

TWO DECADES OF CHANGE IN DISTRIBUTION OF EXOTIC PLANTS AT THE DESERT LABORATORY, TUCSON, ARIZONA

JANICE E. BOWERS¹, TRAVIS M. BEAN², AND RAYMOND M. TURNER¹

U. S. Geological Survey¹ and University of Arizona²

1675 West Anklam Road, Tucson, AZ 85745

jebowers@usgs.gov

ABSTRACT

A gridline survey for exotic plant species was undertaken in 1983 and repeated in 2005 at the Desert Laboratory, a 352-ha natural area just west of downtown Tucson, Arizona, USA. Coordinate data gathered during the surveys were used to plot distributions, determine frequencies (number of coordinate locations), and assess percent change. Fifty-two exotic species were encountered in all, 34 in the first survey, 44 in the second. The proportion of ornamental exotics doubled over time, reaching 50% in 2005. Casual, naturalized, and invasive exotics comprised 44%, 40%, and 15% of species found during the surveys. Minimum residence time increased significantly from casual to naturalized to invasive species, suggesting that the longer a species was present, the more likely it was to surmount barriers to naturalization and invasion. In both 1983 and 2005, casual, naturalized, and invasive species differed in mean frequency by an order of magnitude, with casual species having the lowest frequencies and invasive species the highest. Between surveys, frequency of 18 species decreased; most other species increased in frequency. The recent surge in ornamental exotics, combined with temporal trends in invasiveness, indicates that the proportion of invasive species in the flora will increase with time.

Key Words: alien plants, distribution maps, invasions, nonnative species, Sonoran Desert.

That invasive exotics can irreversibly change natural ecosystems is indisputable (Mack et al. 2000; Levine et al. 2003), but despite all that has been learned in recent years about the autecology and synecology of plants established outside their native range, ecologists and land managers have difficulty predicting which species will become invasive (Mack et al. 2000; Kolar and Lodge 2001). This difficulty results in part from lack of detailed historical information about change in distribution over time (Mack et al. 2000; Hunter and Mattice 2002). When spatial coverage of exotics can be measured, change in area over time can be used to describe rate of spread according to simple reaction-diffusion models (Frappier et al. 2003) or more complex lag-phase models (Mack et al. 2000). Although maps showing the local distribution of exotic species at a single point in time (e.g., Agius 2003) have become increasingly common, repeated mapping of exotic distributions at the local scale is still relatively rare. One notable example is the use of aerial photographs to map distribution of *Phragmites australis* in nine years between 1945 and 1999 (Wilcox et al. 2003). More commonly, changing distributions of exotics have been assessed by repeated censuses of vegetation plots (e.g., Daehler and Carino 1998; Johnstone et al. 1999) or by repeated inventories within local areas (e.g., Hunter and Mattice 2002). Here we present results from two gridline surveys for exotic plants in a 352-ha natural area in the northern Sonoran Desert, USA. The surveys,

made in 1983 and 2005, allowed us to map local distributions of 52 exotic species and assess changes in distribution over 22 years.

Our study site, the Desert Laboratory, was founded as a botanical research station in 1903. It is unique among natural areas in the Sonoran Desert for having been protected from domestic livestock for almost 100 years and for its long and distinguished record of ecological research (White 1985). The Desert Laboratory grounds were colonized by exotics as long ago as 1906 (Spalding 1909). From a total of four species in 1909, the exotic flora increased to 52 species by 1991 (Burgess et al. 1991). Most exotics at our study site were introduced to the Sonoran Desert region from the Old World or Latin America (Wilson et al. 2002). A few species were introduced as ornamental plants from elsewhere in the United States. Exotics of particular concern include winter-annual grasses, especially *Bromus rubens*, *Schismus arabicus*, and *S. barbatus*, and two perennial grasses, *Pennisetum ciliare* and *P. setaceum*. *Bromus rubens* and *P. ciliare* can form a continuous cover of light fuels, increasing fire frequency and severity in desertscrub communities where plants are not adapted to burning (Esque and Schwalbe 2002; Búrquez-Montijo et al. 2002). *Bromus rubens* and *Schismus* spp. significantly reduce the density and biomass of native winter annuals; over the long term, they could also reduce native seed banks, bringing about fundamental alterations in plant community structure and food web dynamics (Brooks

2000; Salo et al. 2005). *Pennisetum setaceum* has the potential to displace native species and promote fire (Wilson et al. 2002). These species are all *transformers*, defined as invasive exotics that “change the character, condition, form or nature of ecosystems over a substantial area” (Richardson et al. 2000).

In spring 1983, we undertook a survey of exotic plants on the Desert Laboratory grounds by walking regular gridlines and recording Cartesian coordinates of exotic species (Burgess et al. 1991). In spring 2005, native and exotic annuals were abundant after a relatively wet winter (precipitation = 151 mm), making it worthwhile to repeat the initial survey, which was undertaken after an unusually wet winter (precipitation = 250 mm). Burgess et al. (1991) discussed geographic origins and breeding systems of invasive exotics found during the original survey and also described the environmental and cultural factors that promoted invasion. Our objectives for the second survey were to: (1) map the distribution of individual exotic species in 2005, (2) use mapped distributions to categorize exotics as casual, naturalized, or invasive, (3) assess changes in distribution and frequency between 1983 and 2005, and (4) identify priorities for monitoring and eradication.

Here and throughout, we have followed the terminology of Richardson et al. (2000) except for our use of the term *exotic* instead of *alien* and for minor modifications to suit the temporal and spatial scales of our study. We defined *exotic* as non-native in the vicinity of Tucson; we needed an unusually narrow definition because several species that are indigenous to Arizona but not to the vicinity of Tucson have spread onto our study site from ornamental plantings in nearby neighborhoods. *Casual exotic plants* are species that have not formed self-replacing populations but rather depend on repeated introduction for their persistence (Richardson et al. 2000). *Naturalized exotics* reproduce consistently and sustain populations over many life cycles, typically recruiting close to the parent plants. Although often associated with disturbance, naturalized exotics are not necessarily restricted to disturbed sites (Richardson et al. 2000). *Invasive exotics* are naturalized species that produce large numbers of offspring at considerable distances from the parents and thus can spread over wide areas in relatively short times, often including successional mature, undisturbed communities; for taxa spreading by seed, the scale of movement is >100 m during <50 years (Richardson et al. 2000). Because we seldom knew the original place or time of introduction for most exotics on our study area, we used a more qualitative assessment to distinguish between naturalized and invasive exotics: naturalized exotics are self-replacing species most likely to be found on disturbed sites or, if more widely distributed, having small

populations at the local scale, whereas invasive exotics are self-replacing species that are ubiquitous and abundant in undisturbed communities. Our modifications retain an important distinction, which is that invasive species have overcome environmental barriers to widespread dispersal and proliferation (Richardson et al. 2000).

METHODS

Study Area

The Desert Laboratory (32°13'N, 111°00'W) is a 352-ha research station and natural area situated west of downtown Tucson, Arizona, USA. The laboratory grounds include Tumamoc Hill, a rocky, basaltic-andesitic knoll (760 to 948 m above sea level), and the level or gently rolling plain to the west (725 to 760 m above sea level). Housing developments, schools, and businesses border upon the Desert Laboratory to the north, south, and west. A small desert park lies on the eastern boundary. Mean maximum and minimum daily temperatures at Tucson are 18.6°C and 2.4°C during January, the coldest month, and 37.9°C and 22.8°C in June, the hottest month (Sellers et al. 1985). Mean annual rainfall at the Desert Laboratory is 300 mm per year. On average, half the yearly total comes during summer (July through September, 152 mm); most of the remainder falls during winter (November through March, 109 mm). The vascular flora of the study area comprises 346 species, subspecies, and varieties, of which 15% are exotic (Bowers and Turner 1985; Burgess et al. 1991). Study site vegetation is typical of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951). Dominant native plants include *Parkinsonia microphylla*, *Carnegiea gigantea*, *Larrea tridentata*, *Acacia constricta*, *Ambrosia deltoidea*, and *Encelia farinosa*. Nomenclature follows Kartesz (1999) insofar as possible.

Status as an ecological reserve has not protected the Desert Laboratory grounds from localized disturbance, starting with construction of laboratory buildings, an access road, and a water system in the early 1900s. Before the grounds were fenced in 1907, wagons carted away surface rock for construction, and cattle, horses, goats, and burros grazed the slopes and flats. After 1907, disturbance was minimal until the 1950s, when easements were granted for construction of petroleum and natural gas pipelines, electric transmission lines, and radio towers. Two clay quarries were dug at some point, and one was used as a landfill in the 1960s. More recently, the petroleum pipeline that crosses the center of the property was replaced (January 2004), as was a portion of the natural gas pipeline that crosses the northeast corner (October 2003).

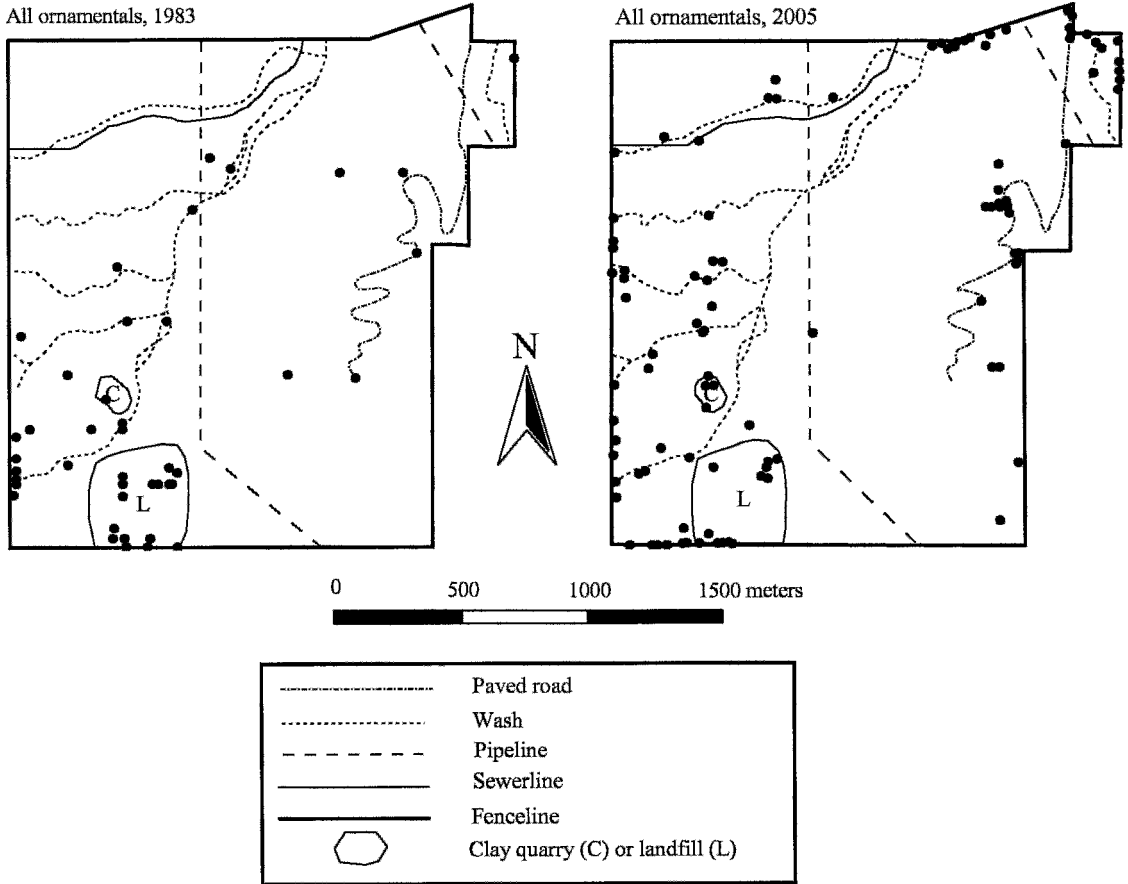


FIG. 1. Distribution of all ornamental species at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

Data Collection

We mapped distribution of exotic species within the Desert Laboratory boundaries in spring 1983 and again in spring 2005. In 1983, we drew a grid of parallel lines on aerial photographs (scale 1:2256) of the study site, then walked each gridline, using the aerial photographs to maintain as accurate a course as possible (Burgess et al. 1991). We also surveyed the paved road and the fenceline that is the boundary of the study site. As we encountered exotic plants, we recorded their Cartesian coordinates within about two meters of the gridline. Distance between coordinate locations varied widely but averaged about 44 m. The gridlines were about 220 m apart and had a total length of about 40 km. In 2005, we repeated the survey on the same gridlines but used a hand-held GPS unit instead of aerial photographs to keep ourselves on course. Every 30 to 40 meters, we recorded latitude and longitude as a GPS waypoint. As we encountered exotic species, we assigned them to the most recent waypoint. We recorded more coordinate locations in 2005 (n = 1349) than in

1983 (n = 976). For convenience, we pooled certain morphologically similar species, treating *Schismus arabicus* and *Schismus barbatus* as *Schismus* spp. and *Sonchus asper* and *Sonchus oleraceus* as *Sonchus* spp.

Data Analysis

The scattered distribution of many species across our study site made it difficult to draw discrete polygons showing areal extent or to calculate rate of spread in meters per year. Instead, we depicted distribution as dot maps from which we determined frequency of observation in 1983 and 2005. Specifically, we used ArcView 3.0a to generate a distribution map for each species found at more than five coordinate locations in either year. For every species, we determined frequency as number of coordinate locations where it was recorded in 1983 or 2005, then determined percent change between years as $([\text{frequency in 2005} - \text{frequency in 1983}] / \text{frequency in 1983}) \times 100\%$. From mapped distributions and our own observations of reproductive behavior and demography, we followed criteria

TABLE 1. FREQUENCY (NUMBER OF COORDINATE LOCATIONS) OF CASUAL EXOTIC PLANTS AT THE DESERT LABORATORY, TUCSON, ARIZONA. Life forms as follows: AF = annual forb, AG = annual graminoid, LS = leaf succulent, PG = perennial graminoid, SH = shrub, SS = stem succulent, TR = tree, O = ornamental. Arrival = year when first reported from Desert Laboratory grounds. Percent change = $([\text{frequency in 2005} - \text{frequency in 1983}]/\text{frequency in 1983}) \times 100\%$.

Species	Life form	Arrival	Frequency		
			1983	2005	% change
<i>Agave americana</i>	LS, O	1985	0	2	—
<i>Agave murpheyi</i>	LS, O	1987	0	3	—
<i>Aloe sp.</i>	LS, O	2005	0	1	—
<i>Aloe vera</i>	LS, O	2005	0	2	—
<i>Castalis tragus</i>	AF, O	1978	17	7	-58.5
<i>Centaurea melitensis</i>	AF	1983	4	6	50.0
<i>Chenopodium album</i>	AF	1983	4	0	-100.0
<i>Chenopodium murale</i>	AF	1983	1	1	0.0
<i>Lantana urticoides</i>	SH, O	1983	1	3	200.0
<i>Lepidium oblongum</i>	AF	1983	4	0	-100.0
<i>Melia azederach</i>	TR, O	1983	1	0	-100.0
<i>Molucella laevis</i>	AF, O	1983	2	0	-100.0
<i>Nicotiana glauca</i>	SH, O	1983	2	0	-100.0
<i>Olea europaea</i>	TR, O	2005	0	1	—
<i>Opuntia basilaris</i>	SS, O	2005	0	2	—
<i>Opuntia ficus-indica</i>	SS, O	2005	0	1	—
<i>Opuntia microdasys</i>	SS, O	1984	0	3	—
<i>Opuntia santa-rita</i>	SS, O	2005	0	1	—
<i>Polypogon monspeliensis</i>	AG	1978	3	0	-100.0
<i>Prosopis sp.</i>	TR, O	2005	0	2	—
<i>Rumex crispus</i>	AF	1983	1	0	-100.0
<i>Sisymbrium altissimum</i>	AF	1983	4	0	-100.0
<i>Tamarix aphylla</i>	TR, O	2005	0	2	—

in Richardson et al. (2000) to categorize the status (casual, naturalized, or invasive) of each species. From published records (Spalding 1909; Bowers and Turner 1985; Burgess et al. 1991), we

determined when each species was first reported from the Desert Laboratory, then calculated minimum residence time after Castro et al. (2005) by subtracting year of first report from

TABLE 2. FREQUENCY (NUMBER OF COORDINATE LOCATIONS) OF NATURALIZED PLANTS AT THE DESERT LABORATORY, TUCSON, ARIZONA. See Table 1 for explanation of column headings.

Species	Life form	Arrival	Frequency		
			1983	2005	% change
<i>Avena fatua</i>	AG	1983	15	26	73.3
<i>Brassica tournefortii</i>	AF	1978	27	66	144.4
<i>Bromus catharticus</i>	AG	1968	7	23	228.6
<i>Caesalpinia gilliesii</i>	SH, O	1989	0	1	—
<i>Cynodon dactylon</i>	PG, O	1909	19	18	-5.3
<i>Cyperus involucratus</i>	PG, O	1985	0	2	—
<i>Eragrostis echinochloidea</i>	PG	2005	0	12	—
<i>Eragrostis lehmanniana</i>	PG	1983	20	8	-60.0
<i>Lactuca serriola</i>	AF	1983	31	27	-12.9
<i>Malva parviflora</i>	AF	1978	6	5	-16.7
<i>Matthiola longipetala</i>	AF, O	1978	16	35	118.8
<i>Melilotus indicus</i>	AF	1983	7	21	200.0
<i>Opuntia engelmannii</i> var. <i>linguiformis</i>	SS, O	1985	0	15	—
<i>Parkinsonia aculeata</i>	TR, O	1968	8	20	150.0
<i>Pennisetum setaceum</i>	PG, O	1983	0	33	—
<i>Phalaris minor</i>	AG	1978	3	3	0.0
<i>Rhus lancea</i>	TR, O	1984	0	16	—
<i>Salsola tragus</i>	AF	1968	54	30	-44.4
<i>Sonchus asper</i> , <i>S. oleraceus</i>	AF	1983	63	58	-7.9
<i>Tamarix chinensis</i>	TR, O	1968	3	6	100.0

TABLE 3. FREQUENCY (NUMBER OF COORDINATE LOCATIONS) OF INVASIVE PLANTS AT THE DESERT LABORATORY, TUCSON, ARIZONA. See Table 1 for explanation of column headings.

Species	Life form	Arrival	Frequency		
			1983	2005	% change
<i>Bromus rubens</i>	AG	1968	355	170	-52.1
<i>Erodium cicutarium</i>	AF	1906	440	392	-10.9
<i>Herniaria hirsuta</i> subsp. <i>cinerea</i>	AF	1985	0	92	—
<i>Hordeum murinum</i>	AG	1906	211	115	-45.5
<i>Pennisetum ciliare</i>	PG	1968	6	485	7983.3
<i>Schismus arabicus</i> , <i>S. barbatus</i>	AG	1968	763	1067	39.8
<i>Sisymbrium irio</i>	AF	1968	424	511	20.5

the year of the second survey. We used a Kruskal-Wallis test to determine whether average residence time differed among categories (casual, naturalized, invasive). We also used Kruskal-Wallis tests to determine whether categories differed in frequency within years.

RESULTS AND DISCUSSION

Changes in the Exotic Flora

Altogether, we found 52 exotic species during the two surveys. Of these, four species (*Agave*

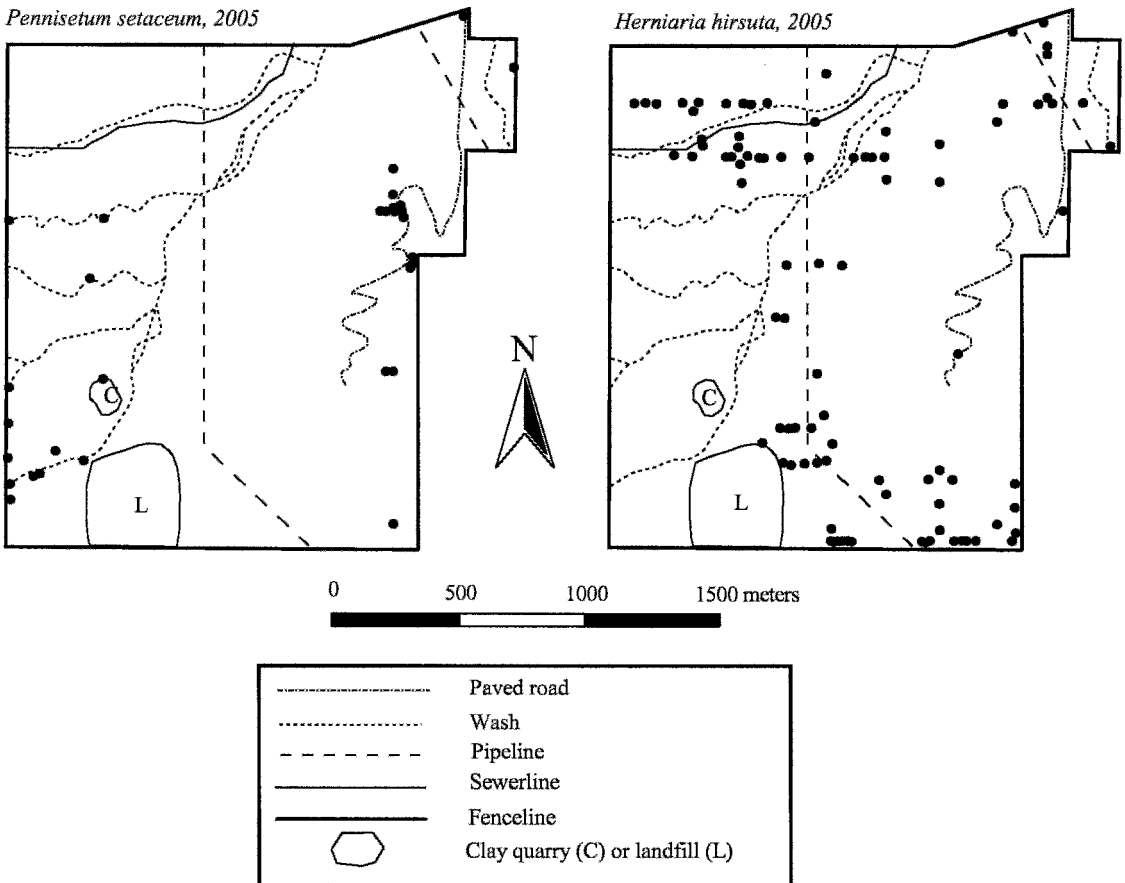


FIG. 2. Distribution of *Pennisetum setaceum* and *Herniaria hirsuta* at the Desert Laboratory, Tucson, Arizona, in 2005.

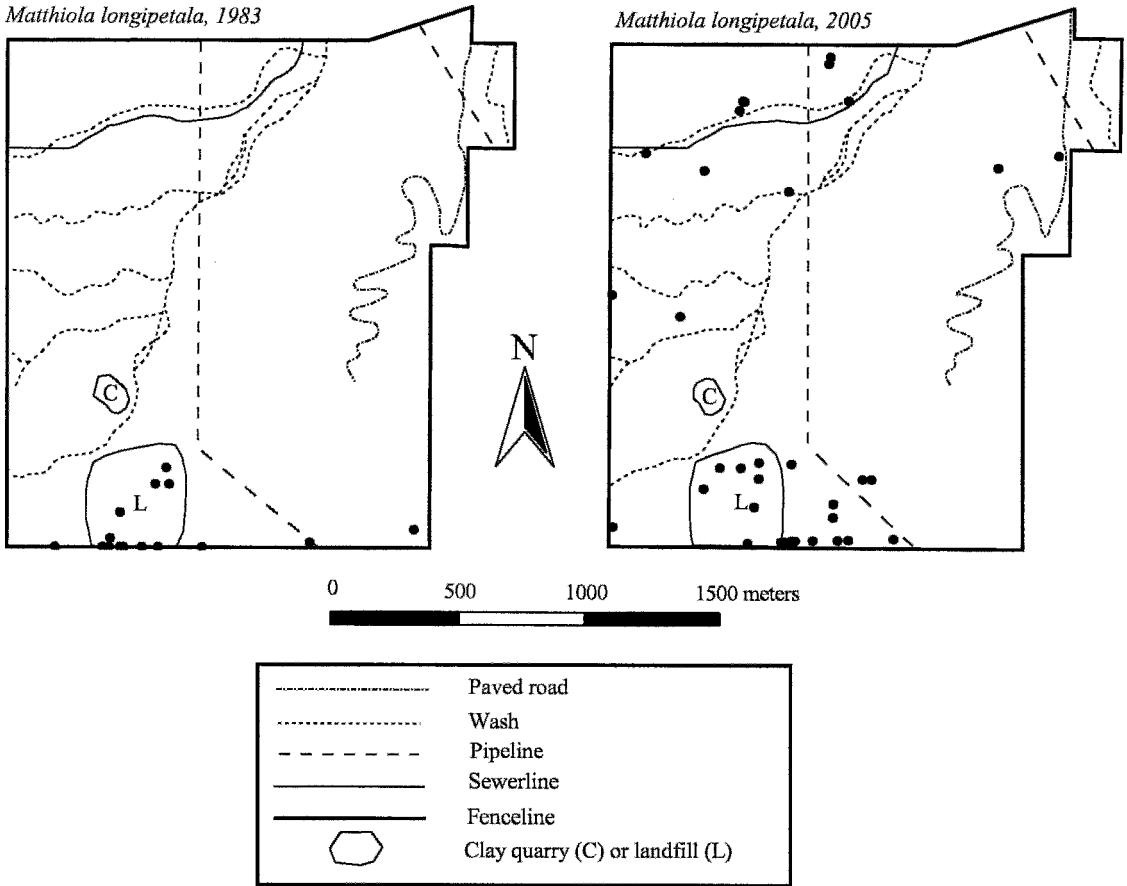


FIG. 3. Distribution of *Matthiola longipetala* at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

murpheyi, *Opuntia basilaris*, *O. santa-rita*, *Parkinsonia aculeata*) are native to Arizona but not to the vicinity of Tucson (Kearney and Peebles 1969, Hodgson 2001). Seedlings of *A. murpheyi* were planted at the Desert Laboratory in 1987 as part of an archeological experiment (S. Fish, personal communication); some persisted without irrigation and eventually reproduced by offsets. The other three are cultivated as ornamentals near our study site. Two exotic species found during the surveys (*Lantana urticoides*, *O. engelmannii* var. *linguiformis*) are native to North America north of Mexico but not to Arizona (Correll and Johnston 1970). Both are grown near our study site as ornamentals. The remaining 46 species were introduced into North America north of Mexico, generally from the Old World or Latin America.

The exotic flora was dynamic during the 22 years between surveys. In 1983, we encountered 34 species of exotics along the gridlines. During the 2005 survey, we found 44 species. Eight species present in 1983 were not found in 2005 and probably no longer occur on our study

site. Eighteen species found in 2005 were not encountered during the 1983 survey. Most were not known from the flora of the Desert Laboratory at the time and probably colonized the study site afterward.

Since 1983, there has been a major shift in the exotic flora from agricultural and ruderal weeds to ornamental plants, that is, species cultivated with or without irrigation in yards, gardens, and lawns. Specifically, ornamentals comprised 26% of exotic species in 1983 and 50% in 2005. In addition, overall frequency of ornamentals increased between 1983 and 2005 (Fig. 1). The growing need for water conservation in the southwestern United States has brought about increased use of arid-adapted ornamentals in urban and suburban landscaping (Mack 2002). Once introduced, ornamentals that are adapted to arid climates elsewhere can spread rapidly in the Sonoran Desert because they tolerate low rainfall, full sunlight, and unenriched soils (Mack 2002). As a consequence, desert areas near towns and cities support ever-increasing numbers of ornamentals. Ornamentals as a group have typically

Pennisetum ciliare, 1983

Pennisetum ciliare, 2005

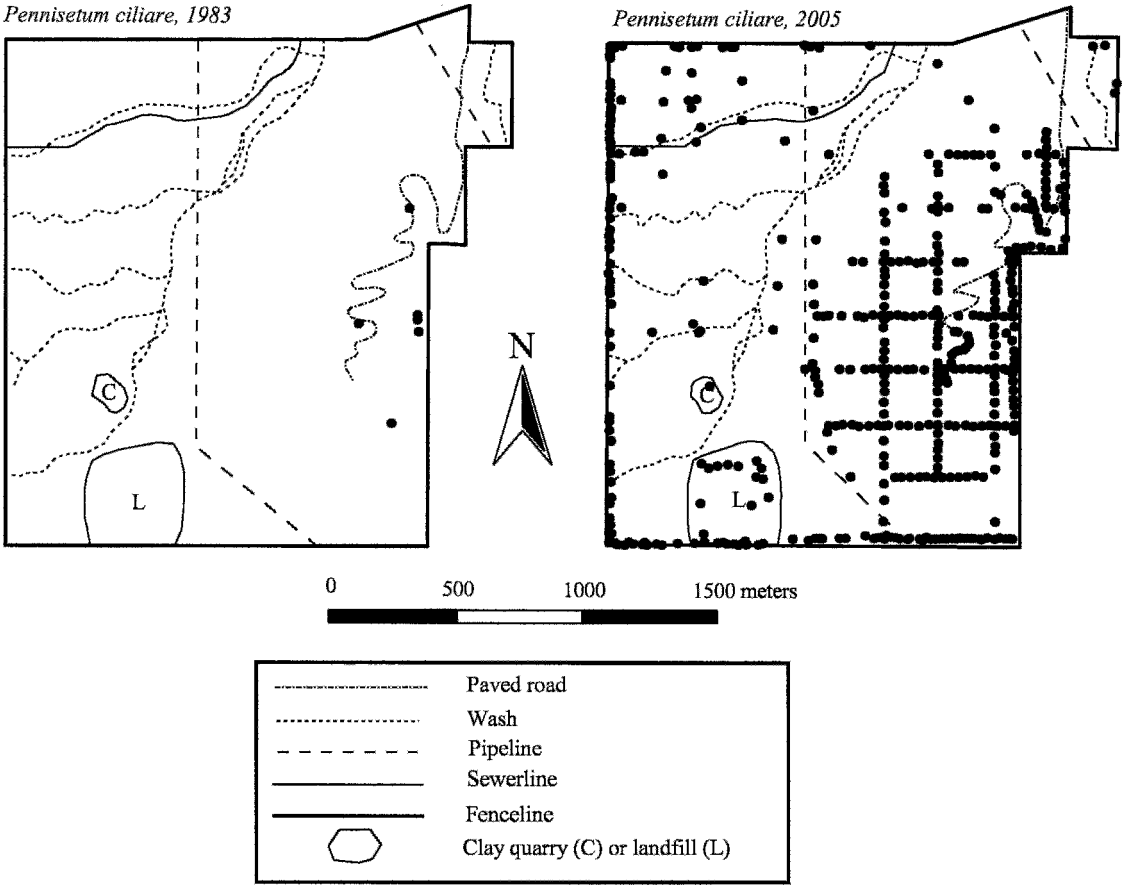


FIG. 4. Distribution of *Pennisetum ciliare* at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

colonized the Desert Laboratory grounds from the perimeter inward, sometimes using washes as corridors (Fig. 1). Virtually all ornamentals on the study site in 2005 also could be found in nearby housing developments, a fact that emphasizes the vulnerability of urban natural areas to urban horticulture. Local and state governments need to take an active role in regulating the sale of invasive ornamental exotics in Arizona.

Status of Exotic Plants

Casual, naturalized, and invasive exotics comprised 44%, 40%, and 15% of species found during the two surveys. All exotics found in 1983 or 2005 are listed in Tables 1, 2, or 3. In 1983, mean frequency (number of coordinate locations) was 3.7 ± 4.40 for casual exotic species, 19.9 ± 18.55 for naturalized species, and 366.5 ± 253.06 for invasive species. (All means are ± 1 SD) Categories differed significantly in mean frequency (Kruskal-Wallis test statistic = 19.15, $P < 0.001$). Means were also significantly different in 2005, when frequency averaged 2.5 ± 1.81 for casual species, 21.3 ± 17.42 for naturalized species, and $404.6 \pm$

339.94 for invasive species (Kruskal-Wallis test statistic = 29.01, $P < 0.001$). (Note that means excluded species with frequency = 0).

Casual exotic plants. After introduction to a site, casual exotic plants must surmount environmental and reproductive barriers before they can be considered naturalized (Richardson et al. 2000). Eight casual species disappeared from our study site between 1983 and 2005 (Table 1), presumably having failed to cross those barriers. Their populations were small in 1983 and therefore vulnerable to extirpation (reproductive barrier); in addition, annual precipitation at the study site in 2001, 2002, and 2004 was $<70\%$ of the long-term average, and severe drought stress might have killed many or most individuals, especially ornamentals that require supplemental water (local environmental barrier). Eleven casual species, all ornamentals, first appeared on our gridlines in 2005 (Table 1). More time is needed to determine whether any can maintain persistent populations.

Naturalized plants. Of 21 naturalized species encountered during the surveys (Table 2), the

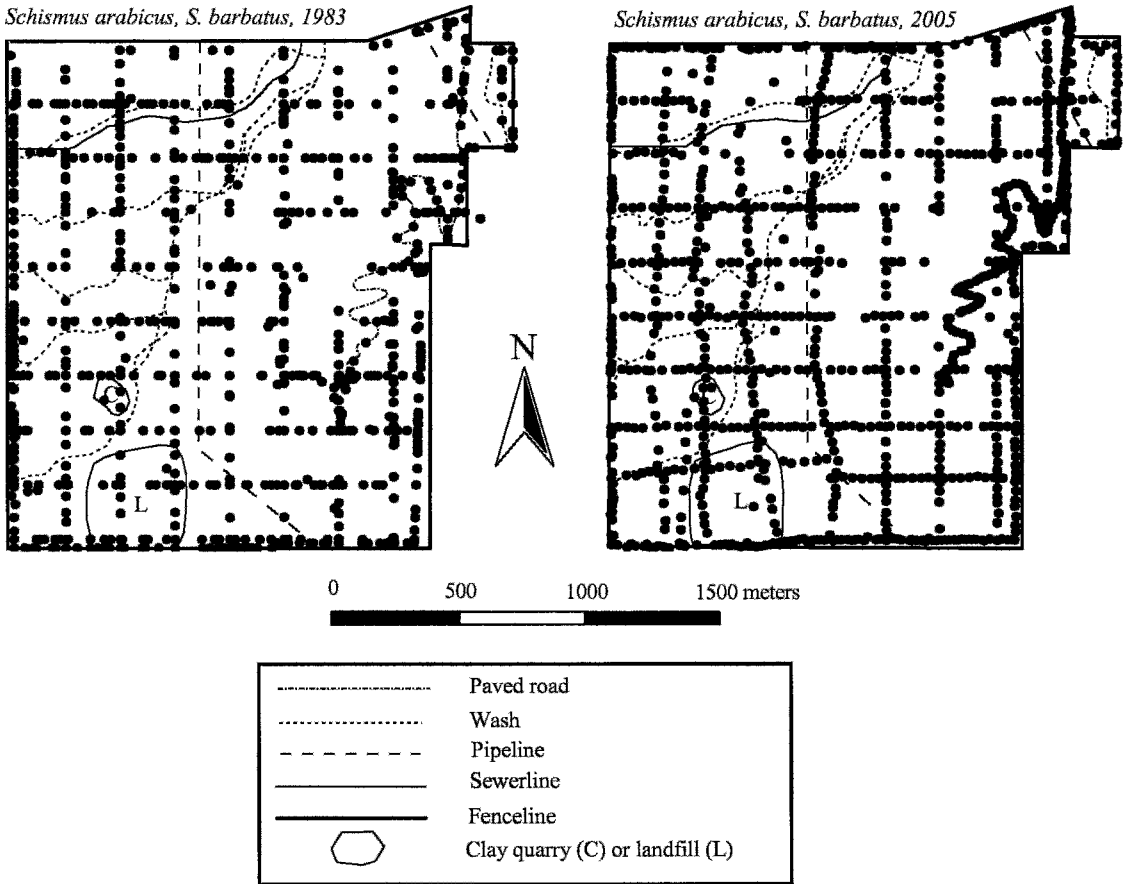


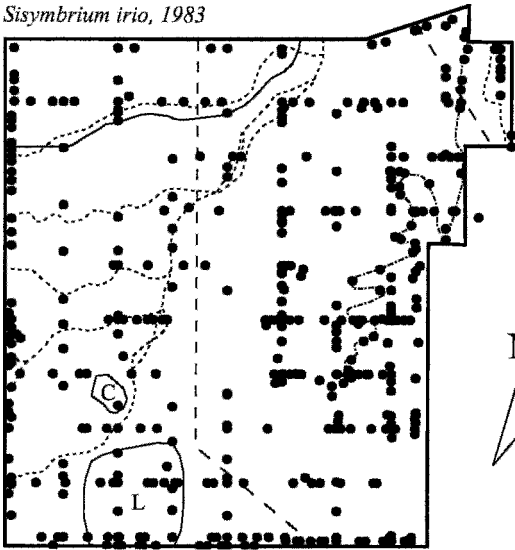
FIG. 5. Distribution of *Schismus arabicus* and *S. barbatus* at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

mapped distribution of 11 expanded noticeably during the past two decades. Two are of particular concern because they have proven invasive elsewhere in the Sonoran Desert. Between 1983 and 2005, *Brassica tournefortii* spread from the perimeter of the study area into the interior and more than doubled in frequency (Table 2); in fact, its 2005 frequency was the highest of any naturalized exotic (Table 2). *Pennisetum setaceum*, not recorded in the 1983 survey, was present in 2005 at a higher frequency than average for naturalized plants (Fig. 2; Table 2). Neither *B. tournefortii* nor *P. setaceum* was ubiquitous and abundant on the Desert Laboratory grounds in 2005, but their invasive potential is well known (Wilson et al. 2002), and both require close monitoring. Although the other nine species are of less immediate concern, they still bear watching. *Bromus catharticus*, *Parkinsonia aculeata*, *Melilotus indicus*, and *Tamarix chinensis*, for example, were present at low frequency in 1983, but that frequency more than doubled by 2005 (Table 2). In 2005, frequency and percent change for *Matthiola*

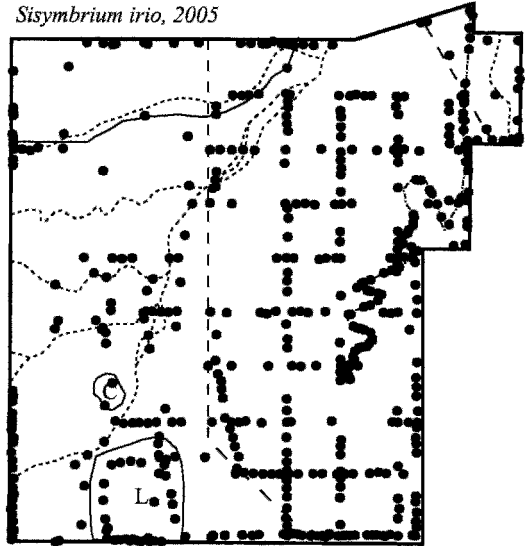
longipetala were still relatively low (Table 2), but the scatter of locations in 2005 was considerably wider than in 1983 (Fig. 3). The same was true of *Avena fatua*. *Eragrostis echinocloidea*, *Opuntia engelmannii* var. *linguiformis*, and *Rhus lancea* apparently colonized the study site after 1983; by 2005 these species were scattered widely enough to be considered naturalized. Frequency of the remaining naturalized species either decreased or stayed the same between surveys (Table 2).

Invasive plants. Invasive species at the Desert Laboratory included seven annual forbs and grasses and one perennial grass (Table 3). Two of these species have become invasive since the original survey. *Herniaria hirsuta* subsp. *cinerea* was rare and local when first reported from the Desert Laboratory (Bowers and Turner 1985) but in 2005 was widespread (Fig. 2). Although its frequency was low relative to long-established invasives such as *B. rubens* and *E. cicutarium* (Table 3), we are treating *Herniaria* as invasive because it has spread widely from its original

Sisymbrium irio, 1983



Sisymbrium irio, 2005



0 500 1000 1500 meters

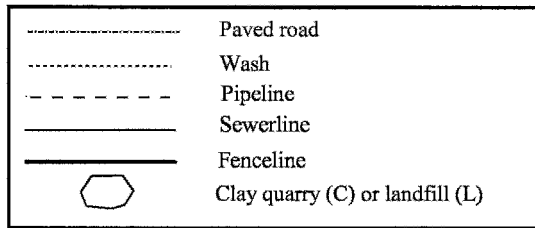


FIG. 6. Distribution of *Sisymbrium irio* at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

location, it has colonized undisturbed as well as disturbed habitats, and it is often abundant where found. In 2005, *Pennisetum ciliare* was declared a regulated and restricted noxious weed in Arizona. Between 1983 and 2005, frequency of this species on our study site changed by almost 8000%, by far the largest increase for any species (Fig. 4; Table 3). During those 22 years, plants spread from “isolated pockets” (Burgess et al. 1991) to form several continuous stands, the largest of which occupied about 50 ha in 2004. This species is abundant not only on disturbed sites such as the landfill and roadsides, but also on undisturbed rocky slopes (Fig. 4). It tends to become the dominant species wherever it occurs.

In contrast to the dramatic spread of *H. hirsuta* and *P. ciliare*, increases in *Schismus* and *Sisymbrium irio* were relatively modest (Table 3). Although the increase in *Schismus* could conceivably reflect differences in sampling methods, careful comparison of the distribution maps shows that this species evidently colonized additional territory between 1983 and 2005, for example, along the paved road and the northern

boundary (Fig. 5). *Schismus barbatus* often germinates in years that are too dry for native winter annuals (Venable and Pake 1999), which likely facilitates spread (Burgess et al. 1991). Another facilitating factor is that *Schismus* seeds are persistent, lasting in the soil for at least two years (Pake and Venable 1996). Even after dry winters when few seeds germinate, a large reserve of seed remains, enabling populations to rebound given adequate rain in the following winter (Venable and Pake 1999). Seeds of *Sisymbrium irio* are also persistent (Pake and Venable 1996). As for *Schismus*, the buffering effect of a between-year seed bank might explain why its frequency and distribution (Fig. 6; Table 3) did not decline during recent dry winters.

Three invasive species—*B. rubens*, *Hordeum murinum*, and *E. cicutarium*—declined between 1983 and 2005 (Table 3). These declines do not indicate a reversal of status from invasive to naturalized but, rather, likely reflect the combined effects of seed-bank dynamics and climatic variability. Seeds of *B. rubens*, for example, are transient in the soil, lasting no more than one

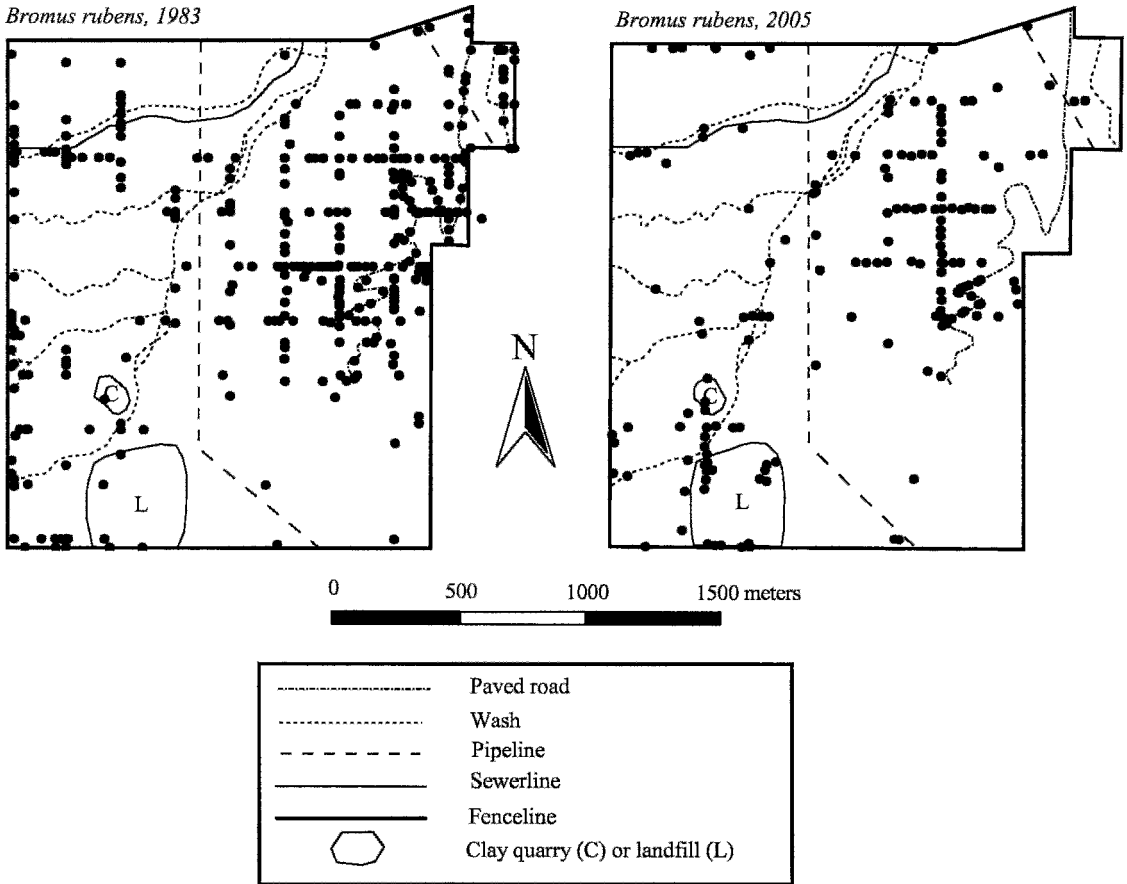


FIG. 7. Distribution of *Bromus rubens* at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

year (Pake and Venable 1996; Salo 2005). During recent dry winters, seeds germinated only in moist microsites, leading to small populations, lowered seed production, and, eventually, decreased frequency in 2005 compared with 1983 (Fig. 7; Table 3). A similar mechanism could account for the decline in *H. murinum*, seeds of which are not likely to persist in the soil between years (Popay 1981). *Erodium cicutarium* was only slightly less frequent in 2005 than in 1983 (Table 3). This species maintains large between-year seed banks in some locations (Roberts 1986; Mayor et al. 1999) but perhaps not at our study site (Pake and Venable 1996). The fact that *E. cicutarium* declined less dramatically than *B. rubens* or *H. murinum* suggests that there is a small reserve of persistent seeds in the soil. Other possible explanations for the decline of *B. rubens*, *H. murinum*, and *E. cicutarium* include competition with *P. ciliare*, especially in dense stands on rocky slopes, competition with native winter annuals, and lower germination as a result of the drier winter (151 mm in 2005 versus 250 mm in 1983).

Residence Time and Status of Exotics

In Chile and doubtless elsewhere, geographical extent of exotic species has increased with time since introduction (Castro et al. 2005). At the Desert Laboratory, casual, naturalized, and invasive exotics differed in minimum residence time, with casual species having been present for the shortest time and invasive species for the longest. Specifically, residence time for casual, naturalized, and invasive species averaged 14.5 ± 10.96 years, 28.1 ± 18.17 years, and 52.3 ± 32.51 years; the difference among categories was significant (Kruskal-Wallis test statistic = 16.146, $P < 0.001$). Moreover, as noted above, frequency in 1983 and 2005 increased across categories from casual to naturalized to invasive. These trends suggest that the longer a species was present on our study site, the more likely it was to surmount barriers to naturalization and invasion. The recent surge in ornamental exotics, combined with temporal trends in invasiveness, indicates that the proportion of invasive species in the flora will increase over time.

ACKNOWLEDGMENTS

We thank K. Giroux and C. Hannum for field assistance during the 2005 survey and B. Wilder for mapping *Pennisetum ciliare* on Tumamoc Hill in 2004. J. Betancourt, S. McLaughlin, and C. Salo reviewed the manuscript. Funding for the 2005 survey was provided by the U.S. Geological Survey and Kinder Morgan Energy Partners.

LITERATURE CITED

- AGIUS, B. 2003. Forging changes in an American landscape: invasive plant species at the Saugus Iron Works National Historic Site. Technical Report NPS/NER/NRTR 2005/10. National Park Service, Woodstock, VT.
- BOWERS, J. E. AND R. M. TURNER. 1985. A revised vascular flora of Tumamoc Hill, Tucson, Arizona. *Madroño* 32:225–252.
- BROOKS, M. L. 2000. Competition between alien annual grasses and native annuals plants in the Mojave Desert. *American Midland Naturalist* 144: 92–108.
- BURGESS, T. L., J. E. BOWERS, AND R. M. TURNER. 1991. Exotic plants at the Desert Laboratory, Tucson, Arizona. *Madroño* 38:96–114.
- BÚRQUEZ-MONTIJO, A., M. E. MILLER, AND A. MARTÍNEZ-YRIZAR. 2002. Mexican grasslands, thornscrub, and the transformation of the Sonoran Desert by invasive exotic buffelgrass (*Pennisetum ciliare*). Pp. 126–146 in B. Tellman (ed.), *Invasive exotic species in the Sonoran Desert region*. University of Arizona Press, Tucson, AZ.
- CASTRO, S. A., J. A. FIGUEROA, M. MUÑOZ-SCHICK, AND F. M. JAKSIC. 2005. Minimum residence time, biogeographical origin, and life cycle as determinants of the geographical extent of naturalized plants in continental Chile. *Diversity and Distributions* 11:183–191.
- CORRELL, D. S. AND M. C. JOHNSTON. 1970. *Manual of the vascular plants of Texas*. Texas Research Foundation, Renner, TX.
- DAEHLER, C. C. AND D. A. CARINO. 1998. Recent replacement of native pili grass (*Heteropogon contortus*) by invasive African grasses in the Hawaiian Islands. *Pacific Science* 52:220–227.
- ESQUE, T. C. AND C. R. SCHWALBE. 2002. Alien annual grasses and their relationships to fire and biotic change in Sonoran desertscrub. Pp. 165–194 in B. Tellman (ed.), *Invasive exotic species in the Sonoran Desert region*. University of Arizona Press, Tucson, AZ.
- FRAPPIER, B., D. LEE-THOMAS, K. F. OLSON, AND R. T. ECKERT. 2003. Small-scale invasion pattern, spread rate, and lag-phase behavior of *Rhamnus frangula* L. *Forest Ecology and Management* 186:1–6.
- HODGSON, W. C. 2001. *Food plants of the Sonoran Desert*. University of Arizona Press, Tucson, AZ.
- HUNTER, J. C. AND J. A. MATTICE. 2002. The spread of woody exotics into the forests of a northeastern landscape, 1938–1999. *Journal of the Torrey Botanical Society* 129:220–227.
- JOHNSTONE, P. D., J. B. WILSON, AND A. G. BREMNER. 1999. Change in *Hieracium* populations in Eastern Otago over the period 1982–1992. *New Zealand Journal of Ecology* 23:31–38.
- KARTESZ, J. R. 1999. A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland, 1st ed. In J. T. Kartesz and C. A. Meacham, *Synthesis of the North American flora*, Version 1.0. North Carolina Botanical Garden, Chapel Hill, NC.
- KEARNEY, T. H. AND R. H. PEEBLES. 1969. *Arizona flora*, 2nd edition, with supplement by J. T. Howell, E. McClintock and collaborators. University of California Press, Berkeley, CA.
- KOLAR, C. S. AND D. M. LODGE. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16:199–204.
- LEVINE, J. M., M. VILA, C. M. D'ANTONIO, J. S. KUKES, K. GRIGULIS, AND S. LAVOREL. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Biological Sciences, Series B* 270:775–781.
- MACK, R. N., D. SIMBERLOFF, W. M. LONSDALE, H. EVANS, M. CLOUT, AND F. A. BAZZAZ. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710.
- . 2002. Natural barriers to plant naturalizations and invasions in the Sonoran Desert. Pp. 63–76 in B. Tellman (ed.), *Invasive exotic species in the Sonoran Desert region*. University of Arizona Press, Tucson, AZ.
- MAYOR, M. D., R. M. BOO, D. V. PELAEZ, AND O. R. ELIA. 1999. Seasonal variation of the seed bank of *Medicago minima* and *Erodium cicutarium* as related to grazing history and presence of shrubs in central Argentina. *Journal of Arid Environments* 43:205–212.
- PAKE, C. E. AND D. L. VENABLE. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology* 77: 1427–1435.
- POPAY, A. I. 1981. Germination of seeds of five annual species of barley grass. *Journal of Applied Ecology* 18:547–558.
- RICHARDSON, D. M., P. PYŠEK, M. REJMÁNEK, M. G. BARBOUR, F. D. PANETTA, AND C. J. WEST. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6:93–107.
- ROBERTS, H. A. 1986. Seed persistence in soil and seasonal emergence in plant species from different habitats. *Journal of Applied Ecology* 23:639–656.
- SALO, L. F. 2005. Red brome (*Bromus rubens* subsp. *madritensis*) in North America: possible modes for early introductions, subsequent spread. *Biological Invasions* 7:165–180.
- , G. R. MCPHERSON, AND D. G. WILLIAMS. 2005. Sonoran Desert winter annuals affected by density of red brome and soil nitrogen. *American Midland Naturalist* 153:95–109.
- SELLERS, W. D., R. H. HILL, AND M. SANDERSON-RAE. 1985. *Arizona Climate*. University of Arizona, Tucson, AZ.
- SHREVE, F. 1951. *Vegetation of the Sonoran Desert*. Carnegie Institution of Washington Publication 591. Carnegie Institution of Washington, Washington, DC.
- SPALDING, V. M. 1909. *Distribution and movements of desert plants*. Carnegie Institution of Washington

- Publication 113. Carnegie Institution of Washington, Washington, DC.
- VENABLE, D. L. AND C. E. PAKE. 1999. Population ecology of Sonoran Desert annual plants. Pp. 115–142 in R. H. Robichaux (ed.), *Ecology of Sonoran Desert plants and plant communities*. University of Arizona Press, Tucson, AZ.
- WHITE, J. 1985. The census of plants in vegetation. Pp. 33–88 in J. White (ed.), *The population structure of vegetation*. Dr. W. Junk, Dordrecht, Netherlands.
- WILCOX, K. L., S. A. PETRIE, L. A. MAYNARD, AND S. W. MEYER. 2003. Historical distribution and abundance of *Phragmites australis* at Long Point, Lake Erie, Ontario. *Journal of Great Lakes Research* 29:664–680.
- WILSON, M. F., L. LEIGH, AND R. S. FELGER. 2002. Invasive exotic plants in the Sonoran Desert. Pp. 81–90 in B. Tellman (ed.), *Invasive exotic species in the Sonoran Desert region*. University of Arizona Press, Tucson, AZ.