By the late 1800s, red brome (*Bromus madritensis* subsp. *rubens*), first collected by Parish in San Bernardino County, had spread throughout the entire Great Basin. Photographs by Matt Brooks.

EXOTIC SPECIES OF CALIFORNIA DESERTS

by Paul R. Kemp and Matthew L. Brooks

The number of exotic species that have become established in the Mojave and Sonoran (Colorado) deserts is rather small in comparison to other regions of California. Only about twenty-five species of exotic plants are widespread (or spreading) into natural habitats of the warm deserts of southeastern California. Nevertheless, several of these species appear to be increasing in abundance as well as range, and may bring about changes in the structure and functioning of the desert plant communities.

Principal Exotic Species: Eurasian Annuals

The number of exotic species reported in local or regional floras of the Mojave and Sonoran desert areas of California (or adjacent southwestern Nevada or western Arizona) varies from about five to twelve percent of the total flora. These percentages typically include some exotic species collected from non-desert habitats within the desert region, such as mountains, riparian, or other natural wetlands, agricultural areas subject to past or present irrigation and fertilization, or disturbed areas subject to runoff (e.g., roadsides). Thus, only a restricted group of recorded exotic species can be considered as having become established and spread into natural desert habitats. Our assessment as to which species make up this group is based upon species distributions in local floras as well as our own observations in the Mojave and Sonoran deserts. Within this group of exotic species there are some differences in regional distributions and, perhaps more important, there are differences in microhabitat distributions, which may reflect how successful some species have been, or will be, at colonizing particular desert habitats. For example, some exotic species are found in wide variety of desert habitats (e.g., under shrub canopies, in open areas, in washes), whereas others may be more restricted to certain habitats. A few species are still confined largely to highly disturbed areas within the desert, but their abundance or establishment in other arid habitats suggests that they should be considered potential invaders of some natural desert habitats in California.

Most of the exotic species that have become established in California's desert habitats are of Eurasian (especially Mediterranean) origin. Three families predominate: Poaceae, Chenopodiaceae, and Brassicaceae. All except Australian saltbush (*Atriplex semibaccata*) are annuals, and for the most part all are found throughout southern California, often in dry, disturbed habitats. Thus, for the most part, the exotic species of the California deserts appear to represent a subset of California's Eurasian exotics that were pre-adapted to the driest habitats associated with their Mediterranean climate origins.

Lack of Perennial Exotics

Riparian and various other desert areas with supplemental water (from high water tables or runoff from roads) have been invaded by a number of exotic woody and herbaceous perennial species. In some areas, species such as tamarisk (*Tamarix* spp.), giant reed (*Arundo donax*), or Bermuda grass (*Cynodon dactylon*) have become the dominant species, resulting in major impacts upon the community. However, aside from these areas, perennial exotic species have not been successful in natural habitats of California's warm deserts. This contrasts with some desert areas elsewhere. In the eastern Sonoran Desert of Arizona, several exotic perennial grass species have become abundant following their introduction. In the northern Chihuahuan desert of Texas and New Mexico native shrubs such as mesquite and creosote bush have invaded some areas that were previously dominated by native grasses.

The lack of exotic perennials in California's deserts may be related to several factors. The exotic perennial grasses that have invaded the Sonoran Desert of Arizona are warm-season grasses that utilize summer rainfall, which greatly diminishes across the Sonoran Desert from eastern Arizona into California. The lack of exotic shrub species in the California deserts may be partly related to the difficulty of shrub establishment in the desert. Most desert shrubs establish only episodically when a sequence of years with favorable moisture allows seedlings to generate sufficient root systems to survive normal drought. This requires a continuous supply of seeds to a region in order to support continuous attempts at establishment. Invasion of the arid grasslands in the Chihuahuan desert by woody perennials has been accomplished through periodically moving fronts adjacent to seed-source shrublands. So far in California, apparently no exotic shrub species has the combination of drought tolerance and abundance of seed sources sufficient to promote establishment in the desert. An additional factor that may favor exotic annuals over perennials in California deserts is that the principal source of exotics for these winter-rainfall deserts has been the Mediterranean region, which has few woody species as potentially invasive as its annuals.


Close-up of red brome.

Historic Establishment of Exotics

Most exotic species apparently first entered the California deserts during the middle to latter part of the nineteenth century, following the Gold Rush of 1849. Some examples include: red brome (*Bromus madritensis* ssp. *rubens*), which Parish collected from San Bernardino County in 1889, and labeled it as a recent introduction); cheatgrass (*B. tectorum*), which spread relatively rapidly throughout the Great Basin in the late 1800s; and Russian thistle (*Salsola tragus*), which was first found in California near Lancaster about 1895. Three others, red-stem filaree (*Erodium cicutarium*), pigweed (*Chenopodium murale*), and barley (*Hordeum murinum*), probably entered the deserts well before this period, as they were established in cismontane California prior to 1800.

Following their introduction, most exotics did not become abundant and widespread in California deserts until after about 1930. For example, Parish noted that in a 1912-1913 survey there were no exotic species found established in the Imperial Valley. However, shortly thereafter several exotic species became relatively abundant, including cheatgrass, red brome, chickweed (*Mollugo cerviana*), and Russian thistle. Red brome was collected at several locations in the Mojave Desert and Great Basin from 1907 to 1917, but not until 1930s and 1940s was it labeled as common or abundant from collections throughout the western Mojave and Sonoran deserts, and it was not common in the eastern Mojave Desert (Nevada) until after 1950. According to Oscar Clarke, U.C. Riverside botanist, *Schismus* species seemed to appear overnight throughout the warm deserts sometime during the 1940s.

Burgess and co-workers outlined five factors that they consider important in fostering establishment and/or spread of exotics into the Sonoran Desert: favorable climate (similar to the exotics' native habitat); prior occurrence in regions with intensive pastoralism; livestock grazing of the habitat; favorable reproductive biology; and minimal integration into food webs. To this list we would add habitat disturbance. Habitat disturbances, including grazing, have played several key roles historically in promoting establishment and spread of exotics into California deserts. Most exotics first appeared in the desert following the boom in cattle and sheep grazing that accompanied the California Gold Rush of 1849. Overstocking of desert ranges probably occurred within two decades following the start of the Gold Rush and resulted in enormous reduction of native grass cover and damage to the cryptogamic desert crusts, both of which had prevented seed germination and seedling establishment of at least some exotic species. An additional disturbance that was important historically to the establishment of exotics in the California deserts was road and railroad construction. This not only provided a huge network of interconnected disturbed sites, but also the means along which seeds of such species as puncture vine (*Tribulus terrestris*) and Russian thistle entered from outside regions. Roadsides also offer refuge (via runoff) for exotics that might otherwise be eliminated during the normal strings of drought years encountered in the desert.

The importance of disturbance to many exotic species in the desert is demonstrated by some subtle differences in their distributions relative to native annual species. Desert areas that have been denuded of vegetation are colonized initially by mostly exotic species, such as red brome, red-stem filaree, and Russian thistle. Many exotic species, such as ripgut brome (*Bromus diandrus*), Russian thistle, and puncture vine, seem to be largely excluded from pristine desert habitats, perhaps by competition with the native annuals or shrubs, or perhaps by the inability of their seeds to germinate on crusted desert soils. However, it seems that some other exotic species are able to enter pristine desert habitats as readily as, or more than, any native annual. This group of exotics includes those whose native distribution was originally desert (e.g, schismus), as well as those with a long history as an exotic in semi-arid regions of North America (e.g, red-stem filaree, red brome).

Current Status of Exotics in the Desert

Biologists studying public lands in California deserts indicate that exotic species appear to be increasing in many areas. In the northeastern Mojave Desert (Nevada test site), Hunter has documented marked increases in red brome and cheatgrass over the period from 1975 to 1988. In the Arizona Sonoran Desert, Burgess and co-workers have found that exotic species have continued to invade pristine habitats and have increased in abundance during the last couple of decades. Brooks has found that exotic species (primarily red brome, schismus, and filaree) now account for the majority of total annual plant biomass in many regions of the California Mojave Desert.

Explanations for causes of recent pulses of exotic expansion in the desert may require looking beyond those historical factors that fostered initial establishments. In the examples cited above, exotic species have greatly increased in relatively undisturbed habitats. Thus, disturbance no longer appears to be such an important prerequisite. Hunter suggests that the recent increases in red brome may be related to some specific biological attributes, or possibly to weather (a sequence of years of abundant rainfall). The biological explanations that Hunter offers, fibrous rooting and surface shading by the exotics, would apparently become effective in favoring exotics over native species only after exotic species achieved a certain threshold density. Fluctuations in weather could conceivably alter growth and survival of any plant species, but it is unclear how these fluctuations might favor exotic species over native species.

The suggestions offered by Hunter for increases in exotics are essentially specific examples from two general categories of factors—extrinsic and intrinsic. Among extrinsic factors that may warrant study for effects on exotic distributions include factors associated with human-induced atmospheric changes: rising atmospheric carbon dioxide (CO_2) and rising levels of atmospheric pollutants. Researchers have found that some weedy exotics respond very strongly to increasing CO_2. They suggest that increasing CO_2 may lead to increased invasiveness and perhaps expanded ranges of exotics. For example, Smith and co-workers found that red brome had greater growth at elevated CO_2 than two native Great Basin perennial

Most Commonly Encountered Exotic Plant Species in California Deserts

Species	Family	Initial Introduction Date	Location	Origin	Current Distribution Desert Range	Habitat	Abundance
Bromus arenarius	Poaceae	1905	San Bern. Co	Australia	Mojave/Sonoran	disturbed	+
B. diandrus	Poaceae	1862	San Francisco	Europe	W Moj./W Son.	disturbed	+
B. madritensis rubens	Poaceae	1880s	Plumas Co	Europe	all CA deserts	natural	+++
B. tectorum	Poaceae	>1889		Eurasia	G. Basin/Mojave	natural	+++
B. trinii	Poaceae			Chile	all CA deserts	natural	++
Hordeum murinum	Poaceae	<1775	Spanish missions	Europe	all CA deserts	disturbed/natural	+
Schismus barbatus, S. arabicus	Poaceae	1930s	Fresno Co	Eurasia	Mojave/Sonoran	natural	+++
Sonchus oleraceus, S. asper?	Asteraceae	<1825		Europe	all CA deserts		+
Brassica tournefortii	Brassicaceae	1930s	Colo. River V	N Africa	Sonoran/Mojave	disturbed/natural	++
Descurania sophia	Brassicaceae			Eurasia	G. Basin/Mojave	disturbed/natural	++
Sisymbrium altissimum	Brassicaceae	1910s		Europe	G. Basin/Mojave	disturbed/natural	+
S. irio	Brassicaceae	1910s		Europe	all CA deserts	disturbed/natural	+
Atriplex semibaccata	Chenopodiaceae			Australia	all saline areas	saline/alkaline	locally abundant
Bassia hyssopifolia	Chenopodiaceae	1920s	San Joaquin V	Eurasia	G. Basin/Mojave	saline/alkaline	locally abundant
Chenopodium murale	Chenopodiaceae	<1775		Europe	all CA deserts	disturbed	+
Halogeton glomeratus	Chenopodiaceae				G. Basin/Mojave	saline/alkaline	locally abundant
Salsola paulsenii	Chenopodiaceae			Eurasia	G. Basin/Mojave	disturbed/natural	++
S. tragus	Chenopodiaceae	1895	Lancaster	Eurasia	all CA deserts	disturbed	++
Erodium cicutarium	Geraniaceae	<1775		Eurasia	all CA deserts	natural	+++
Malva parviflora	Malvaceae	<1825		Europe	all CA deserts	disturbed	++
Mollugo cerviana, M. verticillata?	Molluginaceae	1929	San Bern. Co	Eurasia/ C & S Am.	Mojave/Sonoran	natural	++
Portulaca oleracea	Portulacaceae	1850s	Colo. River V	Europe	all CA deserts	disturbed	+
Tribulus terrestris	Zygophyllaceae	1902	Los Angeles	Eurasia	all CA deserts	disturbed	+

Compiled from Frenkel, Parish, Robbins, and Munz.

grasses. Improved water-use efficiency brought about by increased CO_2 might also partially explain the gradual increase of cheatgrass into drier, lower-elevation sites in the Mojave Desert.

A number of atmospheric pollutants could impact desert plants either through stimulation or inhibition of growth. Most notable among the potential stimulants is nitrogen (N). High rates of N deposition have been suggested as a means of facilitating increases of exotics in native communities. Little is known about rates and distribution of N deposition in California desert areas, but some areas "downwind" of large metropolitan areas can be expected to be receiving large inputs of N. Recent studies by Brooks in desert communities have shown that exotic annual species can be much more responsive (increased biomass/plant) to low-level N amendments than are native annual species.

The second group of factors (intrinsic) that could influence the distribution of exotic species are those brought about by the increased presence of exotic species themselves. Invading exotics are known to compete with native

Sisymbrium irio is one of the exotics that are increasing in California deserts, perhaps in response to human caused atmospheric changes.

species in plant communities of mesic or semi-arid habitats. In arid plant communities, competitive interactions are less well documented. However, Brooks found that removal of red brome and Schismus seedlings increased density, biomass, and diversity of native annual plants at several study sites in the Mojave Desert, and Hunter suggests that the dense cover of red brome almost certainly affects native annuals in the eastern Mojave. Some exotic annuals (e.g, red brome, Schismus) appear to be more regularly abundant from year to year than the native species, with numerous small plants setting seed in all but the most extreme years. Exotic species may have less strict seed dormancy and/or density dependent germination responses. These situations could lead to fundamental changes in the high between-year variation in production and soil seedbanks that has governed much of the interactions among annual species as well as other trophic levels dependent upon annual plants and their seeds.

A significant intrinsic factor that may develop in desert communities with abundant exotic species is fire. Production of large amounts of biomass by exotic species may increase the ability of the community to carry a fire. Frequent fires may remove non-resistant native perennials and foster perpetuation of annual exotics. This situation has been a key factor in the spread of cheatgrass throughout the Great Basin. A similar situation may be developing in some portions of the Mojave and Sonoran deserts where red brome is prevalent. Fires are more frequent where biomass of red brome is high, and fires have become more frequent since the invasion of red brome into this desert region.

What's Ahead

At present we have an incomplete understanding of the factors that are important in controlling the establishment and spread of exotics in desert habitats. We have even less understanding about the potential impacts of these exotic species upon native plants and communities. More basic research is needed to document changes in distributions of exotics in the desert, both spatially and temporally; to correlate distributions of exotics with various extrinsic and intrinsic factors; to determine how various extrinsic and intrinsic factors influence growth and distribution of exotics in relation to native species; and to determine how abundance of various exotic species affects plant community structure and function. In the meantime there is good reason to be concerned that exotic species will continue to increase in numbers and biomass in desert plant communities. Increases in exotics could be expected to have significant impacts upon the native ephemeral species (their most direct competitors), and with the addition of widespread fire, could alter the general nature of desert ecosystems, much as they have in the Great Basin shrub-steppe or Central Valley grasslands.

References

Beatley, J.C. 1966. Ecological status of introduced brome grasses (*Bromus* spp.) in desert vegetation of southern Nevada. *Ecology* 47:548-54.

Billings, W.D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. In G.M. Woodwell (ed.), The Earth in Transition: Patterns and Processes of Biotic Impoverishment. Cambridge Univ. Press, Cambridge, England. pp. 301-22.

Brooks, M. in preparation. Ecology of a biological invasion: alien annual plants in the Mojave Desert. Dissertation. University of California, Riverside.

Brown, D.E. and R.A. Minnich. 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. *Amer. Midl. Nat.* 116:411-22.

Burcham, L.T. 1957. California Rangeland. An historico-ecological study of the range resource of California. Dept. of Natural Res., Sacramento, CA.

Burgess, T.L. J.E. Bowers, and R.M. Truner. 1991. Exotic plants at the desert laboratory, Tucson, Arizona. *Madroño* 38:96-114.

diCastri, F. 1989. History of biological invasions with special emphasis on the Old World. In J.A. Drake, H.A. Mooney, F. diCastri, R.H. Groves, F.J. Kruger, M. Rejmanek, and M. Williamson (eds.), Biological invasions: a global perspective, SCOPE 37, John Wiley and Sons, New York, NY. pp. 1-30.

Frenkel, R.F. 1970. Ruderal vegetation along some California roadsides. Univ. Calif. Press, Berkeley, CA.

Hunter, R. 1991. *Bromus* invasions on the Nevada Test Site: present status of *B. rubens* and *B. tectorum* with notes on their relationship to disturbance and altitude. *Great Basin Nat.* 51:176-82.

Karpiscak, M.M. 1979. Secondary succession of abandoned field vegetation in southern Arizona. Arizona-Nevada Academy of Sciences, Supplement No. 23.

Mack, R.N. 1986. Alien plant invasion into the intermountain west: a case history. In Mooney, H.A. and J.A. Drake (eds.), Ecology of Biological Invasions of North America and Hawaii, Springer-Verlag, New York, NY. pp. 191-213.

Morecroft, M.D., E.K. Sellers and J.A. Lee. 1994. An experimental investigation into the effects of atmospheric nitrogen deposition on two semi-natural grasslands. *J. Ecol.* 82:475-83.

Parish, S.B. 1920. The immigrant plants of Southern California. *S. Calif. Acad. Sci. Bull.* 19(4):3-30.

Robbins, W.W. 1940. Plants growing without cultivation in California. University of California, *Agricultural Experiment Station Bulletin* 637, Berkeley, CA. 128 p.

Smith, S.P., B.R. Strain, T.D. Sharkey. 1987. Effects of CO_2 enrichment on Great Basin grasses. *Func. Ecol.* 1:139-43.

Webb, R.H. and H.G. Wilshire. 1980. Recovery of soils and vegetation in a Mojave Desert ghost town, Nevada, U.S.A. *J. Arid Environ.* 3:291-303.

Williams, R.B. and K.L. Bell. 1981. Nitrogen allocation in Mojave Desert winter annuals. *Oecologia* 48: 145-50.

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