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TAMARIX APHYLLA: A NEWLY INVASIVE TREE IN SOUTHERN NEVADA

Lawrence R. Walker¹, Pamela L. Barnes¹, and Elizabeth A. Powell¹

ABSTRACT.—In the southwestern United States, the nonnative athel pine (*Tamarix aphylla*) was presumed to be sterile and therefore not as likely to spread as its widely distributed, nonnative congener, *T. ramosissima*. However, at Lake Mead National Recreation Area (LMNRA) in southern Nevada, populations of *T. aphylla* have recently spread beyond their limited pre-1990 distribution and now form extensive monospecific stands. Over a 3-year period, we quantified seed production and germination from 60 *T. aphylla* trees at LMNRA. The annual mean seed production period was 50.6 days, and the mean potential germination (under laboratory conditions) was 22%, indicating that *T. aphylla* trees at LMNRA are capable of sexual reproduction in southern Nevada. No seeds germinated in field experiments, apparently because of high soil salt levels. However, seedling regeneration is becoming increasingly common at LMNRA. *Tamarix aphylla* trees occupied a distinct zone along the shoreline of Lake Mead, above *T. ramosissima* in elevation and below native *Larrea tridentata* communities, suggesting either competitive exclusion or differential resource utilization. The *T. aphylla* zone tended to have the highest mean values for total vegetation cover, leaf litter depth, soil salinity, soil moisture, pH, total Kjeldahl nitrogen, and soil organic matter. The capacity for sexual reproduction of this alien plant, combined with a suite of characteristics shared with the invasive *T. ramosissima* (e.g., drought tolerance and copious saline leaf litter), makes *T. aphylla* a potentially invasive species along the shores of LMNRA and other mesic areas in the desert Southwest.

Key words: *Tamarix aphylla*, *Tamarix ramosissima*, invasions, drawdown zone, saltcedar, athel pine, Nevada, reservoir, riparian ecology, Lake Mead.

Floodplains provide corridors for plant invasions (Williams and Wiser 2004), particularly in arid ecosystems where access to water is limited (Brokaw 1998). Extreme fluctuations of water levels around artificial impoundments (Dynesius and Nilsson 1994, Tallent-Halsell and Walker 2002) provide opportunities that favor the invasion of woody plants with deep roots. The shoreline of Lake Mead in the Mojave Desert in southern Nevada, like many impoundments, fluctuates periodically depending on patterns of water removal for irrigation in southern California and rainfall—in this case from the headwaters of the Colorado River. These fluctuations create a drawdown zone that is increasingly dominated by nonnative plants that are capable of surviving periodic inundation and rapidly recolonizing newly exposed banks. Two woody invaders of this drawdown zone are *Tamarix ramosissima* Ledeb. (from central Asia) and *T. aphylla* (L.) Karst. (from North Africa and the Middle East). *Tamarix ramosissima* is an invasive shrub that dominates many watercourses throughout the desert Southwest and alters flooding and erosion patterns, fire frequency, ground water levels, and soil chem-

istry (Busch and Smith 1995, Walker and Smith 1997, Di Tomaso 1998). High water use by *T. ramosissima* leads to lowered water tables (Waisel 1960b, Sala et al. 1996) and competition with native species (Cleverly et al. 1997, Sher et al. 2002, Sher and Marshall 2003). However, very little is known about the ability of *T. aphylla* to invade watercourses or effect ecosystem change.

Tamarix aphylla is larger (up to 10 m tall) than its congener and shares many physiological characteristics such as extreme drought tolerance, rapid growth, and copious saline leaf litter. It grows on sandy soils along riverbanks in its native habitat (Baum 1967, Baum 1978, Abd El-Ghani 2000). Vegetative reproduction from stem (not root) sprouting is common (Lyon 1924), but sexual reproduction is rare (Baum 1967) and seed viability is low (Waisal 1960a). However, sexual reproduction does occur in well-watered areas such as around greenhouses (Danin 1981). The presence of extensive stands of *T. aphylla* reflects flood events (Danin 1999) and high water marks around lake beds (Goldsmith and Smart 1982).

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Tamarix aphylla was introduced in the south-western deserts of the USA in 1911 (Baum 1967), where it has been considered a benign, sterile shade tree that survives arid conditions but rarely spreads (Hoddenbach 1989, Neill 1989, Meyers-Rice 1997; W. Neill, personal communication, 1999). However, following its introduction into Australia in 1930 (Fuller 1998), *T. aphylla* invaded several riparian systems, most notably the Finke River following a 1974 flood (Griffin et al. 1989), resulting in its listing as a weed of national significance (Thorp and Lynch 2000). *Tamarix aphylla* is now also considered a weed in Hawaii (Cronk and Fuller 1995), where it was introduced as an ornamental shade tree (Lyon 1924).

Tamarix aphylla was planted at the Lake Mead National Recreation Area (LMNRA) during the 1950s as part of a program to enhance visitor use of the newly created park by providing shade, windbreaks, and a drought-tolerant ornamental. There has been no apparent concern about the tree spreading in the LMNRA despite efforts to eradicate *T. ramosissima* from shorelines and springs during the last 15 years. Aerial photographs from 1982 show only 4 large trees at Boulder Beach (Study Site 1) where there are now >5000 *T. aphylla* individuals, implying that rapid population growth has occurred in the last 20 years. In 1999 we recognized that *T. aphylla* trees were indeed spreading at Boulder Beach and elsewhere around Lake Mead. A survey in 2002 documented ca. 11,000 individuals along the shoreline of Lake Mead in the LMNRA (Powell unpublished data). In addition, we inadvertently found potential *T. ramosissima*-*T. aphylla* hybrids at LMNRA during this study (Barnes 2003), suggesting continuing changes in the dynamics of *Tamarix*. This paper addresses several questions designed to understand the invasive potential of *T. aphylla*: (1) Do *T. aphylla* trees produce seeds at LMNRA, and, if so, are those seeds capable of germinating? (2) What is the timing and duration of seed production and other phenological stages of *T. aphylla* populations at LMNRA? (3) Do inundation, drought, soil salinity, or leaf litter affect *T. aphylla* germination? (4) Is the distribution of *T. aphylla* linked to soil composition or distance from the lakeshore? (5) Is there a pattern of spatial correlation between *T. aphylla* and *T. ramosissima* or an age gradient within *T.*

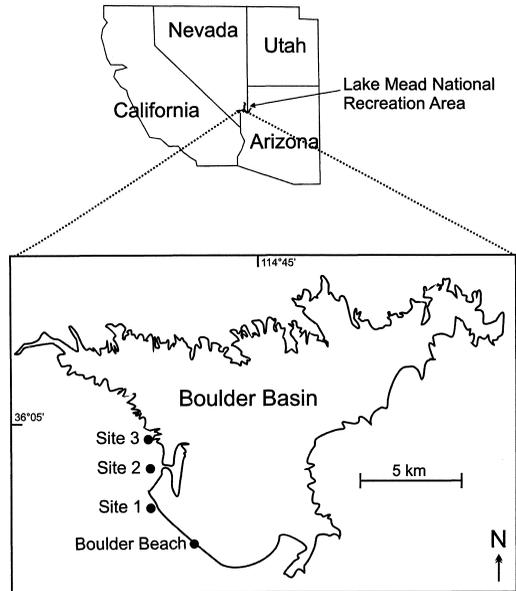


Fig. 1. Location of the 3 study sites on the western edge of the Lake Mead National Recreation Area.

aphylla stands? And (6) do apparent *T. ramosissima*-*T. aphylla* hybrids also produce seeds?

METHODS

Study Area

This study was located in the LMNRA in Nevada, along the western shore of Boulder Basin (Fig. 1). Lake Mead is the reservoir created by Hoover Dam on the lower Colorado River. Located within the Mojave Desert, the study area has mean summer high temperatures >37°C and a mean yearly precipitation of <130 mm. The study (from June 2000 to December 2002) took place at 3 study sites within a 5-km stretch of shoreline. *Tamarix aphylla* stands extended 250, 500, and 300 m along the shoreline at Site 1 (Boulder Beach), Site 2 (Tour Boat), and Site 3 (Saddle Cove), respectively. Vegetation was similar at each site starting with a mudflat filled with snags and seedlings of *T. ramosissima* along the shoreline, then a zone of larger *T. ramosissima*, a zone of overlap between *T. ramosissima* and *T. aphylla*, a *T. aphylla* zone, and, most distant from the shoreline, desert shrubs dominated by *Larrea tridentata* (Sessé & Moc. ex DC.) Coville. At each site, a 75-m-long baseline was placed parallel to the shoreline at water level

at a random location within the *T. aphylla* stand. Within each 15-m section of baseline, a random starting point was selected for a transect perpendicular to the shoreline and baseline. Each of the 15 transects was, in turn, divided into segments 15 m long ($n = 13\text{--}17$ segments, depending on the width of the *T. aphylla* stand). Each transect ended 30 m into the *Larrea* zone. Within each segment, one $6 \times 6\text{-m}$ plot, used for soil and vegetation measurements, was placed randomly on the south side of the transect but at least 1 m from any adjacent plots (see below; $n = 214$ plots). Elevations of each plot were determined with a global positioning system.

Phenology and Seed Germination

From 2000 to 2002, we monitored the reproductive phenology of 20 randomly chosen *T. aphylla* trees (>1 m tall) in each of the 3 sites. Every 2 weeks we noted the presence or absence of flower buds, flowers, fruits, and seeds on each tree. Phenological stages overlapped considerably within trees and thus were not exclusive. When present, seeds from 3 inflorescences per tree were gathered and pooled. We then selected 25 seeds from each pooled sample and placed them (at room temperature and ambient light) in a petri dish on filter paper where they were kept moist with deionized water, providing optimal conditions for germination. Germination, defined as cotyledon emergence, was monitored at least every other day for 30 days. Germination rate was recorded as GT_{50} , or the number of days for 50% of all germination to occur. For a single 7-m *T. aphylla* tree (of average height and productivity), we estimated total seed production from the number of seeds per sampled inflorescence multiplied by the number of inflorescences on that tree.

In October 2001, we conducted paired field and greenhouse germination experiments to determine if drought or surface litter inhibited germination within *T. aphylla* stands. In the field, every 0.5 m along a 30-m transect at Site 2, a plot ($n = 60$) was created by sinking a $6 \times 6 \times 4\text{-cm}$ deep, bottomless plastic form 2 cm into the ground, leaving 2 cm aboveground to contain water. The soil from each hole, with surface litter removed, was replaced to its initial level, and 25 *T. aphylla* seeds (pooled from collections from 25 trees at Site 1) were sown

therein. Ten plots were randomly assigned to each of 6 treatments: (1) leaf litter addition (from a nearby live *T. aphylla*, to a depth of 2 cm, representing natural conditions) with daily watering to a depth of 2 cm (i.e., 75 cm^3); (2) leaf litter addition with weekly watering to a depth of 2 cm; (3) leaf litter addition with only an initial, saturating watering; (4–6) matching watering treatments with no leaf litter addition. To avoid potential interference, other species that germinated in the plots were removed. We also monitored potential germination of voluntary *T. aphylla* in $6 \times 6\text{-cm}$ plots adjacent to each sown plot. In the greenhouse, we established an identical experiment of 6 treatments using trays of identical dimensions (but with drain holes in the intact bottom) filled with field soil. Trays were rotated daily to reduce any differential impacts of variation in the greenhouse environment. Both field and greenhouse germination were monitored for 30 days.

Seed germination was tested under both field and indoor storage conditions using pooled seeds collected in October 2001 from 45 trees at Site 1. Some seeds were immediately placed in 6 petri dishes (25 seeds per dish), wetted, and observed for 30 days. Other seeds were placed in mesh bags on the soil surface at Site 1 (25 seeds in each of 6 bags) at each of 3 new locations of similar elevation and proximity to a *T. aphylla* tree. Two bags from each of the laboratory and 3 field locations were collected, and the seeds were moistened and monitored for germination 1, 4, and 56 weeks following placement. All remaining seeds were stored under dry conditions at room temperature in the laboratory.

Seeds collected in November 2002 from 25 trees at Site 1 were used in soaking (March 2003) and salinity (May 2003) tests to examine tolerance to flooding and salty field conditions. For the first test, 5 subsamples of seeds were soaked in tap water for 0, 1, 3, 5, or 7 days. Then 25 seeds were placed on filter paper in each of 30 covered petri dishes (6 from each soaked subsample) and germination was monitored. For the second test, we created 7 salt solutions (treatments) encompassing the range of salt concentrations observed in the field ($0.08\text{--}3.5 \text{ dS} \cdot \text{m}^{-1}$): 0.05, 0.27, 0.66, 1.29, 1.85, 2.51, and $3.56 \text{ dS} \cdot \text{m}^{-1}$. For each salinity treatment, filter papers in 3 covered petri dishes containing 25 seeds were watered daily and germination was monitored. Solutions were

made with a 2:1 ratio of NaCl to CaCl₂ to most closely resemble field conditions. Although germination potential of these stored seeds probably declined, the nonsoaked seeds and low salt levels served as adequate controls to compare treatment effects.

Soils

Soils were sampled to a depth of 10 cm from every 6 × 6-m plot at all 3 sites in July 2001 (5 samples pooled per plot). After organic debris and large rocks had been removed, the soils were passed through a 2.5-mm-mesh sieve and processed immediately. A 50 g soil sample was removed and allowed to air dry for later nitrogen analysis. The remaining 200 g of soil were weighed and dried at 105°C for 3–4 days and then weighed again to determine gravimetric moisture content ($[\text{wet mass} - \text{dry mass}]/\text{dry mass}$). We measured the pH (1:1 ratio of soil to water; McLean 1982) and soil salinity (electrical resistance with a conductivity bridge on extracted water-soluble salts; Rhoades 1982) of the oven-dried soils. The air-dried sample was digested in sulfuric acid with a mercuric oxide catalyst and analyzed colorimetrically for total Kjeldahl nitrogen using an automated salicylate procedure (Alpkem 1991).

Vegetation

Within each of the 6 × 6-m plots, total vegetation cover and cover of *Tamarix ramosissima* and *T. aphylla* were visually estimated in 5 cover classes (0 = none, 1 = 1%–25%, 2 = 26%–50%, 3 = 51%–75%, 4 = 76%–100%). The number of individuals of both *Tamarix* species was counted, and heights and basal diameters were recorded for each *T. aphylla*. Individual circumferences of multiple-stemmed plants were summed. We also searched each plot for *T. aphylla* seedlings <50 cm tall. We estimated litter depth from 5 randomly chosen locations in each plot. Four vegetation zones were defined by presence of 4 dominant woody species: Zone 1, only *T. ramosissima*; Zone 2, *T. ramosissima* and *T. aphylla*; Zone 3, only *T. aphylla*; and Zone 4, only *Larrea tridentata*. Zone 3 was least common.

We obtained stem cross sections of 24 trees at ground level and aged each tree by counting clearly distinguishable growth rings. Each ring presumably represents 1 year's growth (Brotherson et al. 1983, 1984, Haigh 1998). The trees selected for aging were the tallest and

shortest trees within a 10-m radius of 12 different points. These points were located either 10 m or 30 m above the lowest edge of the *T. aphylla* stand on 2 transects in each of the 3 sites.

Between July 2001 and December 2001, we randomly marked 10 individuals from a group of ca. 100 plants at Site 1 that appeared to be morphologically intermediate between *T. ramosissima* and *T. aphylla* and observed their phenological patterns. Fewer hybrids were observed at Sites 2 or 3.

Statistical Analyses

We analyzed the length of each phenological stage across sites and years with a Friedman nonparametric 2-way ANOVA (Statistix 2000). The percentages of individual trees in each stage were compared with Kruskal-Wallis 1-way ANOVA, a test also used to compare the medians (treatment, percent germination) for the lab and field viability experiments. One-way ANOVA followed by a Bonferroni comparison was used to separate means (treatment, percent germination) in the soak and salinity treatments. All percentages were arcsine square root transformed prior to analysis. Rate of germination (GT_{50}) was represented by the number of days to 50% germination of total germinants. We used simple linear regression to compare each soil variable and vegetation cover (using midpoints from each cover class) against distance from the baseline along the lakeshore. A Kruskal-Wallis 1-way ANOVA was used to compare each soil variable among the 4 vegetation zones following a MANOVA of all soil variables and all zones. Tree age (estimated from growth rings) was analyzed with 2-way ANOVA of ring number by site and distance. The relationship between tree height and ring number was determined by linear regression. Means are reported $\pm 1 s_{\bar{x}}$, and significance was determined at $P > 0.05$.

RESULTS

Phenology

This study documents the 1st record of sexual viability of *T. aphylla* in the USA. Some *T. aphylla* individuals at the 3 study sites passed through all 4 phenological stages (bud, flower, fruit, seed), culminating in substantial seed production. In 2000, 2001, and 2002 there were 37, 18, and 15 individuals, respectively,

TABLE 1. Estimated duration of phenological events based on weekly observations of 20 *T. aphylla* trees at each site. The number in parentheses indicates days in each phenological stage. An asterisk indicates that the earliest dates were not measured.

Year	Site 1	Site 2	Site 3
BUD			
2000	*16 Jul–15 Oct (92)	*24 Jul–8 Oct (77)	*16 Jul–15 Oct (92)
2001	25 Jul–12 Nov (111)	25 Jul–23 Sep (60)	25 Jul–28 Oct (96)
2002	*9 Sep–20 Nov (73)	*9 Sep–20 Nov (73)	*9 Sep–25 Nov (78)
FLOWER			
2000	16 Jul–8 Oct (85)	24 Jul–8 Oct (77)	16 Jul–8 Oct (85)
2001	16 Aug–28 Oct (74)	16 Aug–25 Sep (42)	16 Aug–7 Nov (84)
2002	9 Sep–20 Nov (73)	9 Sep–30 Nov (83)	9 Sep–20 Nov (73)
FRUIT			
2000	21 Aug–1 Jan (133)	10 Sep–8 Oct (29)	4 Sep–1 Jan (119)
2001	16 Sep–24 Dec (100)	16 Sep–23 Sep (7)	23 Sep–24 Dec (93)
2002	19 Sep–13 Nov (56)	26 Sep–6 Nov (42)	3 Oct–6 Nov (35)
SEED			
2000	10 Sep–1 Jan (114)	17 Sep–15 Oct (29)	17 Sep–1 Jan (107)
2001	30 Sep–24 Dec (86)	23 Sep (0)	14 Oct–31 Dec (79)
2002	23 Oct–6 Nov (15)	23 Oct–6 Nov (15)	30 Oct–6 Nov (8)

that produced seeds from a total of 60 trees. There were no significant differences in the duration of any of the phenological stages by site or year (Barnes 2003; Table 1). However, Site 2 generally had a shorter period of seed production, and fewer trees produced seeds than trees at Sites 1 and 3. The year 2000 generally had the longest reproductive season. For all sites and years mean duration was 83.6 ± 5.6 days for buds, 74.2 ± 4.3 days for flowers, 70.6 ± 16.0 days for fruits, and 50.6 ± 15.2 days for seeds.

Seed Germination

Germination decreased over time for seeds collected from Site 1 (Fig. 2), but total germination was higher ($F = 51.74$, $P < 0.0001$) for seeds from Site 1 ($31.9\% \pm 2.3\%$) than from Site 2 ($8.65\% \pm 3.16\%$), or Site 3 ($3.2\% \pm 1.19\%$). Maximum germination for a single tree was 88%, and mean overall germination rate (GT_{50}) was 3.4 days. We estimated that one 7-m *T. aphylla* could potentially produce 250,000–500,000 seeds (7500–150,000 germinable seeds) in 1 season.

In the paired greenhouse and field plots, none of the sown seeds germinated in any of the watering or litter treatments. Seeds stored in the laboratory germinated (when moistened) after 4 weeks of dry storage, but none germinated after 56 weeks of dry storage. Field storage resulted in a more rapid decline, with no germination (under moist laboratory condi-

tions) after 4 weeks in the field. Soaking *T. aphylla* seeds for 7 days significantly reduced germination ($P < 0.0001$) from an initial $41.6\% \pm 6.0\%$ to $1.4\% \pm 0.04\%$ (Barnes 2003). Mean germination was reduced at or above $0.27 \text{ dS} \cdot \text{m}^{-1}$ in $\text{NaCl} + \text{CaCl}_2$ salt solutions, and no germination occurred at or above $2.51 \text{ dS} \cdot \text{m}^{-1}$ (Fig. 3).

Soil and Vegetation

Elevation ($r^2 = 0.0977$, $P < 0.0001$) and soil pH ($r^2 = 0.5588$, $P < 0.0001$) increased with distance from the baseline while all other soil variables showed a weak decline with distance (litter depth: $r^2 = 0.0702$, $P = 0.0001$; soil salinity: $r^2 = 0.0147$, $P = 0.0766$; soil moisture: $r^2 = 0.0461$, $P = 0.0016$; soil nitrogen: $r^2 = 0.046$, $P = 0.0016$). There were significant differences across vegetation zones when vegetation cover and soil variables were combined (Wilks' Lambda = 0.59, $P < 0.0001$). Most of these zonal differences (Table 2) were driven by total vegetation cover (that peaked in Zone 3) and pH (that was least in Zone 1). Litter depth, soil salinity, and soil moisture were lowest in Zone 4. Soil nitrogen did not vary significantly across the vegetation groups. Values for all soil parameters except pH tended to be highest in Zone 3 (*T. aphylla* only).

Height of *T. aphylla* ($r^2 = 0.0305$, $P = 0.0036$), but not diameter ($r^2 = 0.0006$, $P = 0.7085$), increased slightly with distance from

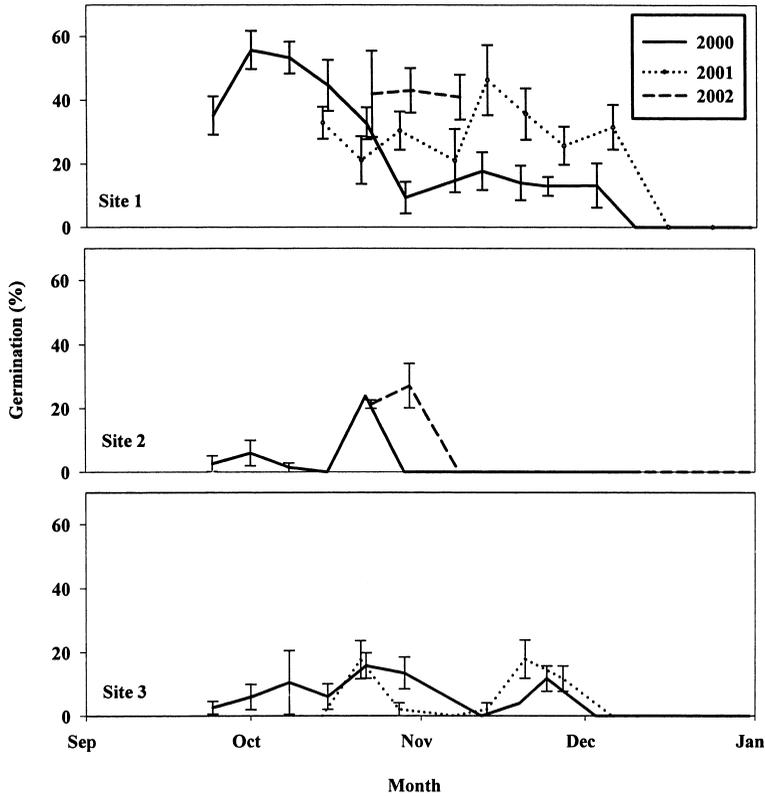


Fig. 2. Mean germination percentages ($\pm 1 s.e.$; $n = 20$ trees per site) for *Tamarix aphylla* seeds by collection date.

the baseline. Mean density of *T. aphylla* was $0.66 \text{ trees} \cdot \text{m}^{-2}$ ($6600 \text{ trees} \cdot \text{ha}^{-1}$), and density was highest 157.5 m from the baseline (Fig. 4A). Maximum height of *T. aphylla* (data not shown) had a similar pattern. Density of *T. ramosissima* peaked at 52.5 m from the baseline. Similarly, cover (Fig. 4B) peaked at 147.5 m (*T. aphylla*) and 67.5 m (*T. ramosissima*). No seedlings were found in the study plots but we observed numerous *T. aphylla* seedlings in adjacent parking lots and beach areas. The presence of taproots and lack of nearby adult trees suggest that the seedlings were not root sprouts from adult trees.

No significant interaction was found between age of *T. aphylla* and site ($P = 0.6176$) or between age and distance into the stand of trees ($P = 0.9269$); however, older trees were significantly taller ($r^2 = 0.676$, $P < 0.0001$). The mean age of the *T. aphylla* trees was 8.04 years. Table 3 summarizes the distribution of ages, with apparent recruitment clusters appearing at 4–6, 8–9, 11–13, and 17–20 years.

The 10 trees that were intermediate to *T. aphylla* or *T. ramosissima* at Site 1 formed flower buds, but only 1 flowered and none set seed. These intermediates resembled *T. ramosissima* with their shrub-like growth habit, yellow green foliage, and floral arrangement on the inflorescences, but they resembled *T. aphylla* in their height and nondeciduous foliage (only *T. ramosissima* is deciduous). They were intermediate in the degree of clasping of leaves (tighter than *T. ramosissima*, looser than *T. aphylla*) and in the yellow color of the autumn leaves. Gaskin and Shafroth (2005) confirmed that these morphological intermediates were genetically distinct hybrids.

DISCUSSION

Tamarix aphylla at Lake Mead National Recreation Area in southern Nevada produces germinable seeds, just as it does in Australia (Griffin et al. 1989) and Israel (Waisel 1960a). This discovery provides the first evidence of

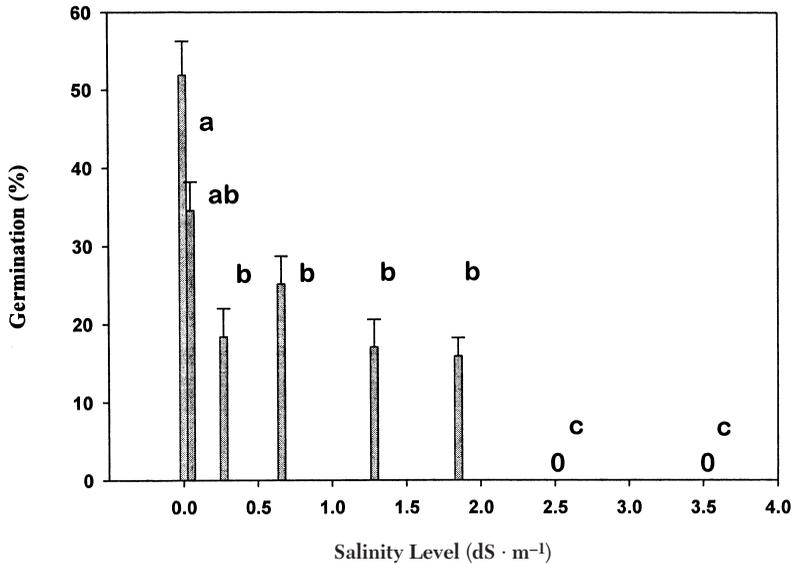


Fig. 3. Mean germination percentages ($\pm 1 s.e.$; $n = 3$ petri dishes per treatment) for *Tamarix aphylla* seeds treated with NaCl:CaCl₂ solutions of varying concentrations. Germination values with the same lowercase letters are not significantly different ($P > 0.05$).

sexual reproduction in the USA and contradicts suggestions that *T. aphylla* is sterile in the southwestern USA (Hoddenbach 1989, Neill 1989). Potentially high seed production, combined with average germination rates of 21% under lab conditions, a seeding season of up to 3 months, some evidence of seedling establishment, and a history of aridland invasion elsewhere, make *T. aphylla* a potential invader of southwestern riparian communities. The production of germinable seeds in *T. aphylla* populations at LMNRA was highly variable among sites (8%–32%) and individual trees (0%–66%), suggesting that potential fecundity is influenced both by environmental factors among sites and more localized micro-site differences. We did not examine intrinsic (i.e., genetic) factors that might also influence fecundity. We further note that potentially substantial genetic mixing since its introduction may have altered the reproductive capacity of *T. aphylla*.

Environmental signals such as photoperiod, irradiance, temperature, and water availability often control phenological events, either promoting or delaying flowering (Lyndon 1992), seed production, or growth (Bazzaz et al. 2000). During our study, a severe drought began, with a concomitant drop in the water level of Lake Mead from 368.0 m above sea level (ASL)

in June 2000 to 351.4 m ASL in December 2002. We found a parallel decline in both the duration of seeding (from 84 to 13 days) and the proportion of *T. aphylla* trees producing seeds (from 62% to 25%), suggesting that groundwater availability is a critical environmental control (Lyndon 1992) at LMNRA for a facultative phreatophyte such as *T. aphylla*.

Low water availability limits germination of *T. aphylla* in its native Israel where seeds are produced in September, long before the seasonal rains in mid-November (Waisel 1960a). Short-term seed viability compounds the issue. Our study showed that *T. aphylla* seeds survived for 4 weeks in dry storage, but <1% germinated after 1 week under (dry) field conditions. Even under ideally moist laboratory conditions, half the seed germination occurred within 3.4 days. We were not able to obtain germination of seeds watered in the field, perhaps due to high soil salinity (see below). Therefore, if adequate soil moisture is not available within a few days of seed release, seeds may not germinate.

The failure of *T. aphylla* seeds to germinate within stands of adult *T. aphylla* at LMNRA (even when we experimentally removed litter and added water) was probably due to inhibition by salty soils. Competition with existing trees for light, water, or nutrients might be an

TABLE 2. Comparison of total vegetation cover and soil variables across vegetation zones that clustered plots by presence of woody species (means with $1 \cdot s_{\bar{x}}$ in parentheses). Results within rows with the same lower case letters are not significantly different ($P > 0.05$).

	<i>T. ramosissima</i> Zone 1	<i>T. ramosissima</i> + <i>T. aphylla</i> Zone 2	<i>T. aphylla</i> Zone 3	<i>L. tridentata</i> Zone 4	df (zones, plots)	H	P
Sample size (n)	125	52	9	28			
Total vegetation cover (%)	21.54 (0.33) a	24.60 (1.26) ab	27.99 (3.90) b	21.36 (0.67) a	3, 207	15.89	<0.001
Litter depth (cm)	1.08 (0.08) a	1.14 (0.13) a	1.91 (0.67) a	0.10 (0.03) b	3, 207	56.94	<0.001
Soil salinity (dS · m ⁻¹)	0.73 (0.05) a	0.92 (0.12) a	1.55 (0.38) a	0.22 (0.03) b	3, 207	52.41	<0.001
Gravimetric moisture (%)	1.58 (0.06) a	1.55 (0.09) a	1.88 (0.30) a	1.25 (0.09) b	3, 207	8.66	0.034
pH	7.51 (0.04) a	7.94 (0.04) b	8.01 (0.07) b	8.03 (0.04) b	3, 207	50.68	<0.001
Total Kjeldahl nitrogen (mg · g ⁻¹)	0.32 (0.02) a	0.27 (0.02) a	0.37 (0.08) a	0.27 (0.03) a	3, 207	2.67	0.446
Soil organic matter (%)	2.55 (0.05) a	2.63 (0.09) a	2.82 (0.29) a	2.45 (0.11) a	3, 207	1.29	0.713

additional restraint, but seedlings of both *T. aphylla* and *T. ramosissima* establish at high densities at LMNRA, so competition among juvenile congeners does not seem limiting. Salty soils, perhaps in combination with seed age (Waisel 1960a), prevented *T. aphylla* germination within the adult stand, yet viable seeds produced by those adults are now germinating on the receding shoreline along with the more numerous *T. ramosissima*. Tallent-Halsell (1998) found that the shoreline of Lake Mohave (immediately downstream from Lake Mead) was less salty than soils in near-shore *T. ramosissima* stands. Native *Populus* and *Salix* species also germinate under conditions of receding water, but limited local seed sources reduce their success (Stromberg 1993, Tallent-Halsell and Walker 2002). Inundation from rising water levels is not conducive to germination of *T. aphylla*, *T. ramosissima*, or native *Populus* or *Salix* trees.

A clearly defined band of *T. aphylla* was found between 67.5 m and 82.5 m (shoreward edge) and 172.5 m and 187.5 m (inland edge) from the baseline (370.0–375.5 m ASL; distances tightly correlated with elevation). *Tamarix ramosissima* was found closer to the baseline than *T. aphylla* and closer to desert vegetation dominated by *Larrea tridentata* and *Ambrosia dumosa* (A. Gray). W.W. Payne delineated the upper elevational boundary of the *T. aphylla* zone. *Tamarix* leaf litter tended to be deepest and soil salinity tended to be highest in the *T. aphylla* zone. *Tamarix aphylla* litter is resistant to decomposition and increased soil salinity in Israel (Litwak 1957). What was unusual at LMNRA, however, was the co-occurrence of *T. aphylla* and *T. ramosissima*.

In Australia, *T. aphylla*, but not *T. ramosissima*, is considered a serious weed (Thorp and Lynch 2000), and we know of no reports of ecological interactions between the 2 species of *Tamarix*. The 2 species appear to partition the drawdown zone at LMNRA because *T. ramosissima* cover declined with increasing distance from the baseline (increased elevation). The taller *T. aphylla* may successfully outcompete the shorter *T. ramosissima* as water table depths increase. Alternatively, because the 2 species lack a complete overlap in their seed dispersal phenology, the zonation may be due to chance coincidences between seed availability and receding shorelines.

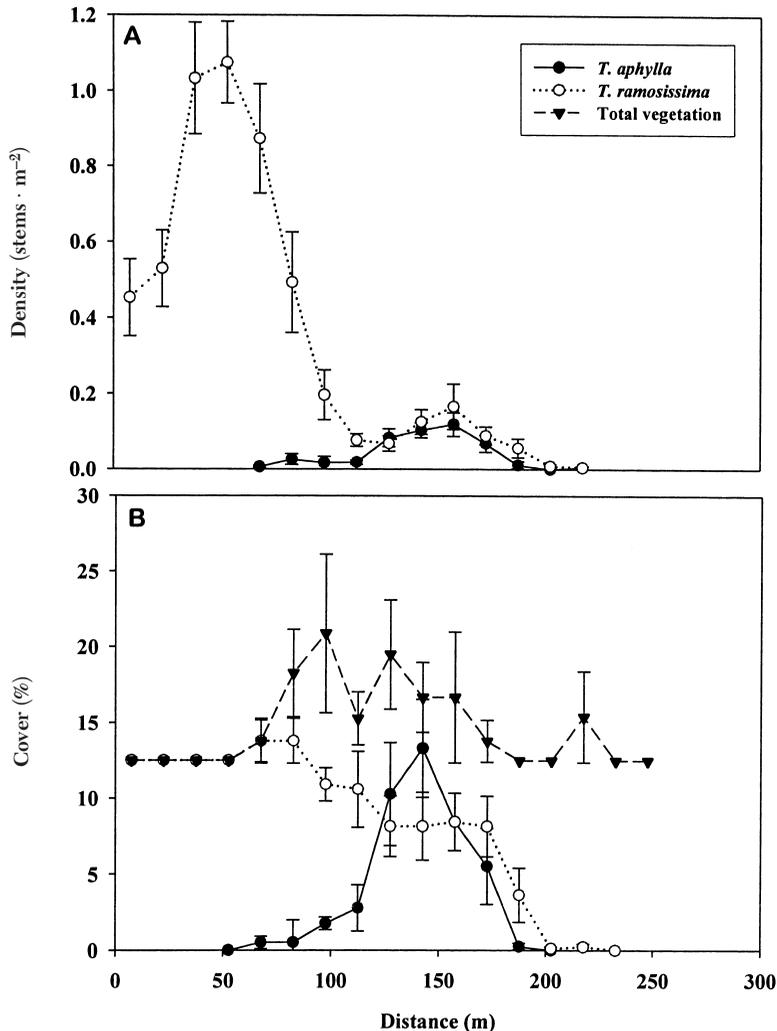


Fig. 4. (A) Mean stem density and (B) cover ($\pm 1 s_{\bar{x}}$; $n = 214$ plots) of *Tamarix ramosissima* and *T. aphylla*. Distance is from the baseline close to the lakeshore. All sites are combined.

Hybrids among species of *Tamarix* are common (Gaskin and Schaal 2002), but this is the first finding of hybrids between *T. aphylla* and *T. ramosissima*. Samples of the 3 phenotypes found at LMNRA represented 3 genotypes (*T. aphylla*, *T. ramosissima*, and a hybrid; Gaskin and Shafroth 2005). We do not know what reproductive or invasive characteristics this hybrid will exhibit, because, to date, no seed production has been observed at Lake Mead. However, Gaskin and Shafroth (2005) report viable seeds from 1 individual of a similar hybrid found along the Colorado River near Blythe, California.

Tamarix aphylla trees are clearly capable of invading riparian areas such as LMNRA. The

high water level of 373.4 m ASL in 1983 roughly corresponds with the elevations of the upper edges of the *T. aphylla* stand at our 3 study sites (370.0–375.5 m ASL) and likely provided a receding shoreline for germination, similar to what is now occurring. The oldest trees at our sites were estimated to be 20 years old, corresponding with the 1983 high water levels. Clusters of younger trees coincide approximately with subsequent fluctuations of Lake Mead levels (due to variable human use and snow pack in the Rocky Mountains upstream). While vegetative reproduction of *T. aphylla* was not examined in this study, we observed a number of stem sprouts from fallen, detached

TABLE 3. Number of *T. aphylla* trees in each age group compared to annual high lake level and precipitation during presumed year of establishment. Ring counts have an assumed accuracy of ± 1 year ($n = 23$ usable tree rings).

Age (annual rings)	Number of trees	Year of establishment	Annual high lake level elevation (ft, m)	Average precipitation (cm)
4	3	1999	1213.96, 370.01	4.01
5	1	1998	1215.95, 370.62	7.47
6	1	1997	1214.65, 370.22	9.06
7	0	1996	1195.04, 364.25	2.41
8	1	1995	1190.92, 362.99	5.76
9	1	1994	1190.98, 363.01	3.94
10	0	1993	1193.75, 363.86	8.52
11	2	1992	1180.55, 359.83	11.18
12	4	1991	1180.19, 359.72	7.87
13	1	1990	1191.88, 363.29	5.34
14	0	1989	1202.57, 366.54	3.03
15	0	1988	1211.82, 369.36	3.01
16	0	1987	1210.83, 369.06	7.43
17	2	1986	1213.20, 369.78	5.09
18	2	1985	1214.36, 369.53	4.13
19	1	1984	1213.73, 369.94	13.36
20	4	1983	1225.85, 373.64	7.35

stems, and we suspect that *T. aphylla* initially spread vegetatively into LMNRA from upstream populations, much as it did in Australia (Griffin et al. 1989).

We expect that, without aggressive control efforts, *T. aphylla* will continue to invade the shorelines of Lake Mead. The production of many seeds, potentially high germination rates, and frequent vegetative reproduction suggest potential for rapid spread (Kolar and Lodge 2001). Once established, *T. aphylla* litter salinizes soils and alters hydrologic regimes in its native habitat (Waisel 1960b, 1961). If such effects are also occurring at LMNRA, there could be a potential altering of ecosystem functions and resulting loss of native riparian species. Further, the impact of *T. aphylla* may compound the well-documented and similar problems stemming from *T. ramosissima* invasions (Brock 1994, Walker and Smith 1997, Everitt 1998) because *T. aphylla* is larger, taller, and produces more salinizing litter than its congener. Further examination of the impacts of *T. aphylla* are clearly important, now that its potential for spread has been suggested. The possibility of hybrids with unknown invasive abilities further suggests that *T. aphylla* should be removed from LMNRA and other riparian corridors throughout the desert Southwest.

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