of Chinook, we counted 163 Russian olive seedlings, 246 saplings, and 102 trees (plus 12 dead trees). We used these counts to calculate an average Russian olive distribution on the floodplain ranging from 40 plants/km near the dam to 300 plants/km between Havre and Chinook. The highest numbers of Russian olive were counted at two nodes within the towns of Havre and Chinook.

Russian Olive on Other Plains Rivers in Montana and North Dakota

We observed Russian olive on most floodplains of eastward-flowing rivers in Montana. Specific river locations with high numbers of Russian olive are indicated on Figure 1. We found only two stands of Russian olive on the Tongue and Powder rivers, and only two trees were noted on the Little Missouri River, in the north unit of Theodore Roosevelt National Park, North Dakota.

Discussion

Flow regulation following construction of dams and reservoirs, livestock grazing and trampling, and beaver harvesting have limited recruitment of plains cottonwood on river floodplains in the northern Great Plains (Rood and Mahoney 1990, 1995, Bradley and others 1991, Hansen and others 1995, Auble and Scott 1998, Lesica and Miles 1999). Recruitment may be threatened further by the introduction of Russian olive and its probable dominance on many of these floodplains within this century (Olson and Knopf 1986a, Lesica and Miles 1999). Our measurements on an unregulated reach of the Milk River in north-central Montana show that Russian olive outnumbers plains cottonwood on many sites between the Alberta/Montana border and Fresno Reservoir. On these sites, Russian olive has colonized similar elevations, parallel to the river channel, as plains cottonwood. Russian olive is also present, but in low numbers, on the Milk River in Alberta upstream of the International Boundary for about 10 km and at

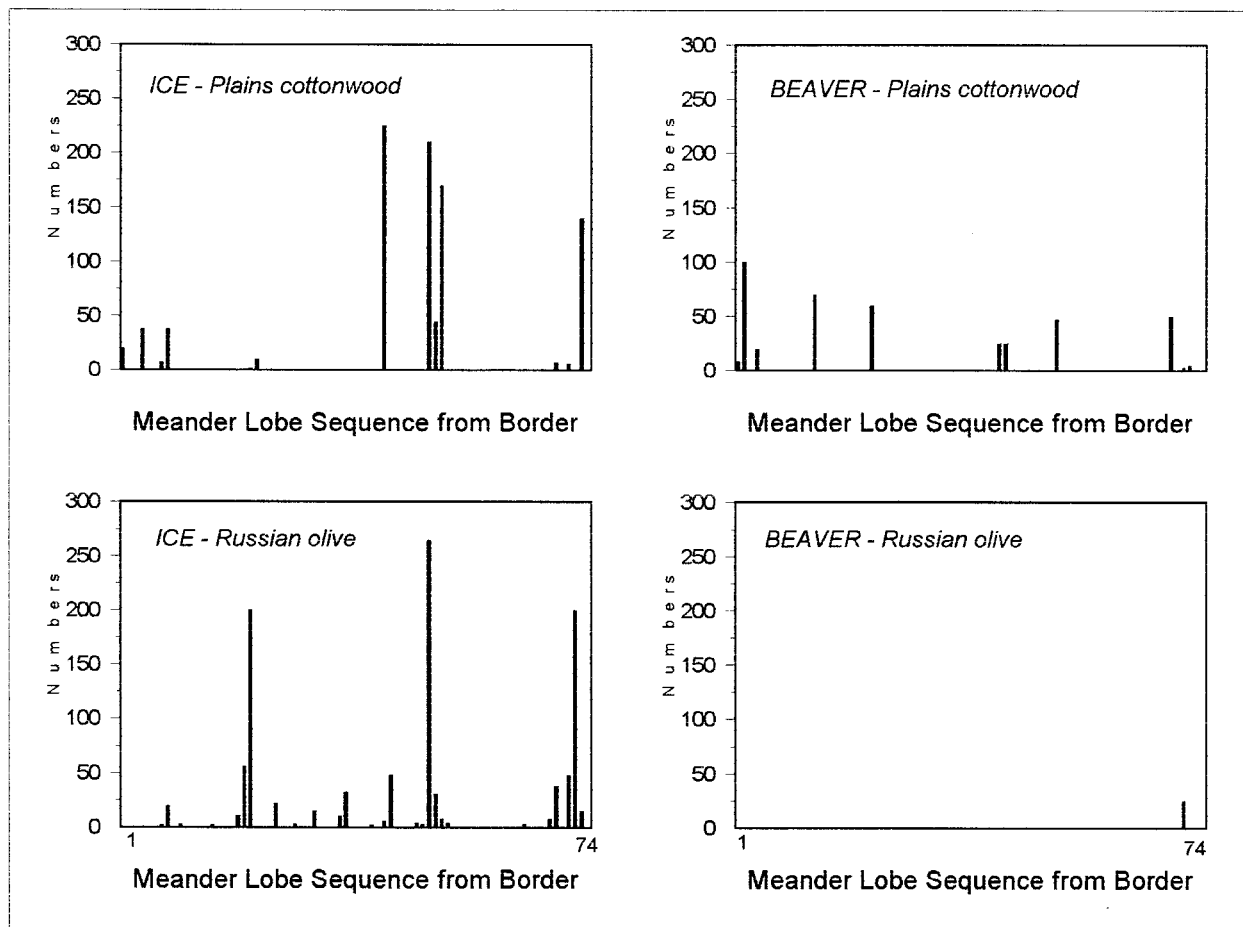


Figure 6. Numbers in 1999 of plains cottonwood and Russian olive damaged by ice and beaver (*Castor canadensis*) on 74 meander lobes, Milk River study reach (segment 2 on Figure 4).

Table 3. Comparison of abundance profiles, Russian olive and plains cottonwood, Milk River, Montana (segment 2)

River reach ^a	RO/CW ^b			
	Seedlings	Saplings	Trees	Dead
All river reaches	0.1216 ³ (>0.10)	0.5946 (<0.001)	0.2432 (<0.05)	0.1757 (>0.10)
Meandering reach	0.1613 (>0.10)	0.6452 (<0.001)	0.1613 (>0.10)	0.2258 (>0.10)
Braiding reach	0.1765 (>0.10)	0.5588 (<0.001)	0.3235 (<0.10)	0.0882 (>0.10)
Backwater reach	0.5750 (>0.10)	0.6000 (<0.10)	0.4250 (>0.10)	0.5000 (>0.10)

^aFor locations of reaches, see Figure 4.

^bRO = Russian olive; CW = plains cottonwood.

^cKolmogorov-Smirnov D_{obs} ; $P(D > D_{obs})$ in parentheses; significant values are in bold type ($P \leq 0.05$).

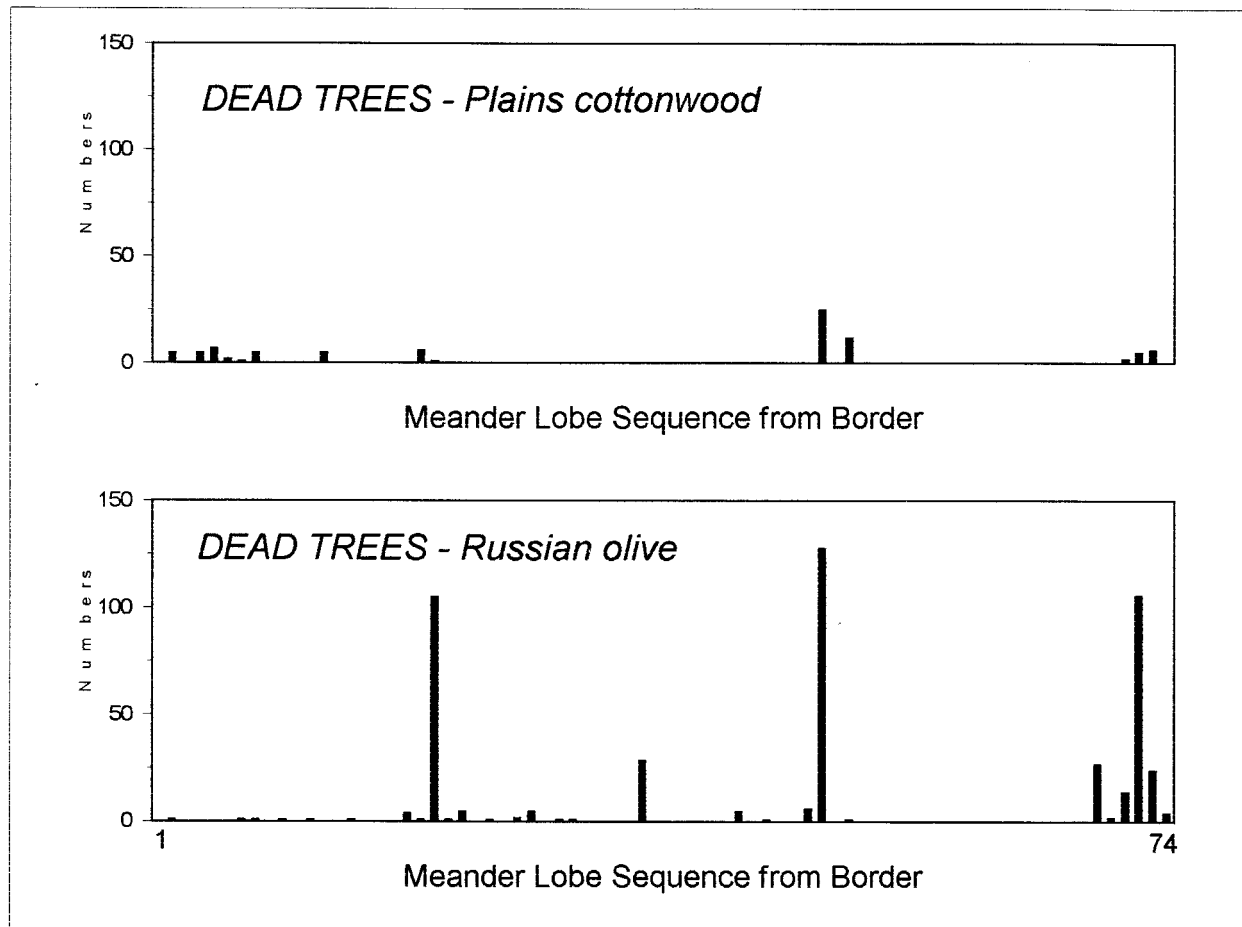


Figure 7. Numbers and distribution in 1999 of dead plains cottonwood and Russian olive saplings and trees on 74 meander lobes, Milk River study reach (segment 2 on Figure 4).

cottage and other recreation facilities on the southeast end of Fresno Reservoir. Between Fresno Dam and Chinook (regulated reach), Russian olive dominates the seedling and sapling size classes, and without recruitment of plains cottonwood, will dominate the tree class, as well, when the old cottonwood trees die. We observed similar patterns on other eastward-flowing rivers in Montana.

We believe that most Russian olive plants between the Alberta/Montana border and Fresno Reservoir originated from seeds dispersed from the Aageson Ranch shelterbelt introduced to the Milk River floodplain in 1950. (The source of Russian olive at the southeast end of Fresno Reservoir and below Fresno Dam appeared to be from windbreak plantings on adjacent uplands rather than from the Aageson Ranch.) Within 50 years, Russian olive has come to comprise 46% of all Russian olive and plains cottonwood seedlings, saplings, and trees, upriver and downriver of the

ranch source, and to dominate the sapling (62%) and tree (61%) size classes compared to plains cottonwood: Although plains cottonwood recruitment has been curtailed on the milk River below Fresno Dam, seed dispersal and germination do not appear to be a problem on unregulated reaches (we counted almost twice as many cottonwood seedlings as Russian olive in 1999). However, successful recruitment occurs only once in 5–10 years on the Milk River (Bradley and Smith 1986). In our study reach, we estimated an attrition rate from seedling to sapling stage of 73% (but only 12% for Russian olive). Losses of cottonwood seedlings on unregulated rivers, including the Milk, have been attributed to livestock grazing and trampling (Rood and Mahoney 1990, Bradley and others 1991, Auble and Scott 1998, Pearce and Smith, unpublished data). If seedlings survive grazing, beaver harvesting reduces their numbers further (Bradley 1982, Lesica and Miles 1999). Russian olive is not so impacted. On the Milk

Table 4. Ecological characteristics, plains cottonwood and Russian olive^a

Criteria	Plains cottonwood	Russian olive
Status in North America	Native	Introduced
Age of first flowering and seed production	10 years	3–5 years
Timing of seed maturation and dispersal	Spring/early summer	Late summer/fall/spring
Seed dispersal mechanisms	Millions of small seeds dispersed by wind and water	Hundreds of large fruits dispersed by animals and possibly by water and ice rafting
Seed viability	7–14 days	up to 3 years
Germination requirements	Bare moist soil	Cold treatment; bare or vegetated moist soil
Asexual reproduction	Suckers, sprouts	Suckers, sprouts
Life span	100–150 years	25–50+ years
Shade tolerance	Low	Moderate
Salt tolerance	Low	High
Drought tolerance	Low	High
Flooding tolerance	High	Moderate
Ice-damage tolerance	Moderate	Low
Fire tolerance	Low	High
Flow regulation tolerance	Low	High
Palatability (cattle, deer, beaver)	Moderate-high	Low-moderate

^aSources: Olson and Knopf (1986a), Rood and Mahoney (1990), Rood and others (1994), Hansen and others (1995), Shafroth and others (1995), Scott and others (1997), Mahoney and Rood (1998), Haber (1999), Lesica and Miles (1999).

River, infrequent (11 times between 1911 and 1999) but devastating river ice drives and ice jams damage and sometimes kill cottonwood saplings and trees, particularly in the braiding reach. However, ice also limits Russian olive establishment in this reach (Smith and Pearce 2000).

Russian olive has several advantages over plains cottonwood at the seed and seedling stages that could promote its eventual dominance on the Milk River and other prairie rivers in the northern Great Plains, if it is not controlled and eradicated (Table 4). Russian olive seeds can be transported at any time of year by birds [e.g., ring-necked pheasant, sharp-tailed grouse (*Tympanuchus phasianellus*), mourning doves (*Zenaida macroura*), robins (*Turdus migratorius*)] and mammals [white-tailed deer (*Odocoileus virginianus*), raccoons (*Procyon lotor*)] (Christiansen 1963, Knopf and Olson 1984, Olson and Knopf 1986a, Lesica and Miles 1999, and personal observations). We propose that olive seeds may also be transported by water and ice rafting. Russian olive seeds are large and viable for up to 3 years, and can germinate on vegetated as well as bare soil (Shafroth and others 1995). Russian olive develops long (up to 5 cm) thorns with maturity and livestock avoid it past the seedling stage. Plains cottonwood seeds, on the other hand, are transported by wind and water within a narrow time window in spring and early summer. Although plains cottonwood can produce millions of seeds per tree each year (which is an advantage), the seeds must germinate within 7–14 days where and when they land, whether the site is favorable or

not, and so mortality is high (Rood and Mahoney 1990, Johnson 1994, Shafroth and others 1995, Auble and Scott 1998, Mahoney and Rood 1998). Once seedlings become established, they are more palatable to livestock than Russian olive (Hansen and others 1995, Pearce and Smith, unpublished data). Selective harvesting of plains cottonwood by beaver (*Castor canadensis*) may also be favoring establishment of Russian olive (this paper and Lesica and Miles 1999).

While we are unable to document with certainty the upriver transport of Russian olive seeds from the ranch source by small mammals and birds on the Milk River, our measurements suggest this is the probable mode of dispersal. We found no Russian olive along a 6-km reach of the Milk River at the Pinhorn Ranch in Alberta (50 km upriver from the Montana seed source). Most Russian olive identified on 1997 aerial photographs flown between the Pinhorn and international border were located close to the border. During a recent (1999) exotic plant eradication program along a 25-km reach of the Milk River upstream of the international boundary, 23 Russian olive saplings and trees (upto 35 years old) were cut down and a herbicide was applied to the stumps (T. Hood, personal communication, 2000). (The remaining plants will be cut in 2001.) There are no records of Russian olive plantings on or close to the Milk River floodplain in southeastern Alberta, suggesting that the 1950 planting at the Aageson Ranch was the original seed source. This also suggests upriver seed dispersal by wildlife. Like Russian olive, ring-necked pheasants were introduced to the northwest United

States in the late 1800s (Weigand and Janson 1976). Ring-necked pheasants may have used Russian olive fruits as a food source in their native Asia. Although we do not know when pheasant moved into the Milk River valley, periodic visits to the valley in Alberta between 1975 and 1999 (Pearce, unpublished data), and observations by others in Alberta (Wallis 1976, Bradley 1982) and Montana (M. Forsyth and S. Huhtala, personal communication, 1999), suggest that ring-necked pheasants are very common on the floodplain, especially in fall and winter, and may be an important wildlife vector for dispersal of Russian olive seeds [perhaps an example of facilitative interaction between introduced species as suggested by Simberloff and Von Holle (1999)].

Seed dispersal by water and ice transport, rather than solely by wildlife transport, may explain the presence on the Milk River of large numbers of Russian olive downriver from the ranch seed source, although this mode of dispersal has not been documented in the literature. Within the last 50 years, Russian olive has invaded the floodplain to 40 km down river from the source, and many seedlings and saplings have colonized on sites close to and paralleling the channel (Figure 3). In addition to the plantings at the Aageson Ranch, numbers are high at three concentration nodes, two in the braiding reach and one in the backwater reach. Although Russian olive on these sites could have been introduced as seeds transported by birds or small mammals from distant (3–7 km from valley) upland shelterbelt plantings, we suggest that this distribution pattern most likely indicates overbank hydrologic transport processes (rainfall-induced floods and ice rafting during river breakup).

Russian olive seeds could enter the river by one of several mechanisms: (1) directly falling into the river or onto ice from overhanging branches; (2) seed-bearing branches and even entire trees being toppled into the river by bank erosion; (3) wildlife defecating seeds onto low-elevation channel banks, bars, or ice; and (4) overbank flows entraining seeds deposited onto the floodplain. Seeds and seed-bearing branches can then be deposited onto other floodplain sites down river during overbank flooding and ice rafting. Overbank processes on the Milk River have a calculated 12-year return period for rainfall-induced floods, an 8-year return period for ice-drive floods, and a combined rainfall/ice flood return period of 5.5 years (Smith and Pearce 2000). There have been seven ice-induced floods and two rainfall-induced floods on the Milk River since 1955 [allowing 5 years for the Russian olive seedlings planted in 1950 to recover from transplant shock and to reach seed-producing age (Haber 1999, Lesica and Miles 1999)]. The three concentration nodes of Russian olive

down river from the ranch source (Figure 5) may have seeded in by hydrological processes. The two high-density nodes in the braiding reach are characterized by even-aged, closely spaced, Russian olive saplings and small trees that may have colonized originally from ice-block rafted seeds and grounded seed-bearing trees, followed by seed dispersal by birds and small animals. However, Russian olive can be killed as well as dispersed by ice: on some sites in the braiding reach, numbers of Russian olive were reduced by 50%–90% after established plants were killed by ice damage in 1996 (Smith and Pearce 2000). The third high-density node, in the backwater, could represent a dumping area where river velocity slows substantially before entering Fresno Reservoir and organic material (e.g., seeds and dislodged trees) and ice blocks are grounded and deposited onto the floodplain. Once established, birds and small mammals could disperse seeds to nearby locations on the floodplain.

Human activities that impact riparian systems, such as flow regulation and livestock grazing, have resulted in conditions unfavorable for the establishment of plains cottonwood. Because Russian olive has dispersal and recruitment advantages compared to cottonwood, it may transform a floodplain from productive native riparian forests and woodlands to dense, thorny thickets with limited species diversity. In Montana undisturbed colonizing and established cottonwood communities support as many as 114 and 58 plant species, respectively, compared to only 29 species in undisturbed Russian olive stands (Hansen and others 1995). As well, Russian olive degrades and narrows river channels, contributes to declines in river-stage levels, blocks irrigation canals, interferes with farm machinery (e.g., thorns puncturing tires), and reduces forage for livestock (Currier 1982, Olson and Knopf 1986a). Knopf and Olson (1984) suggest that naturalization of Russian olive on floodplains in the Rocky Mountains has provided additional wildlife habitat between riparian cottonwood forests and adjacent grass-dominated uplands. In the northern Great Plains, however, Russian olive on some floodplains is forming dense, monodominant stands, and at some locations appears to be replacing early successional cottonwood communities, thus potentially reducing habitat options for wildlife in this region (Olson and Knopf 1986a). Russian olive may have value for landowners on otherwise treeless prairie uplands for windbreaks, soil stabilization, and ornamental plantings, but this value must be weighed against potential negative impacts to native communities on floodplains. Once these problems are recognized by floodplain stakeholders, control and eradication of Russian olive may become a priority.

Introduced plants now comprise almost 14% of the regional flora in the Great Plains (Vitousek and others 1996). In Montana, the introduced Russian olive now outnumbers plains cottonwood as the dominant tree on many sites along the Milk River between the Canada/United States border and Fresno Reservoir. Based on present recruitment levels, it appears that it will outnumber cottonwood in all size classes, both upriver and downriver of the point source, within 10 years. Russian olive has become naturalized on many rivers in Montana because it does well on sites optimal for, as well as unfavorable for, plains cottonwood recruitment (Hansen and others 1995, Shafroth and others 1995, Lesica and Miles 1999). Russian olive and other introduced invasive plants do not respect international borders. Although Russian olive is widespread throughout Montana and other western states, especially in riparian zones, Canada may have a better chance to control it, given its later (1970) distribution for shelterbelts and the much smaller numbers of trees that have been observed, so far, on river floodplains in the prairie provinces (Haber 1999, B. Adams, T. Hood, and W. Thompson, personal communication, 1999). Removing Russian olive once it is established is time-consuming, expensive, and difficult (Olson and Knopf 1986a,b, Hansen and others 1995, Shafroth and others 1995), but Canada has not yet declared Russian olive an alien plant that must be controlled. Unfortunately, invasions of introduced species appear to receive attention only when they cause environmental and economic problems for landowners. By then it may be too late to eradicate them.

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