WETLANDS, Vol. 23, No. 4, December 2003, pp. 763–777

BIOLOGY, ECOLOGY AND MANAGEMENT OF *ELAEAGNUS ANGUSTIFOLIA* L. (RUSSIAN OLIVE) IN WESTERN NORTH AMERICA

Gabrielle L. Katz[1,3] and Patrick B. Shafroth[2]
[1] *Department of Geography*
University of Colorado
Boulder, Colorado 80309

[2] *U.S. Geological Survey, Fort Collins Science Center*
2150 Centre Avenue, Bldg. C
Ft. Collins, Colorado, USA 80526

[3] *Present address:*
Department of Geography and Planning
Appalachian State University
ASU Box 32066
Boone, North Carolina, USA 28608
E-mail: katzgl@appstate.edu

Abstract: *Elaeagnus angustifolia* (Russian olive) is an alien tree that is increasingly common in riparian habitats of western North America. This paper reviews the pertinent scientific literature in order to determine the status of *E. angustifolia* as a riparian invader and to suggest ecological reasons for its success. *Elaeagnus angustifolia* meets the biogeographic, spread, and impact criteria for invasive species. Ecological characteristics likely enabling its invasiveness include adaptation to the physical environmental conditions that characterize semi-arid riparian habitats, lack of intense pressure from herbivores, and tolerance of the competitive effects of established vegetation. We believe that the success of this species is at least partly due to its ability to take advantage of the reduced levels of physical disturbance that characterize riparian habitats downstream from dams. Control of *E. angustifolia* is likely to be most promising where natural river flow regimes remain relatively intact.

Key Words: biological invasions, *Elaeagnus angustifolia*, riparian vegetation

INTRODUCTION

Biological invasions constitute a major component of anthropogenic global change (Vitousek 1994) and threaten native biodiversity and ecosystem functioning in a variety of settings (Mack et al. 2000). Whereas all ecosystems are invasible in principle (Williamson 1996), alien species are more abundant in some ecosystems than in others. In particular, riparian ecosystems commonly provide habitat and dispersal corridors for alien species (DeFarrari and Naiman 1994, D'Antonio et al. 1999, Prieur-Richard and Lavorel 2000). For example, North American Great Plains riparian areas support greater alien species richness than do adjacent grassland uplands (Stohlgren et al. 1998), and riparian areas in the Pacific Northwest support greater numbers and cover of aliens than uplands (DeFarrari and Naiman 1994).

Theories put forth to explain patterns of biological invasion include those emphasizing the roles of physical disturbance (Hobbs and Huenneke 1992, D'Antonio et al. 1999), resource availability (Stohlgren et al. 1999), and habitat diversity (Lonsdale 1999). However, the ability of a particular alien species to establish successfully and spread in a new region depends on both the attributes of the alien and the characteristics of the ecosystem being invaded (Lonsdale 1999, Prieur-Richard and Lavorel 2000). Unless otherwise noted, in this paper, we use the term ''invasion'' to refer to the successful establishment and spread of an alien species within an ecosystem. Although we recognize the problematic negative connotation associated with common use of the term ''invader'' (Daehler 2001, Davis and Thompson 2001), we believe that it may still be a useful and efficient term describing the role of certain species within ecological communities.

In this paper, we review literature on the biology, ecology, and management of *Elaeagnus angustifolia* L. (Russian olive, also called oleaster), an alien tree

Figure 1. Naturalized stand of *Elaeagnus angustifolia* along the Snake River, Idaho. (Photo by F.L. Knopf).

that escapes from cultivation in much of western North America. In particular, we examine (1) the status of *E. angustifolia* as an invader in riparian ecosystems of interior western North America, (2) some likely reasons for its ecological success, (3) the available information on management and control of this species, and (4) promising areas for future research.

Plant Description

Elaeagnus angustifolia is a member of the Elaeagnaceae family, which contains three genera (*Elaeagnus*, *Sheperdia*, and *Hippophae*) and approximately 50 species (Heywood 1993). In western North America, common native species closely related to *E. angustifolia* include *Elaeagnus commutata* Bernhardi (silverberry), *Shepherdia argentea* (Pursh) Nuttall (silverberry), and *Shepherdia canadensis* (L.) Nutall (buffaloberry, Weber and Wittman 1996). *Elaeagnus umbellata* Thunb. (autumn olive) is a related Asian species that was introduced to North America for ornamental purposes and has spread from cultivation in parts of the mid-western and the eastern United States (Ebinger and Lehnen 1981, Sternberg 1996).

Elaeagnus angustifolia is a small tree or large multi-stemmed shrub (Figure 1). It is deciduous, with alternate, lanceolate leaves. Leaves, petioles, and current-year branchlets are covered in distinctive silvery-gray peltate scales (Great Plains Flora Association 1986). Its bark is reddish and sometimes shredding, and branches may possess sharp thorns. Fragrant yellow flowers are produced in spring and are insect-pollinated (Figure 2a). Fruits are oval-shaped, 1–1.5 cm long, and contain a single, relatively large seed (Figure 2b,Young and Young 1992). Fruit dispersal occurs during the fall and winter, primarily by birds (VanDersal 1939, Borell 1962, Olson and Knopf 1986b, Kindschy 1998) and other vertebrates (G. Katz, personal observation), and possibly also by fluvial transport (Brock 1998, Pearce and Smith 2001). *Elaeagnus angustifolia* has been shown to have vesicular-arbuscular mycorrhizae (Riffle 1977). It is also an actinhorizal species, participating in a nitrogen-fixing symbiosis with actinomycetes of the genus *Frankia* (Zitzer and Dawson 1992, Johnson 1995).

ELAEAGNUS ANGUSTIFOLIA AS A RIPARIAN INVADER

Recent criteria proposed for classifying a species as an invader commonly include a ‘‘biogeographic criterion’’: the species must be new to the region (Davis and Thompson 2000, Richardson et al. 2000). Additional criteria have been the subject of considerable

Figure 2. (a) Branchlet of *Elaeagnus angustifolia* showing leaves and flowers (Photo by F.L. Knopf). (b) *Elaeagnus angustifolia* leaves and fruits (Photo by G. Katz).

debate (e.g., Daehler 2001, Davis and Thompson 2001) and have included a ‘‘spread criterion’’: the species must reproduce and spread in the new environment (Davis and Thompson 2000, Richardson et al. 2000), or an ‘‘impact criterion’’: the species must have a significant impact on the new environment (Davis and Thompson 2000). Although some workers have recommended exclusion of the impact criterion (e.g., Daehler 2001), we believe that examination of all three criteria provides a useful framework for assessing the ecological role of *E. angustifolia* in North America.

The Biogeographic Criterion

Elaeagnus angustifolia is native to southern Europe and to central and eastern Asia (Hansen 1901, Shishkin 1949, Little 1961). Within this region, it occurs primarily on coasts, in riparian areas, and in other rel-

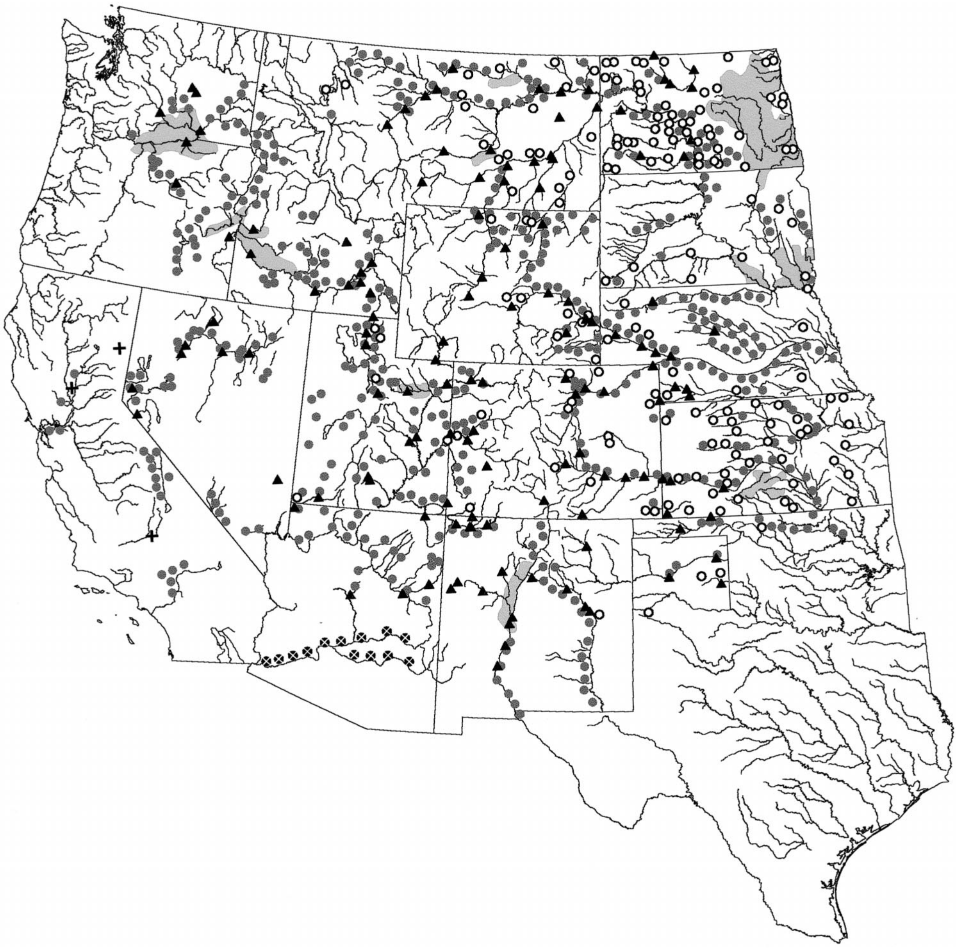

Figure 3. Distribution of *Elaeagnus angustifolia* in 17 western United States. Figure is modified from Olson and Knopf (1986). ● = occurrences of *E. angustifolia* reported by Olson and Knopf (1986). ○ = occurrences reported by the Great Plains Flora Association (1977). ⊗ = occurrences reported by Olson and Knopf (1986), but excluded by Brock (1998). Shaded areas represent regions of extensive naturalization, according to Olson and Knopf (1986). ▲ = occurrences noted between 1997–2001 (J. M. Friedman, unpublished data).

atively moist habitats (Shishkin 1949, Zhang 1981). It is a component of several forest types, including mixed *Tamarix-Elaeagnus* forests, *E. angustifolia*-dominated stands, and *Populus-Elaeagnus* and *Haloxylon* woodlands (Shishkin 1949, Bakhiev and Treshkin 1994, Petrov and Kuz'michev 1994).

Elaeagnus angustifolia was intentionally introduced to North America as a horticultural plant. According to Hansen (1901), it was brought to Nebraska, Kansas, the Dakotas, and Minnesota by Russian Mennonites who used it for hedgerows and as a shade tree. It was recommended for cultivation in several western states in the early 1900s (Christensen 1963, Tellman 1997), was planted in Minnesota prior to the 1930s (Deters and Schmitz 1936), and was used extensively in windbreaks throughout the Great Plains by the 1940s (Read 1958).

Public and private agencies have continued to advocate planting *E. angustifolia* for windbreaks and other horticultural purposes. As recently as the 1980s and 1990s, many state and federal agencies were subsidizing the distribution of *E. angustifolia* seedlings in the western U.S. and Canada (Olson and Knopf 1986a, Haber 1999). It has been promoted and planted in the western U.S. as a source of nectar for bees (Hayes 1976), for wildlife habitat (Borell 1962), and for erosion control. In the eastern U.S., *E. angustifolia* has been planted on reclaimed mine spoils (Côté et al. 1988) and in coastal areas because of its ability to withstand ocean salt spray and deposition of wind-blown sand (Morehart et al. 1980). Continued horticultural interest in *E. angustifolia* is evidenced by recent research addressing such topics as chemically regulating the growth of *E. angustifolia* in nurseries to maintain a compact form (Warren 1990), herbicide-resistance of *E. angustifolia* seedlings (Abrahamson 1986, Porterfield et al. 1993), treatments that facilitate rooting in *E. angustifolia* cuttings (Chong et al. 1992),

Table 1. Quantitative assessments of naturalized *Elaeagnus angustifolia* in western North America.

River or Location	Density (plants/ha)	Cover (%)	Source
Rio Grande, NM	52–357[a]	N/A	Freehling 1982
Rio Grande, NM	0–566[b]	0–43.3	Hink & Ohmart 1984
Rio Grande, NM	N/A	11.1–34.8	Howe & Knopf 1991
Chinle Wash, AZ	430–1150[c]	25–78	Brock 1998
Duchesne R., UT	N/A	50	Knopf & Olson 1984
Milliken, CO	N/A	40	Knopf & Olson 1984
Arikaree R., CO	0.7–225.2	N/A	Katz 2001
S. Fk. Republican R., CO	4.3–314.3	N/A	Katz 2001
Platte River, NE	N/A	2.2–24.5	Currier 1982
Marias R., MT	20–760	N/A	Lesica & Miles 2001
Yellowstone R., MT	20–5120	N/A	Lesica & Miles 2001
Snake R., ID	N/A	80	Knopf & Olson 1984
Snake R., ID	940	81.2	Brown 1990
Snake R., ID	0–55	N/A	Dixon & Johnson 1999

[a] Only individuals >8 cm diameter at breast height and >2 m tall sampled.
[b] All individuals sampled.
[c] Estimated from figure.

and methods of propagating *E. angustifolia* from leaf segments (Economou and Maloupa 1995) and shoot segments (Iriondo et al. 1995).

The Spread Criterion

Elaeagnus angustifolia occurs in most of the continental U.S., absent only from 13 states in the southeast (USDA, NRCS). In the 17 western states it has spread from its original plantings without direct human assistance and is now widely established outside of cultivation (Figure 3; Olson and Knopf 1986b, Brock 1998). It is reported to be spreading from cultivation in the Canadian provinces of British Columbia, Alberta, Manitoba, and southern Ontario (Scoggan 1979). While it is present in much of the central and north-eastern United States, it is generally described as only occasionally or rarely escaping from cultivation (e.g., Steyermark 1963, Rhoades and Block 2000, Wisconsin State Herbarium). Similarly, *E. angustifolia* is occasionally cultivated in far southern New Mexico and Arizona (Olson and Knopf 1986b) but is generally not abundant along the Rio Grande below ca.175 km south of Albuquerque, New Mexico (Campbell and Dick-Peddie 1964) and is not widely naturalized south of the Mogollon Rim, Arizona (Brock 1998). We know of no documented occurrences of *E. angustifolia* in Mexico; however, suitable sites may exist in parts of the Sierra Madre of Chihuahua and Sonora. It has also spread from cultivation in semi-arid parts of South America (Klich 2000).

Elaeagnus angustifolia was introduced to western North America by 1900 but did not become prominent outside cultivated areas until 2–5 decades later (Christensen 1963, Olson and Knopf 1986a). The time lag between initial introduction and widespread invasion reflects a pattern commonly observed for invasive horticultural plants (Ewel et al. 1999, Reichard and White 2001). Although reasons for the ''lag phase phenomenon'' are often poorly understood (Ewel et al. 1999), in this case, it was likely associated with (1) a low rate of introduction in the early part of the 20th century, with significantly greater rates in the 1930s and 1940s in association with government programs, (2) the approximately ten-year lag before newly established *E. angustifolia* individuals become reproductively mature and provide seeds for establishment in new areas (Lesica and Miles 2001), and possibly (3) the inherently slow rates of spatial spread expected for species such as *E. angustifolia* that possess relatively large, primarily vertebrate-dispersed seeds.

The Impact Criterion

Vegetation Effects. Given the complex and varied interactions that occur in most ecosystems, all invaders are likely to have ecological effects in their new ranges (Daehler 2001). The presence of *E. angustifolia* has influenced vegetation composition and structure, as evidenced by high stem densities and canopy cover values measured at several sites in western North America (Table 1). At various sites, *E. angustifolia* is present in monotypic stands or within multi-species canopies. For example, at sites on the Middle Rio Grande, New Mexico, *E. angustifolia* was co-dominant with *Populus fremontii* S. Wats. (Fremont cottonwood) as an overstory species, and dominant or co-dominant in the shrub understory (Freehling 1982).

Invasion by *E. angustifolia* may alter the successional dynamics of riparian forests. In much of interior western North America, native riparian forests are dominated by pioneer species (primarily *Populus* and *Salix* spp.) that rely on physical disturbance to create bare, moist patches for seedling establishment (Braatne et al. 1996, Auble and Scott 1998). These species are generally intolerant of shade (Shafroth et al. 1995) and do not become established within intact vegetation (Katz et al. 2001). In the western Great Plains, shade-tolerant or late-successional tree species are rare or absent from the native riparian forest flora. In the absence of physical disturbance, riparian forests eventually succeed to non-forested communities such as prairie (Friedman et al. 1997), or sagebrush steppe (Lesica and Miles 2001). Here, *E. angustifolia* constitutes a new functional guild; it can establish beneath the canopy of native riparian trees (see below) and can form self-replacing stands. In more humid parts of western North America, *E. angustifolia* may compete strongly with native species such as *Fraxinus pennsylvanica* Marsh. (green ash) and *Acer negundo* L. (box elder), which are seral in *Populus* stands (Lesica and Miles 2001).

Faunal Effects. Alien plants that successfully establish and spread in new environments may alter the use of ecosystems by animals. Although *E. angustifolia* has been promoted for use in wildlife habitat plantings (Borell 1962), there has been relatively little research on its use by animal species. Borrell (1962) noted 42 bird species and 5 mammals that eat *E. angustifolia* fruit, and Freehling (1982) reported an average of up to 24 bird species that use *E. angustifolia-P. fremontii* forests along the Middle Rio Grande in New Mexico. However, except for mourning dove (*Zenaida macroura* L.), it was not clear to what extent the bird species were using *E. angustifolia* versus co-occurring vegetation (Freehling 1982). Knopf and Olson (1984) found that bird species richness and alpha diversity in monotypic *E. angustiolia* stands were intermediate to those of native riparian and native upland vegetation types in Colorado, Idaho and Utah. For small mammals, species richness was greater in *E. angustiolia* stands than in the native riparian and upland vegetation types (Knopf and Olson 1984). Stoleson and Finch (2001) found nests of 11 bird species in *E. angustifolia*, a minor forest component out of a total of 29 species observed to be nesting in riparian woodlands of the Gila River in New Mexico. Of these, only mourning dove, willow flycatcher (*Empidonax traillii* Aud.) and yellow-breasted chat (*Icteria virens* L.) nested frequently in *E. angustifolia*. Black-billed magpies (*Pica pica* L.) nested almost exclusively in *E. angustifolia* on the Snake River Plain in southeastern Idaho prior to experimental treatment but appeared to shift nest sites successfully to big sagebrush (*Artemisia tridentata* Nutt.) following removal of *E. angustifolia* from a management area (Gazda et al. 2002).

In some cases, *E. angustifolia* may provide important structural habitat for wildlife species. It can form an intermediate-height understory canopy layer that is lacking in some native riparian forest communities and may increase the spatial extent of woody habitat by establishing on the outer edge of native riparian forests (Knopf and Olson 1984) or within former grasslands and herbaceous wetlands (Gadza et al. 2002). A test of the structural importance of *E. angustifolia* was provided by Brown (1990), who compared bird use of *Salix* and *E. angustifolia* habitats of similar structure along the Snake River in Idaho. In the winter season, more foraging guilds were found in *Salix* than in *E. angustifolia* stands, but no other differences existed. In the breeding season, species richness, abundance and density were significantly greater in *Salix* than in *E. angustifolia* habitats, and all foraging guilds avoided *E. angustifolia* (Brown 1990). Certain bird guilds, such as cavity nesters, appear to be consistently absent from *E. angustifolia* stands in New Mexico (Stoleson and Finch 2001).

Differences in bird use between *E. angustifolia*- and *Salix*-dominated habitats might be due to relatively low insect abundance in *E. angustifolia* stands (Brown 1990). In other settings, greater insect species richness has been associated with trees historically abundant in a region compared to recently introduced trees (Southwood 1961). Waring and Tremble (no date) examined this question in their study of invertebrate herbivore communities associated with dominant native (*Salix exigua* Nutt. and *P. fremontii*) and alien (*E. angustifolia* and *Tamarix ramosissima* Ledeb.) plants along the San Juan River in Utah. Species richness of insect herbivores was much lower on *E. angustifolia* (8.23 ± 3.08 species/100 sweeps) than on the native *S. exigua* (24.25 ± 4.39), but numbers were similar on the native *P. fremontii* (8.22 ± 3.59). Insect densities were also lowest on *E. angustifolia* (13.53 ± 5.92), greatest on *S. exigua* (210.34 ± 115.83), and intermediate on *P. fremontii* and *T. ramosissima* (Waring and Tremble no date).

Ecosystem Level Effects. Alien species may alter ecosystem processes such as disturbance regimes (Mack and D'Antonio 1998, D'Antonio et al. 1999) and nutrient cycling (Vitousek et al. 1987). Invasion by *E. angustifolia* potentially influences hydrogeomorphic processes, for example by increasing floodplain roughness in habitats where woody vegetation would otherwise not occur (Tickner et al. 2001). However, we know of no research that has addressed this issue. Invasion by *E. angustifolia* also potentially affects ecosystem nutrient levels, although we know of no studies that have demonstrated this in natural settings.

Elaeagnus angustifolia is an actinorhizal species, forming nitrogen-fixing root nodules in symbiotic association with actinomycetes of the genus *Frankia* (Miller and Baker 1985, Zitzer and Dawson 1989, Moretti 1993). Degree of nodulation in *E. angustifolia* was related to soil type, soil pH, and possibly soil aeration in central Illinois (Zitzer and Dawson 1989, Zitzer and Dawson 1992) and to salinity in experimental treatments (Kefu and Harris 1992). As is typical of nitrogen-fixing plant species, *E. angustifolia* has high leaf nitrogen content (Royer et al. 1999, Simons and Seastedt 1999). Leaf litter from *E. angustifolia* populations contained 3.08% N in Spain (Bermúdez de Castro et al. 1990), 2.25% N in France (Domenach et al. 1994), and 1.8–2.7% N in Colorado, compared to 0.7–1.4% N for *Populus deltoides* Marsh. ssp. *monilifera* (Aiton) Eckenwalder (plains cottonwood, Simons and Seastedt 1999). Leaves of *E. angustifolia* contained 3.1–3.3% N in Spain (Llinares et al. 1992), 2.9% N on the Rio Grande in New Mexico (Johnson 1995), and 1.6% N in southern Idaho, compared to values of $<1\%$ for native *Populus tremuloides* Michx.(aspen), *Cornus stolonifera* Michx.(dogwood), and *Populus balsamifera* ssp. *trichocarpa* (Torr. & Gray ex Hook.) Brayshaw (black cottonwood, Royer et al. 1999). Leaves of laboratory-grown *E. angustifolia* seedlings contained 3.3% N, which was associated with a high photosynthetic rate (Côté et al. 1988).

Because of its actinorrhizal nature, high leaf nitrogen content and deciduous habit, *E. angustifolia* may contribute significant additional nitrogen to ecosystems that it invades (Bermúdez de Castro et al. 1990). Indeed, *E. angustifolia* has been used as a ‘‘biofertilizer’’ or nurse crop in silvicultural settings because the decomposition of its leaves and sloughed root tissue adds nitrogen to plantation soils (Dawson and Sambeek 1993, Domenach et al. 1994). Further, Llinares et al. (1994) suggested that allelopathic chemicals in *E. angustifolia* litter inhibit microbial nitrification and may result in considerable N-conservation on sites dominated by *E. angustifolia*. Although Domenach et al. (1994) found that complete leaves of *E. angustifolia* had relatively high lignin:N ratios, they also concluded that a large proportion of the leaf components were water-soluble and N-rich and, therefore, were probably prone to ready biodegradation. On the other hand, Royer et al. (1999) found slow processing rates of *E. angustifolia* leaves in some Idaho streams and suggested that slowed litter processing might alter local and downstream aquatic communities.

INVASION ECOLOGY

Most attempted general explanations of biological invasions have focused on either the attributes of successful invaders (Bingelli 1996, Rejmánek and Richardson 1996, Crawley et al. 1997) or on the attributes of invasible communities (Lavorel et al. 1999, Prieur-Richard and Lavorel 2000). Another approach, presented by Lonsdale (1999), is to view the relative success of an invader as a function of both its rate of introduction and its rate of survival in the new range. The survival rate includes at least four sub-components: survival considering maladaptation (or adaptation) to the physical environment of the new range, survival given the effects of herbivores and pathogens, survival as influenced by competition from native vegetation, and survival after chance extinction events (Lonsdale 1999). The overall survival rate is influenced by both the attributes of the alien plant and by the properties of the ecosystem potentially being invaded. Below, we examine the first three of these components and the role of physical disturbance.

Adaptation to the New Physical Environment

Tolerance of the abiotic conditions that characterize a new region is a prerequisite for invasion there. Because it is native to temperate areas of Eurasia, *E. angustifolia* is pre-adapted to the general climatic conditions that characterize much of interior western North America. However, within this region, the success of *E. angustifolia* may be due to its ability to tolerate a broad range of physical conditions and to its relative lack of specialization with respect to fluvial processes. Baker (1965) argued that weeds should possess ‘‘general purpose’’ genotypes, which pre-adapt them to grow under a wide variety of environmental conditions. There is some evidence that *E. angustifolia* fits this description, especially in comparison to native woody riparian taxa. Below, we review the currently available published information on the tolerance of *E. angustifolia* to varying levels of (1) soil alkalinity and salinity and (2) moisture availability.

Soil Chemistry. In experimental studies, *E. angustifolia* has been shown to possess high alkali tolerance. Seeds and recently germinated seedlings of *E. angustifolia* rated as the most alakali tolerant of twenty common shelterbelt species tested for tolerance of Na_2SO_4 and Na_2CO_3 (Stoeckeler 1946). Field observations are consistent with this result, as *E. angustifolia* is reported to be naturalized on some alkaline sites (e.g., on a gypsaceous alkaline gley solonchack in Spain; Bermúdez de Castro et al. 1990), and several workers have stated that *E. angustifolia* is generally tolerant of alkaline conditions (Read 1958, Bertrand and Lalonde 1985).

Elaeagnus angustifolia seems to be fairly tolerant of salinity in experimental studies. Using leakage of UV-absorbing substances as a measure of cellular injury from salt treatments, Redmann et al. (1986) determined that *E. angustifolia* leaf tissue was very tolerant of both NaCl and KCl. Monk and Wiebe (1961) conducted salt irrigation experiments with equal parts NaCl and $CaCl_2$ and found *E. angustifolia* seedlings to be tolerant of a 10.3 g/L salinity level, grouping it among the most salt-tolerant species studied. Further, Kefu and Harris (1992) cited data indicating that growth of *E. angustifolia* seedlings was unaffected by weekly application of an 8 g/L solution of NaCl, with only slight injury resulting from a 10 g/L salinity level, severe injury occurring at 14 g/L, and frequent mortality at 16 g/L and higher. By comparison, *P. fremontii* seed germination was inhibited by irrigation with a mixed-salt solution of 4.0 g/L (Shafroth et al. 1995), and decreased performance of rooted cuttings has been reported at salinity levels of 4.0 g/l (Glenn et al. 1998), 5.3 g/L (Vandersande et al. 2001), and 6.0 g/L (Jackson et al. 1990), with mortality occurring at 6 g/L (after 120 days, Jackson et al. 1990) to 16 g/L (after 60 days, Glenn et al. 1998). For *P. deltoides* rooted cuttings, significant reductions in growth have been observed at NaCl concentrations of 5.8–11.7 g/L (Singh et al. 1999).

Although *E. angustifolia* is somewhat salt-tolerant, it cannot survive the extremely high salinities that characterize some western U.S. habitats. Although Kefu and Harris (1992) cited data indicating that *E. angustifolia* can grow in soils with salinities of 10–15 g/L in China, sites supporting non-cultivated *E. angustifolia* populations in Utah had average soluble soil salt concentrations of 2.0 g/L (range 0.1–3.5 g/L), compared to 5.2 g/L (range 0.7–15.0 g/L) on sites supporting saltcedar (*Tamarix* spp.; Carman and Brotherson 1982). In another study, all *E. angustifolia* seedlings planted in a highly saline (EC 9.2 dS/m) and sodic (SAR 33.1) bentonite soil in Wyoming died within two weeks (Uresk and Yamamoto 1994).

Soil Moisture. In the western United States, drought stress is commonly experienced by vegetation, even in riparian areas (Albertson and Weaver 1945, Tyree et al. 1994). Although many authors mention drought tolerance as an important part of the horticultural appeal of *E. angustifolia* (Hansen 1901, Deters and Schmitz 1936, Little 1961, Sprackling and Read 1979), there is relatively little published research that can be drawn upon to support this claim. Deters and Schmitz (1936) studied shelterbelts in Minnesota following a 1930s drought and found that *E. angustifolia* showed very high survival, although it was a minor shelterbelt component. However, in the more arid Southern Plains, *E. angustifolia* planted in windbreaks suffered considerable drought-induced mortality following dry conditions in the 1950s (Read 1958). Further evidence for only moderate drought-tolerance is provided by Carmean (1976), who found that *E. angustifolia* grew best on a moderately drained silty clay loam soil in western Minnesota and that it performed most poorly on a very well-drained sandy loam.

Although at the landscape scale, *E. angustifolia* is naturalized primarily in moist sites, at the local scale it occurs on sites with a variety of moisture conditions. Campbell and Dick-Peddie (1964) observed naturalized *E. angustifolia* populations on xeric, mesic, and hydric sites along the Rio Grande in New Mexico. *Elaeagnus angustifolia* has been characterized as typical of moist pastures and rangeland (Carman and Brotherson 1982) and frequently flooded wetland meadows with saturated soils (Currier 1982). However, Knopf and Olson (1984) characterized sites supporting *E. angustifolia* stands in Colorado, Idaho, and Utah as intermediate in moisture, compared to riparian and upslope areas. Similarly, *E. angustifolia* occurred at intermediate elevations within the bottomland of the Snake River, Idaho (Johnson et al. 1995). On the Marias and Yellowstone Rivers in Montana, *E. angustifolia* was restricted to the cottonwood understory on dry high terraces but occurred with and without a cottonwood canopy on moist, lower-elevation terraces (Lesica and Miles 2001).

Elaeagnus angustifolia may be similar to native riparian tree taxa that possess few adaptations to drought (Stromberg and Patten 1992, Tyree et al. 1994, Rood et al. 1995) in that it sometimes survives in arid environments as a facultative phreatophyte, avoiding drought stress by tapping into a relatively constant supply of ground water. Zhang (1981) reported that *E. angustifolia* was much less physiologically drought-tolerant than the xerophytes *Nitraria tangutorum* Bobrov. and *Haloxylon ammodendron* (C. A. Mey.) Bunge, and that its survival in the Min-Qin area of China was primarily due to its ability to extend its roots 1 to 3 meters downwards to ground-water sources. For the seedling stage, Shafroth et al. (1995) found no difference in the response of *E. angustifolia* and *P. deltoides* seedling establishment to various water accessibility treatments. For both species, the lowest numbers of seedlings survived when ground-water levels were farthest from the soil surface.

Relative to many native riparian trees in western North America, however, *E. angustifolia* does seem to possess some adaptations for drought-tolerance. Whereas Shafroth et al. (1995) found that biomass did not differ between *E. angustifolia* and *P. deltoides* seedlings grown under varying water accessibility treatments, root:shoot ratios were higher for *P. deltoides* than for *E. angustifolia*, suggesting that *E. angustifolia* may have additional drought adaptations that compensate for its relatively small root mass. Indeed, compared to native riparian tree taxa, *E. angustifolia* seedlings and adults possess some apparently xeromorphic attributes, including reflective silvery foliage, a relatively thick cuticle, and sunken stomata (Zhang 1981). Klich (2000) argued that morphological and anatomical leaf variation within individual *E. angustifolia* canopies constituted an adaptive advantage in semi-arid riparian habitats characterized by strong variations in solar radiation, air temperature, and humidity.

Effects of Herbivores and Pathogens

When a species is introduced into a new area, it usually leaves behind specialized predators and pathogens that prey on it in its native range. Therefore, the success of invasive species has sometimes been attributed to this release from ‘‘natural enemies’’ (Crawley et al. 1997, Mack et al. 2000). However, if generalist native predators (including herbivores, granivores) and pathogens are present in the new region, they can potentially have a large influence on the survival of the alien species (Katz et al. 2001). Herbivory by introduced livestock and attack by introduced pathogens may also influence the success of a plant invader.

Herbivory does not seem to limit *E. angustifolia* invasion in western North America to any great extent. Population densities of invertebrate herbivores were low on *E. angustifolia* along the San Juan River in Utah (Waring and Tremble no date). Native beaver (*Castor Canadensis* Kuhl) harvested very few *E. angustifolia* trees, and the severity of beaver damage was low compared to the mortality and damage inflicted to native *P. deltoides* on both the Marias (Lesica and Miles 1999) and Milk Rivers (Pearce and Smith 2001) in Montana. Although domestic livestock will browse *E. angustifolia* (G. Katz, *personal observation*), the observation that *E. angustifolia* commonly invades into grazed meadows and pastures (Currier 1982) suggests that herbivory does not prevent its survival. In addition to large seed reserves that may enhance the survival of seedlings following browsing (Armstrong and Westoby 1993), *E. angustifolia* adults possess several adaptations to deter grazers, including sharp thorns (Hansen 1901) and leaves containing abundant defense compounds (T. R. Seastedt, *personal communication*). On the other hand, granivory by generalist mammals (primarily house mice, *Mus musculus* L. and deer mice, *Peromyscus maniculatus* Wagner) completely prevented germination of *E. anugustifolia* seeds outside of small mammal exclosures in study plots in Colorado (Katz et al. 2001).

Elaeagnus angustifolia is subject to several diseases, both in nurseries and in field settings. Published reports of diseases in *E. angustifolia* nursery stock include documentation of several fungal cankers (Arnold and Carter 1974, Morehart et al. 1980, Krupinsky and Walla 1986, Morton and Krupinsky 1986, Peterson and Morton 1986) and a leaf spot fungus (Lorenzini et al. 1984). Read (1958) stated that disease caused considerable mortality of *E. angustifolia* planted in windbreaks in the Dakotas, and there is increasing concern about disease and die-back of ornamental *E. angustifolia* plants in the Midwest and Great Plains (e.g., anonymous 1987, Pottorff and Jacobi 1998, Tisserat 2002). For native *E. angustifolia*, Petrov and Kuz’michev (1995) described die-back of native *E. angustifolia* in forests near the Caspian Sea due to vascular bacteriosis carried by a bark beetle. Episodes of widespread mortality and bark beetle infestation are apparently common for *E. angustifolia* in its native range (Petrov and Kuz’michev 1994).

Competition and Disturbance

It is often generalized that physical disturbance facilitates biological invasions (Fox and Fox 1986, Hobbs and Huenneke 1992), presumably by removing competing vegetation (Lonsdale 1999) and releasing resources. In many settings, biological invasions are enhanced by increased levels of physical disturbance or by the introduction of new kinds of disturbance into native ecosystems (D’Antonio and Vitousek 1992, Hobbs and Huenneke 1992, Crawley et al. 1997). Such patterns result from the fact that, in the ecosystems studied, invasive alien species are better able to colonize, grow, and reproduce in disturbed habitats than are the native species (McIntyre and Lavorel 1994) or are better able to tolerate novel kinds of disturbance to which the native species are not adapted (e.g., Mack and Thompson 1982).

The case of *E. angustifolia* invasion in western North America provides a contrasting example to these general patterns (Lesica and Miles 1999). In the present example, the invader seems to have ecological characteristics typical of later-successional species, while native riparian trees tend to be pioneers, dependent on physical disturbance for recruitment (Shafroth et al. 1995, Katz et al. 2001). Field observations indicate that *E. angustifolia* is relatively tolerant of the competitive effects of established native vegetation, invading beneath woody overstories or within herbaceous vegetation. Along the Rio Grande in New Mexico, *E. angustifolia* occurs as an understory species (Howe and Knopf 1991) and without an overstory on some reaches (Campbell and Dick-Peddie 1964). Knopf and Olson (1984) observed naturalized *E. angustifolia* individuals growing both within cottonwood floodplain forests and colonizing wet meadows in Colorado, Idaho, and Utah. Along the Bighorn River in Montana, *E. angustifolia* occurred beneath the open canopy of middle-aged cottonwood woodlands, as well as on the outskirts of cottonwood stands (Akashi 1988). Currier (1982) considered *E. angustifolia* to be typical of heavily grazed pastures along the Platte River, Nebraska, although it also occurred in some riparian forest understories. *Elaeagnus angustifolia* has been characterized as typical of moist pastures in Utah (Christensen 1963) and pasture land along the North Platte River in Nebraska (Bovey 1965).

Two experimental studies support these field observations by suggesting that *E. angustifolia* is relatively shade-tolerant compared to native *P. deltoides* and that it is able to establish within intact vegetation. Shafroth et al. (1995) found that artificial shade decreased growth of *P. deltoides* seedlings more than *E. angustifolia* seedlings in experimental planters but that there was no effect on seedling survival of either species. Katz et al. (2001) found that seedlings of *E. angustifolia* became established within dense, undisturbed herbaceous vegetation, while those of *P. deltoides* did not.

Seed Size, Dormancy and Longevity. Ecological attributes contributing to the later-successional regeneration traits of *E. angustifolia* may include large seed size and seed longevity. Seeds of *E. angustifolia* weigh approximately 0.09 g, compared to 1.7×10^{-4} g for *Salix amygdaloides* Anderss. (peachleaf willow; Young and Young 1992) and between 2.0×10^{-3} g (Young and Young 1992) and 6.04×10^{-4} g (Friedman et al. 1995) for *P. deltoides*. Large seed size is associated with several ecological attributes including establishment, growth, and survival in the shade (Grime and Jeffrey 1965, Foster 1986, Saverimuttu and Westoby 1996), the ability of seedlings to establish within intact groundcover (Reader 1993), seedling survival following defoliation (Armstrong and Westoby 1993), and possibly seedling establishment under arid conditions (Baker 1972, Leishman and Westoby 1994, Westoby et al. 1997). On the other hand, because of the trade-offs between seed size, seed number, and dispersability (Harper 1977, Rees 1997), good invaders might be expected to produce abundant, widely dispersed, small seeds, rather than fewer large seeds requiring specialized dispersal. However, when efficient dispersal agents are present, the potential disadvantages of large-seededness may be overcome (Rejmánek and Richardson 1996) or outweighed by benefits such as increased competitive ability (Crawley et al. 1997) and increased tolerance of environmental stresses. Indeed, large-seededness may be an important factor enabling *E. angustifolia* to establish within intact vegetation and litter, thereby liberating it from the dependence on physical disturbance that characterizes the establishment of native cottonwoods and willows.

A relatively long seed-viability period may be another important aspect of the invasion ecology of *E. angustifolia*. In contrast to native cottonwoods and willows, whose seeds are germinable when dispersed and remain viable for only a short period following dispersal (Young and Young 1992), *E. angustifolia* seeds are dispersed during the late fall and winter in a dormant state and remain viable for one to three years in the laboratory (Young and Young 1992). To break dormancy, *E. angustifolia* seeds require a period of after-ripening (Hogue and LaCroix 1970, Hamilton and Carpenter 1976, Belcher and Karrfalt 1979). In general, under laboratory conditions, cleaned seeds germinate best after pre-chilling for approximately 90 days under moist conditions at 5 °C (Hogue and LaCroix 1970, Belcher and Karrfalt 1979).

The exact mechanism or mechanisms responsible for *E. angustifolia* seed dormancy are unknown. Hogue and LaCroix (1970) found that seed germinability of non-after-ripened seeds was increased by removal of both the seed endocarps and the seed coats and argued that germination inhibition appeared to be caused by non-leachable substances in these structures. Hamilton and Carpenter (1976) analyzed growth substances in *E. angustifolia* seed endocarps and embryos and attributed dormancy regulation to coumarin-like substances present in both structures. It has been proposed that treatment with sulfuric acid improves germinability and may replace pre-chilling for the purposes of horticultural propogation (Heit 1967).

Long-term seed viability may allow *E. angustifolia* to exploit suitable germination conditions over a relatively lengthy time period compared to native taxa (Howe and Knopf 1991, Shafroth et al. 1995). In establishment experiments, Shafroth et al. (1995) found that the timing of *E. angustifolia* seed germination varied fairly widely depending on treatment conditions. They argued that the success of *E. angustifolia* was probably at least partly due to its ability to germinate whenever conditions at a particular site became suitable. However, this attribute is only advantageous on substrates old enough and stable enough to contain seeds that arrived in previous years.

The later-successional characteristics of *E. angustifolia* contrast sharply with the ecological traits of many native riparian trees and with those of saltcedar (*Tamarix* spp.), the dominant woody riparian invader in most of the southwestern U.S. Like native pioneer species, *Tamarix* produces abundant quantities of small

(1.0×10^{-4} gram) seeds that are dispersed by wind and water to bare moist substrates where seedling establishment occurs (Brock 1994). In contrast to native pioneer species, however, *Tamarix* seeds are dispersed throughout the growing season (Warren and Turner 1975), and established plants are relatively tolerant of salinity, drought, and fire (Jackson et al. 1990, Brock 1994, Shafroth et al. 1998). During the 20th century, *Tamarix* spread quickly and become very abundant along rivers in the southwestern United States (Robinson 1965, Everitt 1998). However, it is unlikely that *Tamarix* can maintain long-term dominance of riparian sites in the absence of occasional disturbance.

On most rivers in western North America, river flow regimes have been altered by humans (Graf 1999), and in most cases, flood frequency and intensity have been reduced (Williams and Wolman 1984). Downstream from dams, reduced rates of fluvial disturbance have led to reduced recruitment of native pioneer riparian trees on many formerly meandering rivers (Bradley and Smith 1986, Johnson 1992, Friedman et al. 1997). This reduced recruitment results from the fact that these species typically become established on >fluvial disturbance patches= created by sediment erosion and deposition accompanying natural river flow fluctuations (Auble and Scott 1998). Where river regulation has resulted in diminished rates of creation of these disturbed patches, recruitment of native floodplain species has been reduced. In such settings, *E. angustifolia* is at an advantage relative to native and alien disturbance-dependent taxa because its reproduction is not as closely linked to flood disturbance (Shafroth et al. 1995, Lesica and Miles 1999, Katz 2001).

CONTROL AND MANAGEMENT

There is little published research addressing effective techniques to control or remove *E. angustifolia* from invaded sites, although Stannard et al. (2002) assessed a variety of suppression methods, including mechanical and chemical approaches. Techniques such as mowing, cutting, girdling, chaining, and bulldozing can suppress *E. angustifolia* on invaded sites, although the disadvantages to such approaches can be significant, including the necessity for frequent treatment repetition, the indiscriminate removal of other woody species, and severe soil disturbance (Stannard et al. 2002). Burning does not seem to be an effective control technique, since *E. angustifolia* will resprout vigorously from root crowns, and at present, no targeted biocontrol agents exist (Stannard et al. 2002).

Most published accounts of effective *E. angustifolia* suppression employ a chemical treatment, either alone or combined with mechanical techniques. Bovey (1965) reported successful control of *E. angustifolia* invasion by aerial spraying of herbicides (1:1 mixture of 2,4-D and 2,4,5-T, at 1.8–3.7 kg/ha), and Ohlenbusch and Ritty (1978) also reported effective control using foliar (2,4,5-T, Silvex (2,4,5-TP)), dicambra, and picloram in a 9:1 carrier solution of water and diesel oil) and basal (2,4,5-T, Silvex (2,4,5-TP)), dicambra, and tryclopyr ester in a 100% diesel oil carrier) herbicide applications. Edelen and Crowder (1997) reported significant initial damage to adult *E. angustifolia* when foliage was sprayed with a 4% solution of imazapyr (Contain, 14% active ingredient), although long-term response was not assessed. These approaches may not be feasible or desirable in many riparian settings (Ohlenbusch and Ritty 1978, Caplan 2002).

Dieter (1996) reported that the most effective means of *E. angustifolia* control employs a combination of (1) pulling out small individuals from moist soil using a weed wrench and (2) cutting larger individuals at ground level and then immediately applying a small amount of herbicide to the cut stumps. Similarly, Caplan (2002) described controlling small (<10cm diameter) *E. angustifolia* stems with a mulching tractor and controlling large stems with cutting and immediate application of a 50-percent solution of Garlon-4® (triclopyr) to stump surfaces. However, several annual follow-up applications of herbicide to the foliage of root sprouts were also required. In general, any initial control method requires at least some ongoing suppression of stem and root sprouts and of new recruitment from seed (Edelen and Crowder 1997, Stannard et al. 2002). Such labor-intensive control techniques might be avoided if it were possible to limit initial seedling establishment in an area using management techniques such as targeted grazing, granivory, or temporary inundation.

Attempts to limit further invasion by *E. angustifolia* will benefit from recognition of the ecosystem and management contexts in which invasion occurs. In much of western North America, native riparian ecosystems have been impacted by floodplain and river management techniques. Hydrologic alterations have been implicated in the widespread decline of some riparian forest types (Johnson 1992, Stromberg, 2001) and in facilitating invasions by opportunistic alien species (Everitt 1998). Indeed, it is likely that reduced levels of fluvial disturbance downstream from dams favor invasion by *E. angustifolia* (Shafroth et al. 1995, Lesica and Miles 1999, Katz et al. 2001). However, current interest in changing river-flow management strategies to restore native riparian forests (Molles Jr. et al. 1998, Richter and Richter 2000, Patten et al. 2001, Stromberg 2001) provides hope for the possible control of invasive riparian plant species via restoration of ecosystem processes. At present, it is unclear how prescribed flows, such as those aimed at maintaining a mosaic of native riparian forest patch types (Richter and Richter 2000), might influence the spread or abundance of *E. angustifolia*. Ideally, river flow regimes designed to improve regeneration and survival of native riparian forest species will also limit the success of alien invaders.

RESEARCH NEEDS

Despite the increasing prevalence of the alien *E. angustifolia* in riparian environments throughout the western United States, much remains unknown regarding the ecology and invasion effects of this species. For example, there is little quantitative information on the historic and present-day rate of spread of *E. angustifolia* (except Pearce and Smith 2001) or its potential for range expansion in this region. We suggest that research addressing the ecological factors limiting the geographical range of *E. angustifolia* could examine the possibility that seed dormancy is not effectively broken in the warm southern deserts and the question of whether pathogens may limit its spread in more humid areas. Further, there is little published information on the tolerance of *E. angustifolia* to drought stress, inundation, or the physical effects of fluvial disturbance, and there have been no studies of competition or facilitation between *E. angustifolia* and co-occurring species. Elucidation of the effects of *E. angustifolia* invasion on ecosystem nutrient levels is also needed. With increasing interest in using managed river flows as a tool in riparian forest restoration, research addressing the effects of river flow regimes on invasion by *E. angustifolia* merits particular attention.

ACKNOWLEDGMENTS

During preparation of this paper, G. Katz was supported by the Graduate School of the University of Colorado-Boulder and by a U.S. Environmental Protection Agency STAR Graduate Fellowship. We are grateful to Jonathan Friedman, Susan Beatty, Peter Lesica, and one anonymous reviewer for providing helpful reviews of an earlier version of the manuscript.

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Manuscript received 5 August 2002; revisions received 4 February 2003; accepted 4 August 2003.