Germination and Establishment of the Native Plains Cottonwood (*Populus deltoides* Marshall subsp. *monilifera*) and the Exotic Russian-olive (*Elaeagnus angustifolia* L.)

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Abstract: *Russian-olive* (Elaeagnus angustifolia) *is a small Eurasian tree that has escaped from cultivation and become naturalized, primarily along watercourses throughout the western United States. We examined germination and establishment of Russian-olive and plains cottonwood* (Populus deltoides), *the principal native riparian tree of the Great Plains, under a range of experimental moisture and light conditions. The fewest seedlings established under the driest conditions; seedling biomass was predictably lower in the shade; root-to-shoot ratios were higher for cottonwood, higher in the sun, and higher under drier conditions. Several interactions were also significant. The timing of germination and mortality varied between plains cottonwood and Russian-olive: cottonwood germinated in mid-June in all treatments in a single pulse with subsequent mortality; the timing and amount of Russian-olive germination differed substantially across treatments with little net mortality. Differences in life-history traits of these species, including seed size, viability, and dispersal, help explain treatment differences. Russian-olive will likely remain an important component of riparian communities along both unregulated and regulated western rivers because it succeeds under conditions optimal for cottonwood establishment and under many conditions unfavorable for cottonwood. Furthermore, many western states still encourage planting of Russian-olive, and control techniques tend to be labor-intensive and expensive.*

Germinación y establecimiento del álamo nativo de las planicies (*Populus deltoides* Marshall subsp. monolifera) y el olivo ruso exótico (*Elaeagnus angustifolia* L.)

Resumen: *El olivo ruso (Elaeagnus angustifolia) es un árbol pequeño nativo de Europa y Asia que ha escapado de ser cultivado y se ha naturalizado principalmente a lo largo de cursos de agua en el oeste de los Estados Unidos. Examinamos la germinación y el establecimiento del olivo ruso y del álamo del llano (Populus deltoides), el principul árbol nativo rivereño de las Grandes Planicies, bajo un amplio espectro de condiciones experimentales de humedad y luz. La menor cantidad de retoños se estableció bajo las condiciones más secas; la biomasa de los retoños fue predeciblemente menor en la sombra; la proporcián raiz: vástago fue más alta para el álamo, mayor bajo el sol y más alta bajo condiciones más secas. También fueron significativas varias interacciones. El tiempo de germinación y la mortalidad para el álamo del llano y el olivo ruso fue diferente. El álamo del llano germinó durante un único pulso a mediados de Junio en todos los tratamientos con la mortalidad subsiguiente, mientras que los tiempos y la cantidad de germinación del olivo ruso difirieron substancialmente entre los distintos tratamientos con muy poca mortalidad neta. Diferencias en los caracteres de la historia de vida de estas especies, incluyendo el tamaño de la semilla, la viabilidad y la dispersión ayuda a explicar las diferencias entre tratamientos. El olivo ruso permanecerá probablemente como un com-*

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ponente importante de las comunidades ribereñas a lo largo de ríos regulados y no-regulados del oeste. Esto es posible porque el olivo ruso se desempeña exitosamente bajo condiciones que son óptimas para el establecimiento del álamo del llano y bajo condiciones diversas desfavorables para álamo. Más el aún, varios estados del oeste todavía fomentan la plantación del olivo ruso y las técnicas de control requieren una labor intensiva y costosa.

Introduction

Understanding invasions of ecosystems by exotic species is central to many applications of conservation biology. Russian-olive (*Elaeagnus angustifolia* L.) is a small Eurasian tree that has escaped windbreak and horticultural plantings and become naturalized in riparian areas throughout the western United States (Olson & Knopf 1986*a*), forming extensive monotypic stands in some areas (Knopf & Olson 1984; Brown 1990). The native woody riparian species that Russian-olive has displaced or with which it occurs are usually members of the Salicaceae (cottonwoods, willows). Plains cottonwood (*Populus deltoides* Marshall subsp. *monilifera* (Aiton) Eckenwalder; Weber 1990) is the dominant native tree within riparian forests throughout the North American Great Plains.

Russian-olive has been reported both as beneficial and detrimental to wildlife, but it is unquestionably a threat to native plant communities. Characteristics of Russian-olive beneficial to wildlife include a small size that provides structural habitat intermediate to grasses and low-shrubs typical of uplands and the larger trees associated with riparian areas (Knopf & Olson 1984) and the production of abundant edible fruit (Borell 1962). Knopf and Olson (1984) and Brown (1990), however, found that bird species richness and density were higher in native riparian vegetation than in Russian-olive stands. Russian-olive is able to grow under the cottonwood (*Populus* sp.) canopy and can ultimately dominate such sites when the overstory cottonwoods die (Currier 1982). Conversion of sites with both cottonwood and Russian-olive to monotypic Russian-olive would be harmful to the estimated 31% of native bird species that depend on the larger cottonwoods for cavity nesting or insect foods (F. L. Knopf, personal communication).

Given the current wide distribution and likely continued spread of Russian-olive in western riparian ecosystems (Currier 1982; Knopf 1989; Howe & Knopf 1991), more information on its germination and establishment requirements, especially in relation to the native plains cottonwood, is needed to better understand the success of Russian-olive and to manage its spread. We quantified which site conditions might favor one species over the other, and we considered the influences of river management and interspecific differences in key life-history traits.

Methods

We examined germination, establishment, and one season of growth of Russian-olive and plains cottonwood. We placed four planters (30 cm diameter by 100 cm depth) in each of 15 outdoor tanks (122 cm diameter by 135 cm depth) near Fort Collins, Colorado. We drilled a series of 1.3-cm holes into the lower 10 cm of each planter to allow water exchange, and we filled the planters to 92 cm with coarse sand (78% of particles 300—2000 μm). We added Steam's Miracle-Gro (15-30-15, N-P-K) in solution to the top of each planter prior to planting (1.7 g Miracle-Gro to 1.89×10^{-3} m^3 water). The experimental design was a randomized complete block, split-split plot, with three blocks of five whole plots (tanks), each subjected to one of five treatments and containing two subplots and two sub-subplots. We used a block design because we suspected that differences in morning shading from a nearby cliff might significantly affect response variables.

The five whole-plot treatments were designed to represent a streamside elevational gradient ("elevation" A, B, C, D, and E). A 10-cm difference in water level separated successive elevations above groundwater, but the rates of water rise and decline were the same across treatments (Fig. 1). Therefore, water levels for elevation A, the lowest streamside elevation, were always 40 cm higher than for elevation E, the highest streamside elevation. Water levels in the tanks were controlled by adding water (drawn from the Cache la Poudre River) to the tanks or by draining water from faucets attached near the bottom of each tank. From 15 April to 15 May, we held groundwater levels constant at 12, 22, 32, 42, and 52 cm below the soil surface in tanks A, B, C, D, and E, respectively. Between 15 May and 15 June, we raised the water tables 20 cm (0.66 cm per day), and after 15 June we dropped the water tables 0.40 cm per day. The rise and fall of the water table mimicked the timing of peak runoff in Great Plains streams. In a similar experiment (Segelquist et al. 1993), the decline of 0.40 cm per day was optimal for plains cottonwood seedling survival and growth.

The subplot treatments consisted of two light levels: full sun and 89% shade. We mounted shade cloth on wooden frames and positioned the frames 15 cm over the three northernmost planters in each tank so that oblique shade did not affect any of the full-sun planters. To

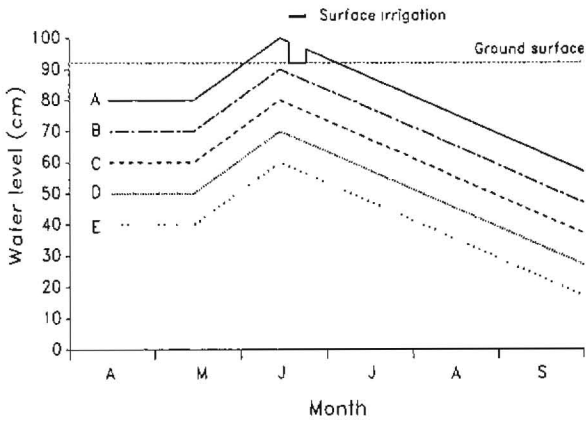

Figure 1. Water levels over time (April-September) for elevational treatments (A-E). The ground surface was at 92 cm in all treatments, and surface irrigation was applied in all treatments for one week following the cottonwood planting.

keep low-angle sunlight of morning and evening from reaching the shaded planters, we covered the east and west ends of the frames with shade cloth.

The sub-subplots consisted of germination treatments for Russian-olive and plains cottonwood seeds. We collected Russian-olive seeds from 20 trees in Larimer County, Colorado, in September and October 1990. We removed the fleshy fruit from the seeds and stored them in sealed containers at 3°C over the winter. We planted 50 Russian-olive seeds on 10 April. Because Russian-olive seeds are often dispersed by birds (Young & Young 1992), we scarified some of the seeds to ensure some germination. Of the 50 Russian-olive seeds, we soaked 25 in concentrated sulfuric acid for one hour (American Nurseryman 1967), notched 10 with a file, and left 15 untreated. We collected plains cottonwood seeds on 17 June 1991 from 20 trees in Larimer County, Colorado, and planted 100 seeds in designated planters on 18 June. To ensure germination of plains cottonwood seed in all treatments, we irrigated the surface of the cottonwood planters with 4.45×10^{-4} m^3 of water every day for the first week.

We counted all seedlings in all planters at two-week intervals throughout the growing season. Seed from nearby plains and narrowleaf cottonwood trees fell into the experimental planters, resulting in some seedling establishment. More cottonwood seeds from nearby trees established themselves in the full-sun planters because the shade cloth prevented these seeds from landing in the shaded planters. Because we could not distinguish volunteer cottonwoods from planted cottonwoods, we did not remove any cottonwood seedlings from any of the planters. We corrected results from the end-of-the-growing-season sampling based on the numbers of cottonwood seedlings in the corresponding Russian-olive planters.

We harvested all seedlings during the first week of October 1991. For every recovered plant we measured shoot and root lengths, separated the roots and shoots, and separately oven-dried and weighed the above- and belowground plant parts.

Results

Elevation above groundwater had a significant effect on the volunteer-corrected fraction of planted seeds present as seedlings at the end of the growing season. The lowest numbers of seedlings were found at the highest elevation E (Tables 1 and 2). Light and species had no significant effect on the number of seedlings established at the end of the growing season, although the two-way interaction of light and elevation above groundwater and

Table 1. Treatment means ± 1 standard error of the mean for number of volunteer-corrected, live seedlings at the end of the growing season as percentage of planted seeds and average seedling biomass of surviving seedlings (grams per seedling)[a]

	Cottonwood				*Russian Olive*			
	Sun		*Shade*		*Sun*		*Shade*	
Elevational Treatment[b]	*Seedlings*	*Biomass*	*Seedlings*	*Biomass*	*Seedlings*	*Biomass*	*Seedlings*	*Biomass*
A	19 ± 2	0.22 ± 0.01	19 ± 7	0.05 ± 0.02	9 ± 1	0.03 ± 0.01	36 ± 3	0.04 ± <0.01
B	29 ± 7	0.36 ± 0.08	25 ± 4	0.05 ± 0.02	44 ± 4	0.34 ± 0.05	18 ± 3	0.15 ± 0.11
C	36 ± 4	0.45 ± 0.23	22 ± 10	0.08 ± 0.04	40 ± 1	0.48 ± 0.15	28 ± 2	0.09 ± 0.01
D	10 ± 4	3.72 ± 1.91	31 ± 4	0.06 ± 0.02	22 ± 1	0.25 ± 0.02	13 ± 2	0.13 ± 0.04
E	0 ± 0	—	1 ± 1	0.04[a]	1 ± 1	0.29[c]	5 ± 4	0.14 ± 0.07[d]

[a] *Values are the mean of three planters unless otherwise indicated.*
[b] *Water levels in the elevational treatments are depicted in Fig. 1.*
[c] *n = 1*
[d] *n = 2.*

Table 2. Effects of elevation above groundwater, light, and species on live seedlings at the end of the growing season as a fraction of seeds in each planter.[a]

Source of Variation	*df*	*MS*	*F*
Whole Plot			
Block	2	0.0002	0.04
Elevation (E)	4	0.5159	87.04[b]
Error	8	0.0059	
Subplot			
Light (L)	1	0.0001	0.01
E × L	4	0.0703	6.41[b]
Error	10	0.0110	
Sub-Subplot			
Species (SP)	1	0.0225	1.89
E × SP	4	0.0043	0.36
L × SP	1	0.0054	0.45
E × L × SP	4	0.0618	5.18[b]
Error	20	0.0119	

[a] *ANOVA was performed with a split-split plot design using an arcsine (fraction)$^{1/2}$ transformation.*
[b] $p \leq 0.01$.

Table 3. Effects of elevation above groundwater, light, and species on average biomass and root biomass/shoot biomass of surviving seedlings in each planter.[a]

		Average Biomass per Plant		*Root Biomass/ Shoot Biomass*	
Source of Variation	*df*	*MS*	*F*	*MS*	*F*
Whole Plot					
Block	2	0.476	0.76	0.306	4.19
Elevation (E)	3	4.707	7.50	0.724	9.90[b]
Error	6	0.628		0.073	
Subplot					
Light (L)	1	30.114	75.51[c]	10.170	193.89[c]
E × L	3	1.442	3.62	0.223	4.26
Error	8	0.399		0.052	
Sub-subplot					
Species (SP)	1	0.899	2.15	7.888	194.93[c]
E × SP	3	1.567	3.75[b]	0.106	2.61
L × SP	1	6.667	15.97[c]	1.857	45.89[c]
E × L × SP	3	1.548	3.71[b]	0.090	2.23
Error	16	0.418		0.040	

[a] *ANOVA was performed with a split-split plot design, restricted to the four wettest treatments, and used the natural logarithm of average per-plant biomass.*
[b] $p \leq 0.05$.
[c] $p \leq 0.01$.

the three-way interaction of light, water, and species were significant. Light regime interacted with elevation above groundwater to produce less decline in numbers at the higher elevations in the shade than in the sun. Furthermore, this interaction differed by species, with a stronger sun-shade difference in the response to elevational treatment for cottonwood than for Russian-olive (Table 1).

Treatment means of the average individual biomass of surviving cottonwood seedlings in each planter ranged from 0.04 grams per seedling in the shade at the highest elevation E to 3.72 grams per seedling in the sun at elevation D (Table 1). Average Russian-olive biomass ranged from 0.03 grams per seedling in the sun at the lowest elevation A to 0.48 grams per seedling in the sun at elevation C. In an analysis of variance restricted to the four lowest elevational treatments that had surviving seedlings in all planters, elevation and light regime, but not species, had significant effects on average seedling biomass (Table 3). Seedling biomass was higher in the sun than the shade and tended to be higher at intermediate elevations (Table 1). Cottonwood had a significantly greater difference in seedling biomass between sun and shade than did Russian-olive. Cottonwood also had significantly greater differences across elevational treatments than did Russian-olive. The three-way interaction among species, water, and light regimes was also significant, with a larger interaction between light and elevation above groundwater for cottonwood than for Russian-olive.

Excluding the highest elevation above groundwater, there were significant treatment effects on the root-to-shoot biomass ratios of surviving seedlings at the end of the growing season for elevation, light, and species (Table 3). Cottonwood had larger ratios than Russian-olive, ratios in the sun were higher than in the shade, and higher elevations tended to have higher ratios (Fig. 2). Two interaction terms were also significant for root-to-shoot biomass ratios. The difference between sun and shade was much greater for cottonwood than for Russian-olive, and the pattern of higher ratios at higher elevations above groundwater was more pronounced in the sun than in the shade.

Although light and species had no effect on volunteer-corrected numbers of seedlings present at the end of the growing season (Tables 1 and 2), there were important differences in the timing of germination and mortality (Fig. 3). Cottonwood germination was essentially synchronous across treatments, with a pulse of germination in mid-June. For cottonwood, treatments differed in the magnitude of the initial pulse and the rate of subsequent mortality. The inclusion of cottonwood volunteers in Figure 3 confounds some treatment differences. Cottonwood numbers are falsely inflated, and there were more cottonwood volunteers in the sun than in the shade because of the shielding effect of the shade cloth on seed fall. The difference in temporal pattern between cottonwood and Russian-olive is clear, however, even in the presence of volunteer cottonwoods. Russian-olive exhibited a much more monotonic increase in seedling numbers in all treatments. Treatments differed substantially in the timing and magnitude of germination, with little net mortality in any treatment combination.

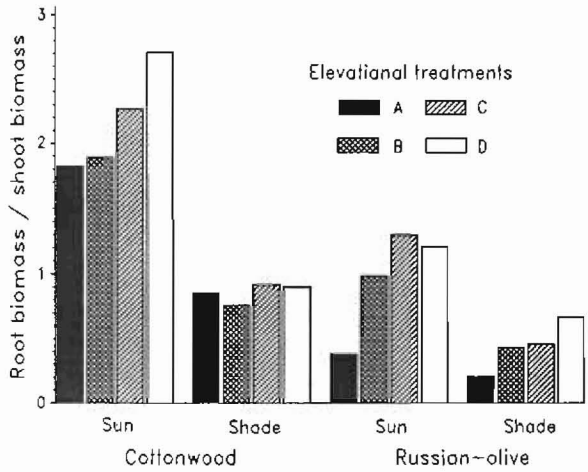

Figure 2. Mean root-to-shoot biomass ratios at the end of the growing season. Total root biomass was divided by total shoot biomass for each planter. The values are the mean of three replicate planters for each treatment combination. Water levels in the elevational treatments are depicted in Fig. 1. The highest elevational treatment (E) is excluded because some planters had no surviving seedlings.

Discussion

Hobbs and Huenneke (1992) suggest that any alteration in the pattern or frequency of a historical disturbance regime will result in a decline in native species diversity. Successful plant invasions are often associated with increased disturbance (Hobbs 1989; Rejmanek 1989; Hobbs & Huenneke 1992; Parker et al. 1993). In situations where the frequency or intensity of a natural disturbance is decreased, however, the invasion of competitively superior non-natives may be promoted (Cowling et al. 1986; Hobbs & Huenneke 1992).

In semiarid and arid regions of western North American, the plains cottonwood is a disturbance-dependent species with relatively specific germination and establishment requirements. Its relatively small seeds (400–1260 seeds per gram; Hardin 1984), dispersed by wind and water, are released over several weeks (Engstrom 1948) and remain viable for only 1–2 weeks (Moss 1938; Ware & Penfound 1949; Kapustka 1972). The timing of this germination window corresponds to the high flows of snowmelt runoff (Scott et al. 1993). These flows produce the bare, moist, mineral-substrate sites on which cottonwood normally become established (Moss 1938; Schopmeyer 1974). After germination, cottonwood seedlings require continued supplemental moisture to avoid desiccation (Mahoney & Rood 1991; Segelquist et al. 1993). These conditions are frequently provided by the descending limb of a natural snowmelt hydrograph but may not be provided by rapid declines following a thunderstorm peak flow or reservoir release. Furthermore, cottonwood is considered intolerant of shade (Van Haverbeke 1990), regenerating at the landscape scale on newly created disturbance sites rather than under existing stands.

We manipulated surface elevation and light in order to represent the range of physical site conditions that might be present in the riparian zone of a river with a hydrograph close to optimal for cottonwood establishment (Scott et al. 1993; Segelquist et al. 1993). We found no evidence that Russian-olive is intolerant of the physical conditions optimal for cottonwood establishment. There were no overall species differences in the fraction of planted seeds alive at the end of the growing season or in the average biomass of surviving seedlings. Optimum site conditions for cottonwood, however, seem to be more narrowly defined than for Russian-olive. Cottonwood displayed greater sun-shade contrasts in average seedling biomass and root-to-shoot biomass than did Russian-olive, and stronger interactions between light and elevation above groundwater for seedling numbers, average seedling biomass, and root-to-shoot ratios. The average biomass of surviving seedlings in the worst treatment combinations were similar for cottonwood and Russian-olive, but cottonwood had more than seven times higher average seedling biomass than did Russian-

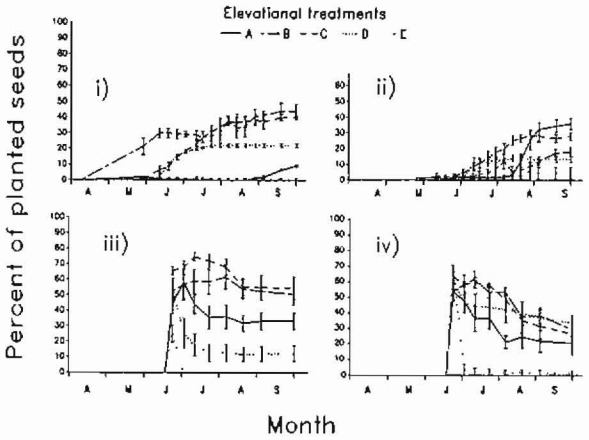

Figure 3. Seedling numbers over time (April-September) as a percentage of planted seeds. Vertical bars are ± 1 SE of the mean (n = 3). Water levels in the elevational treatments are depicted in Fig. 1. Species and light treatments: Russian-olive, sun (i); Russian-olive, shade (ii); cottonwood, sun (iii); and cottonwood, shade (iv). Cottonwood numbers are not corrected for volunteers.

olive in the best treatment combinations for each species.

Seed characteristics and dispersal of the Russian-olive differ substantially from those of the plains cottonwood. Russian-olive seeds are much larger, (about 11.4 Russian-olive seeds per gram; Young & Young 1992), have a hard endocarp, require a period of after-ripening (Hogue & LaCroix 1970), and are dispersed mostly by birds and animals (Hansen et al. 1988; Young & Young 1992). Furthermore, Russian-olive seedlings are reported to be tolerant of shade, and mature trees thrive under a wide range of soil and moisture conditions (Borell 1962; Carman & Brotherson 1982; Currier 1982).

Summarizing these differences in terms of alternative reproductive strategies, plains cottonwoods saturate the floodplain with large numbers of small, short-lived seeds at the time when a natural snowmelt runoff pattern is most likely to provide suitable bare, moist surfaces. The probability of an individual cottonwood successfully establishing and becoming a mature tree is very low. Many sites are not suitable for germination within the relatively brief period of germinability, mortality is extremely high on sites that are not ideal, and there is substantial mortality of seedlings germinating on ideal sites. At the landscape level, this strategy results in many small patches of cottonwood on suitable sites (such as point bars) produced by frequent small-scale disturbances and in fewer, large patches of relatively even-aged cottonwood on suitable sites (such as flood deposits or former channel bed) produced by more extreme, less frequent disturbances (Scott et al. in press).

In contrast, Russian-olive has a much higher investment in each seed and is able to establish over a wider range of sites. Part of the Russian-olive's ability to establish in a wider variety of floodplain sites apparently is due to its ability to germinate only when conditions at each particular site are suitable. In contrast to the cottonwood's synchronous pulse of germination and subsequent mortality across treatment combinations (Fig. 3), Russian-olive germinated at quite different times under different treatment combinations of elevation and light and suffered little or no net mortality of seedlings following germination. This temporal variation in germination may be due to differences in scarification or to variation in the hardness of the seed coat (Young & Young 1992). In a natural setting, these differences, along with varying degrees of cold stratification, could result in germination of a cohort of Russian-olive seeds across multiple growing seasons.

The differences in reproductive strategies and requirements between Russian-olive and plains cottonwood may favor invasion by Russian-olive along many regulated western rivers. Historically in the semiarid west, cottonwood stands along unregulated rivers in the absence of exotic plant species likely were replaced by native upland grass and shrub communities or were damaged or destroyed by flooding (Akashi 1988). In many regulated systems today, however, Russian-olive may replace cottonwood stands over time. For example, invasion of a cottonwood-dominated riparian forest by Russian-olive might proceed as follows on a river system with significantly reduced flood magnitude and frequency: (1) Russian-olive seedlings become established under, at the margins of, or in gaps of the canopy of an existing stand of cottonwoods; (2) as cottonwoods die, Russian-olive becomes the dominant overstory species; and (3) recruitment of Russian-olive seedlings continues in the shade of the new canopy, but cottonwood recruitment is restricted to the narrow, frequently-disturbed margins of the active stream channel, where annual high flows may bury or scour seedlings.

The ability of Russian-olive to establish and grow in the absence of a bare, mineral substrate has also led to its successful naturalization in situations where cottonwoods do not occur. For instance, Currier (1982) notes that Russian-olive is a frequent invader of wetland meadows on the Platte River in Nebraska; areas within the floodplain not suitable for cottonwood establishment. Russian-olive is also known to have spread in sufficiently moist upland areas, such as prairie sites where precipitation provides enough moisture or near irrigated fields (Olson & Knopf 1986*a*).

Russian-olive will probably continue its invasion into and spread throughout western riparian ecosystems. Invasions will continue through reproduction of existing plants and through future introductions. Forestry and extension agencies in almost every western state promote and often subsidize the planting of Russian-olive (Olson & Knopf 1986*b*; F. L. Knopf, personal communication), and Russian-olive is commonly sold in nurseries. Russian-olive will likely become a more prominent component of western landscapes as the cottonwood canopy of existing stands along regulated rivers is replaced by Russian-olive now present in the understory.

Because control techniques are labor-intensive, expensive, and not 100% effective (Olson & Knopf 1986*b*), and because Russian-olive occurs across federal, state, and private lands, prospects for control appear to be limited to small management areas, such as a particular wildlife area or nature preserve. In regulated river environments, improved regeneration of native cottonwood stands might be achieved through simulating flood disturbance by scraping the soil surface and irrigating at the time of cottonwood seed dispersal (Friedman 1993), by occasionally releasing flows of appropriate timing and magnitude to promote establishment (Bradley & Smith 1986; Scott et al. 1993), or by planting poles or nursery stock (Swenson & Mullins 1985; Carothers et al. 1990). Our results suggest, however, that Russian-olive would not be completely excluded even under physical conditions most favorable for the establishment of plains cottonwood.

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