Alien Plants and Fire in Desert Tortoise (Gopherus agassizii) Habitat of the Mojave and Colorado Deserts

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ABSTRACT. – Alien plants and fire have recently been recognized as significant land management problems in the Mojave and Colorado deserts. Annual species dominate the alien flora, although only *Bromus rubens*, *Schismus* spp., and *Erodium cicutarium* are currently widespread and abundant. These species can compete with native plants, and *B. rubens* in particular has contributed to significant increases in fire frequency since the 1970s. Native desert plants are often poorly adapted to fire, and recurrent fire has converted native shrubland to alien annual grassland in some areas. Changes in plant communities caused by alien plants and recurrent fire may negatively affect native animals such as the desert tortoise by altering habitat structure and the species composition of their food plants. The dominance of alien annual plants and the frequency of fire may increase in the future due to increased levels of urbanization and atmospheric nitrogen and carbon dioxide. Increases or decreases in rainfall could also cause changes in alien plant dominance and fire frequency. Land managers should focus on early detection and eradication of new alien species, especially those that pose significant fire threats, and on law enforcement to minimize the frequency of ignitions by humans. Additional information on the ecology and effects of invasive plants and fire in the Mojave and Colorado deserts are needed to develop effective management plans.

KEY WORDS. – Reptilia; Testudines; Testudinidae; Gopherus agassizii; Bromus; Schismus; conservation; management; disturbance; fire; exotic species; invasive plants; plant invasions; Mojave Desert; Colorado Desert; USA

Threats from alien species currently rank second to habitat destruction in causing species endangerment (Wilcove et al., 1998), and about 42% of federally threatened or endangered species are listed because of threats from alien species (The Nature Conservancy, 1996; Babbitt, 1998). Approximately 5000 alien plant species have become established in natural habitats outside of agricultural areas in the United States, and many of these species are believed to have displaced native plants and altered ecosystem integrity (Morse et al., 1995). Alien plants invade approximately 700,000 hectares of wildlife habitat per year (Babbitt, 1998). Accordingly, the control of alien plants is now a top priority for land management agencies in the United States.

The Federal Wildland Fire Policy defines fire as a critical natural process that should be reintroduced for the benefit of ecosystem integrity (Glickman and Babbitt, 1995). It also recognizes fire hazards that can result as fuels accumulate where fire has been previously suppressed and recommends that fire be used to reduce these high fuel loads. However, in some ecosystems fire may not be a natural ecosystem component or an appropriate tool to reduce fuel loads. Such ecosystems include the Mojave and Colorado deserts, where fire appears to be historically rare (Humphrey, 1974; R. Minnich, unpubl. data). Plant communities in these deserts are generally slow to recover from fires (O'Leary and Minnich, 1981; Brown and Minnich, 1986), and fires often increase landscape flammability due to postfire dominance of alien annual grasses (Brooks, 1999a; Esque and Schwalbe,

2002). These conclusions are based on limited data, but they indicate that fire may have mostly negative effects in this region.

The Mojave population of the desert tortoise (Gopherus agassizii) is a Federally Threatened species that is listed partly due to the negative effects of alien plants and fire. The Mojave population occupies critical habitat in the California, Nevada, and Utah parts of the Mojave and Colorado deserts located north and west of the Colorado River (U.S. Fish and Wildlife Service, 1994). Members of the multiagency Desert Tortoise Management Oversight Group ranked alien species and fire second only to disease as major threats to the desert tortoise (annual meeting, 29 March 2000). Bioregional management plans such as the West Mojave Coordinated Management Plan (California), Clark County Habitat Conservation Plan (Nevada), and Washington County Habitat Conservation Plan (Utah) have been structured primarily around conservation of the desert tortoise, and have accordingly placed the management of alien plants and fire high on their list of management priorities. However, limited information about methods for control hinders the implementation of comprehensive management actions.

In this paper we present information that can be integrated into land management plans and used to establish priorities for future studies in desert tortoise habitat. We evaluate the current status of alien plants and fire, describe their effects, discuss future trends, propose management actions, and suggest research priorities.

ALIEN PLANTS

Alien plants comprise a relatively small portion of desert floras worldwide (Lonsdale, 1999), and the Mojave and Colorado deserts are no exception. By the end of the 1970s the California portion of the Mojave Desert contained 1836 vascular plant species, of which only 156 (9%) were alien species (Rowlands et al., 1982). In 1998 it was estimated that 13% of all plant species were alien at the Lake Mead National Recreation Area (J. Haley, *pers. comm.*). These percentages compare to an average of 16% alien plant species among 184 sites located in various ecosystems worldwide, and an average of 32% on island ecosystems (Lonsdale, 1997, 1999). As a result, most research on the ecology and effects of alien plants has focused on island ecosystems, and very little research has been done in the Mojave and Colorado deserts.

Annual plant species currently dominate the alien flora in wildland areas of the Mojave and Colorado deserts (Table 1). Although the most extensively studied alien species in this region are the perennials *Tamarix* spp. and *Arundo donax*, the riparian habitats that they occupy comprise less than 3% of the entire Mojave Desert (Rowlands et al., 1982). The remaining upland area is occupied almost exclusively by alien annuals, which can comprise 66–97% of the total annual plant biomass (Brooks, 1998, 1999b) and are present in at least 50% of wildland desert sites (K. Thomas, unpubl. data). Thus, alien annuals are the most widespread and abundant alien taxa in the Mojave and Colorado deserts, and we focus on the ecology and management of alien annual species in this paper.

Dominant Alien Taxa

Although relatively few alien plant species have invaded this region, and even fewer have invaded natural habitats (Kemp and Brooks, 1998), many are either locally abundant or widespread and abundant and pose various ecological problems for land managers (Table 1). Some species are recognized by states as noxious agricultural weeds, but none are federal noxious weeds. More are recognized as alien plants of significant ecological concern in wildland areas (California Exotic Pest Plant Council, 1999).

Poaceae and Asteraceae dominate alien floras worldwide (Mack et al., 2000), and along with Brassicaceae and Chenopodiaceae dominate the alien flora of the Mojave and Colorado deserts (Table 1). The most widespread and abundant species are the annuals *Bromus madritensis* ssp. *rubens* (hereafter called *Bromus rubens*), *Schismus* spp., and *Erodium*

Table 1. Alien plant species in critical desert tortoise habitat of the Mojave and Colorado deserts. This list only includes species that are currently found in or threaten to invade wildand areas. **** Compiled from information in Hickman (1993), CalFlora Database (2000), California Exotic Pest Plant Council (1999), Southwest Exotic Plant Mapping Program (2000), The Nature Conservancy (2000), Fire Effects Information System (2000), and information cited in the text. Life Form: AG = annual grass; AF = annual forb; BH = biennial herbaceous; PG = perennial grass; PH = perennial herbaceous; PW = perennial woody shrub or tree. Weed Ranking: CalEPPC = California Exotic Pest Plant Council [A1, A2, B, RA (red alert), NI (need more information), AG (annual grasses)]; CA = California Department of Food and Agriculture [A, B, C]; AZ = Arizona Department of Agriculture [Restr (restricted), Regul (regulated), Prohib (prohibited)]; UT = Utah Department of Agriculture [NW (noxious weed)]; NV = Nevada Department of Agriculture [NW (noxious weed)] abundant: ****** = widespread and abundant. Effects: A = allelopathic; C = competition with other plants; F = promotes fire; T = toxic to livestock. (*Table 1 continues on next page*).

Family	Scientific Name	Common Name	Life Form	Weed Ranking	Abundance	Effects
Amaranthaceae	Amaranthus albus	prostrate pigweed	AF		*	
Apiaceae	Apium graveolens	celery	AF		*	
Apocynaceae	Nerium oleander	South American oleander	PW		-10	
Asteraceae	Centaurea melitensis	tocalote	AF	CalEPPC-B	*	C
	Centaurea repens	Russian knapweed	AF	CA-B, AZ-Restr, UT-NW,	傘	C, A, T
	Centaurea solstitialis	vellow starthistle	AF	CalEPPC-A1, CA-C, AZ-Restr, UT-NV	V *	C, T
	Cirsium ochrocentrum	yellow-spined thistle	PH	CA-A	- 10	
	Convza bonariensis	South American conyza	AF			
	Dimorphotheca sinuata	African daisy	AF	AZ-Regul	*	
	Grindelia squarrosa var. serrulata	curly cup gumweed	BH	5	*	Т
	Heterotheca psammophila	camphor weed	AF		*	
	Lactuca serriola	prickly lettuce	AF		*	
	Sonchus arvensis	perennial sow thistle	PH	CA-A, AZ-Prohib, NV-NW	*	C
	Sonchus asper ssp. asper	prickly sow thistle	AF			1.000
	Sonchus oleraceus	sow thistle	AF		*	
	Taraxacum officinale	common dandelion	AF			
	Tragopogon dubius	goat's beard	AF		*	
Brassicaceae	Brassica juncea	Indian mustard	AF		\$	
	Brassica tournefortii	mustard	AF	CalEPPC-A2	***	
	Capsella bursa-pastoris	shepard's purse	AF	cultificitie	*	
	Chorispora tenella	blue mustard	AF	CA-B	*	
	Descurania sophia	tansy mustard	AF	CalEPPC-NI	nije zije zije	
	Erysimum repandum	waliflower	AF	callifern	*	
	Hirschfeldia incana	Mediterranean mustard	BH	CalEPPC-NI	***	
	Lepidium perfoliatum	shield cress	BH	callarent		
	Lobularia maritima	sweet alyssum	PH		柴	
	Malcolmia africana	African mustard	AF		*	
	Sisymbrium alitissimum	tumble mustard	AF		***	
	Sisymbrium irio	london rocket	AF		alle alle alle	
	Sisymbrium orientale	Oriental mustard	AF		0.00.0000	
	Thlaspe arevense	fan weed	AF		*	
Chenopodiaceae	Atriplex semibaccata	Australian saltbush	PW	CalEPPC-A2	*	
enenopoulaceae			AF		***	Т
	Bassia hyssopifolia	bassia	AF	CalEPPC-B	de de de	1

Table 1, continued

	Character France Revenue	louble months	AF		*	
	Chenopodium album Chenopodium murale	lamb's quarters	AF		*	
	Corispermum hyssopifolium	Corispermum	AF		*	
	Cycloloma atriplicifolium	winged pigweed	AF		* *	(Tr)
	Halogeton glomeratus Kochia scoparia	halogeton Kochia	AF AF	CalEPPC-RA, CA-A, AZ-Restr	*	Т
	Salsola paulsenii	barbwire Russian thistle	AF			
	Salsola tragus	Russian thistle	AF	CalEPPC-NI, CA-C	***	C
Convolvulaceae		bindweed Bussien alive	PH PW	CA-C, AZ-Regul, UT-NW,	市 水	С, Т
Elaeagnaceae Euphorbiaceae	Elaeagnus angustifolius Chamaesyce maculata	Russian olive spotted spurge	AF		15. 1	
Fabaceae	Alhagi pseudalhagai	camel thorn	PW	CalEPPC-RA, CA-A, AZ-Restr, NV-NW	*	
	Medicago lupulina	black medick	AF			
	Medicago sativa	alfalfa	PH			
	Melilotus alba Melilotus indica	white sweetclover sourclover	AF AF			
	Melilotus officinalis	yellow sweetclover	BH			
	Parkinsonia aculeata	Mexican palo verde	PW		*	
Gerenaceae	Trifolium repens	white clover	PH AF		****	С
Lamiaceae	Erodium cicutarium Marrubium vulgare	red-stemmed filaree horehound	PH		**	C
Liliaceae	Asparagus officinalis ssp.officinalis	garden asparagus	PH			
Malvaceae	Malva neglecta	common mallow	AF		*	
Molluginaceae	Malva parviflora Mollugo cerviana	cheeseweed carpet-weed	AF AF		來 水	
Myrtaceae	Eucalyptus spp.	gum tree	PW		*	
Moraceae	Ficus earica	edible fig	PH	CA-B	*	
Plantaginaceae	Plantago lanceolata	English plantain	PH		22	
Poaceae	Plantago major Agrostis stolonifera	common plantain creeping bent grass	PH PG		*	
roaccae	Agrostis viridis	water bent grass	PG			
	Arundo donax	giant reed	PG	CalEPPC-A1	*	C, F
	Avena barbata	slender wild oat	AG	CalEPPC-AG	*	
	Avena fatua Avena sativa	wild oat	AG	CalEPPC-AG	*	
	Bromus catharticus	cultivated oat rescue grass	AG AG	91.	*	
	Bromus diandrus	ripgut brome	AG	CalEPPC-AG	34.34	C, F
	Bromus inermis	smooth brome	AG		*	F
	Bromus madritensis ssp. madritensis Bromus madritensis ssp. rubens	foxtail chess red brome	AG AG	CalEPPC-A2	新建市港	C, F
	Bromus tectorum	cheatgrass	AG	CalEPPC-A1	***	C.F
	Bromus trinii	chilean chess	AG	Callarierin	**	F
	Chloris virgata	fingergrass	AG		*	22
	Cynodon dactylon Digitataria sanguinalis	Bermuda grass crab grass	AG AG	UT-NW	**	С
	Echinochola crus-galli	barnyard grass	AG		*	
	Hordeum marinum	Mediterranean barley	AG		**	С
	Hordeum murinum ssp. glaucum	blue-gray barley	AG			
	Hordeum murinum ssp. leporinum Lolium multiflorum	barley perennial ryegrass	AG AG	CalEPPC-AG	34	
	Pennisetum glaucum	pearl barley	AG	callifend		
	Pennisetum setaceum	fountain grass	PG	CalEPPC-A1	*	
	Phalaris canariensis	canary grass	AG			
	Poa annua Poa compressa	annual bluegrass Canadian bluegrass	AG PG			
	Polypogon interruptus	ditch beard grass	PG			
	Polypogon monspeliensis	rabbitfoot grass	AG		**	
	Schismus arabicus	Mediterranean grass	AG	CalEPPC-AG	****	C,F
	Schismus barbatus Sorghum halepense	Mediterranean grass Johnsongrass	AG PG	CalEPPC-AG NV-NW	*	C, F
	Vulpia myuros	zorro fescue	AG	********	*	
Polygonaceae	Polygonum argyrocoleon	silver-sheathed knotweed	AF		1212	
Portulaceae	Rumex crispus Portulaca oleracea	curley dock	PH AF	AZ Bagul	**	
Primulaceae	Anagallis arvensis	common purslane scarlet pimpernel	AF	AZ-Regul	75	
Ranunculaceae	Ranunculus testiculatus	buttercup	AF		*	т
Rosaceae	Rubus discolor	Himalayan blackberry	PW			
Simaroubaceae Scrophulariacea	Ailanthus altissima	tree of heaven	PW	CalEPPC-A2	*	A, C
Scrophulariacea	e Verbascum thapsus Veronica anagallis-aquatica	wooly mullein water speedwell	BH PH	CalEPPC-B		
Solanaceae	Nicotiana glauca	tree tobacco	PW	CalEPPC-NI	*	
	Physalis lancifolia	lanceleaf ground-cherry	AF			
	Solanum elaeagnifolium Solanum nigrum	white horse-nettle	PH PH		*	
	Solanum rostratum	black nightshade buffalo berry	AF		81. 	
	Solanum sarrachoides	hairy nightshade	AF			
T	Solanum trifolium	cutleaf nightshade	AF	o imposibili	*	
Tamariaceae	Tamarix aphylla Tamarix ramosissima	athel	PW	CalEPPC-NI CalEPPC A1 NW NW	****	ACE
Ulmaceae	Ulmus minor	saltcedar English elm	PW PW	CalEPPC-A1, NV-NW	de la construction.	A, C, F
Zygophyllaceae	Kallstroemia grandiflora	Arizona caltrop	AF		*	
	Kallstroemia parviflora	few-flowered caltrop	AF		*	
	Tribulus terrestris	puncturevine	AF	CA-C, AZ-Regul, NV	*	Т

cicutarium. These species invaded this region during the late 1880s and early 1900s or earlier, and became widespread or locally dominant after the 1950s (Parish, 1913, 1920; Jackson, 1985; Heady, 1988; Brooks, 2000a,b; Brooks and Esque, 2000; Minnich and Sanders, 2000).

Bromus rubens is classified within section Genea of the genus Bromus (Pavlick, 1995), along with its close relative B. tectorum. Bromus rubens became common in most parts of the Mojave Desert by 1950 (Hunter, 1991), and dramatically increased in dominance since the 1970s (Beatley, 1966; Hunter, 1991). Bromus rubens is considered an invasive weed in its Mediterranean home range (Jackson, 1985), and is recognized as a potential wildland pest in the Mojave and Colorado deserts (California Exotic Pest Plant Council, 1999). Its dominance is positively correlated with rainfall, soil nitrogen, fire frequency, and elevation (Brooks, 1998). and negatively correlated with low winter temperatures (Hulbert, 1955). It is typically most abundant under shrubs where soil moisture and nitrogen levels are highest (Brooks, 1999b). It appears to experience high seedling mortality during years of low rainfall and can subsequently become locally rare (R. Minnich, pers. comm.), but actual mortality rates during drought have not been quantified. We hypothesized that Bromus rubens can reproduce in relatively mesic refugia at high elevations, on north-facing slopes, and along roads even during the driest years, allowing it to persist in this region (Esque et al., 2001).

Schismus spp. is comprised of two closely related species, S. arabicus and S. barbatus. It was first reported in California around 1935 (Hoover, 1936; Robbins, 1940), invaded the Mojave and Colorado deserts during the 1940s, and became abundant there by the 1950s (O. Clarke pers. comm.). Schismus spp. is not considered an invasive weed in its Middle East home range (Brooks, 2000 b), but is considered a potential wildland pest in the Mojave and Colorado deserts (California Exotic Pest Plant Council, 1999). Its abundance is negatively correlated with that of B. rubens, possibly due to competition between them (Brooks, 2000c). It benefits from increased levels of water and nitrogen, but is also well adapted for arid, low-nutrient conditions (Brooks, 1998, 2000b). It can germinate and reproduce even during very dry years (Burgess et al., 1991; Brooks, 1999b), and can proceed from germination to reproduction faster than many other desert annual plants (Szarek et al., 1982).

Erodium cicutarium is often not considered a weedy plant, perhaps because it has been naturalized in southwestern North America for so long. It has been present in this region since the 1600s, in contrast to most other alien annuals that invaded in the late 1880s and early to mid-1900s (Heady, 1988). Nevertheless, this species is widespread and appears to compete with native plants in the Mojave (Brooks, 2000c) and Sonoran (Inouye et al., 1980) deserts.

There are a number of alien species that are only locally abundant in specific habitats such as road verges, agricultural fields, livestock watering sites, off-highway vehicle staging areas, riparian corridors, sand dunes, or at high elevations. These species include the perennial *Tamarix* spp., and the annuals *Brassica tournefortii*, *B. tectorum*, *Bromus trinii*, *Centaurea melitensis*, *C. repens*, *Descurania sophia*, *Hirschfeldia incana*, *Pennisetum setaceum*, *Salsola* spp., *Sisymbrium altissimum*, and *S. irio* (Table 1). Many of these species cause significant ecological problems in other ecosystems (California Exotic Pest Plant Council, 1999), and should be high priorities for monitoring and control efforts in the Mojave and Colorado deserts.

Brassica tournefortii is one of the locally abundant species that is of particular concern for land managers because of its rapid rate of colonization and profuse production of biomass. This species first appeared in California in 1927, became dominant in coastal southern California during the 1980s, and is currently spreading north and east in the Mojave and Colorado deserts (Minnich and Sanders, 2000). It has been observed as far north as the southern Owens Valley in California and in St. George, Utah (MLB and TCE, pers. obs.). It primarily spreads along roads, especially in sandy soils, and at an eastern Mojave Desert site was observed to spread > 1.5 km away from a paved road in 6 years (K. Berry, unpubl. data).

Ecological Effects of Alien Annual Plants

Bromus tectorum can effectively compete with native species for water in the Great Basin Desert (Eissenstat and Caldwell, 1988; Melgoza et al., 1990; Melgoza and Nowak, 1991), and *B. rubens*, *Schismus* spp., and *E. cicutarium* appear to compete effectively with native annuals for soil nitrogen in the Mojave Desert (Brooks, 1998; 2000c; in press). Experimental thinning of alien annual seedlings reduced density, biomass, and species richness of native Mojave Desert annuals (Brooks, 2000c). Although the displacement of native species by alien species has not been documented, a previously common native annual grass, *Vulpia octoflora*, appeared to become uncommon during the 1940s after the invasion of the ecologically similar *Schismus* spp. (O. Clark, *pers. comm.*).

Densely packed alien annual plant seedlings and accumulated plant litter may inhibit the germination of native annual plants. After germination, alien annual plants such as E. cicutarium, Bromus spp., and Schismus spp. initiate vegetative growth earlier than most native species in the Mojave Desert (Jennings, 2001). Established annual plants seedlings can inhibit the subsequent germination of annual plants seeds (Inouye, 1980, 1991), although the specific effects of alien seedlings on germination of native seeds has not been evaluated. Plant litter created by alien annual grasses decomposes more slowly than that of native annuals because shoot fiber content is higher in alien than in native plants (DeFalco, 1995) and accumulates during successive years. Thick plant litter may impede germination of plant seeds by shading the mineral soil, reducing the amount of water that reaches the mineral soil, and suspending seeds above and out of contact with the mineral soil (Facelli and Pickett, 1991).

Alien annual grasses alter the fuel structure and fire behavior in the Mojave and Colorado deserts, making them more susceptible to frequent fires. Stems of alien annual grasses in the genera *Bromus* and *Schismus* remain rooted and upright into the summer fire season and can accumulate over successive years, whereas those of most native forbs and aliens such as *E. cicutarium* crumble soon after senescence (Brooks, 1999a). High frequency and cover of standing dead annual grass stems creates continuous fine fuel beds that facilitate the spread of fires (Duck et al., 1997; Brooks, 1999a; Esque and Schwalbe, 2002; Esque et al., in review).

FIRE

Changing fire regimes threaten tortoises worldwide. Of the 40 tortoise species listed by Swingland and Klemens (1989), 12 were listed as threatened by fire. Only one other threat, general habitat destruction, was listed for more species (23 species). Of the 12 species threatened by fire, direct effects of fire threatened 3 and indirect effects, particularly habitat loss from fire, threatened 9. For all but one species, increased rather than decreased fire frequency constituted the threat. Tortoise species may be poorly adapted to fire because most evolved in arid or semi-arid habitats (Swingland and Klemens, 1989) where fire is often historically rare. Fire management is therefore an important factor for the conservation of at least 30% of the world's tortoise species, especially those that live where rainfall is low.

The desert tortoise is one species threatened by altered fire regimes due to alien plant invasions. Although fire was not included as a threat for this species in Swingland and Klemens (1989), increased fire frequency due to annual grass invasions (*Bromus* and *Schismus* spp.) was one reason the Mojave population was listed as Threatened by the U.S. Fish and Wildlife Service (1990, 1994).

Recent Fire History

In this section we describe patterns of fire occurrence since the 1970s in the Mojave and Colorado deserts. We rely primarily on a BLM-CDD database of 2103 recorded fires that burned 73,099 ha (180,490 acres) in the California desert between 1980 and 1995 (DI-1202 fire reports). This dataset does not include desert tortoise habitat in Arizona, Nevada, and Utah. It also is an underestimate of the number of fires that occurred and the amount of area burned within the California deserts, because it does not include unreported fires or fire records for large expanses of lands managed by the National Park Service, the Department of Defense, and other local or privately owned lands. However, the BLM-CDD dataset is the largest single collection of fire records for the Mojave and Colorado deserts, and we use it this paper to evaluate the recent status and trend of fire across a large portion of desert tortoise habitat. We supplement this dataset with our personal knowledge of recent fire history in desert tortoise habitat outside of California.

The percentage of fires and total area burned in the BLM-CDD from 1980 to 1995 was much higher in the Mojave (94% and 77%) than the Colorado desert (6% and

Table 2. Fire history data from the Mojave and Colorado desert portions of the Bureau of Land Management, California Desert District (BLM-CDD), 1980-1995 (n = 2103 fires).

Region	Annual Mean	(SD)	Annual Range
Mojave Desert			
No. Fires	123	(53)	42-223
Hectares	3526	(3410)	58-12280
Hectares	/fire 42	(70)	1-292
Lightnin	g 27	(15)	7-70
Human	97	(47)	21-186
Colorado Desert			
No. Fires	5 8	(5)	2-19
Hectares	1042	(2447)	< 1-9911
Hectares	/fire 94	(149)	<1-522
Lightnin	g 2 7	(5)	1
Human	7	(2-18)	1-4
Total			
No. Fire	s 131	(56)	47-236
Hectares	4569	(4383)	181-14282
Hectares	/fire 48	(71)	2-279
Lightnin	g 28	(15)	7-72
Human	104	(50)	25-196

23%) (Table 2). This could be partly attributed to the larger size of the Mojave Desert, although much of this area is not managed by BLM and is not included in the BLM-CDD database. In contrast, the average fire size was 55% larger in the Colorado Desert, due to the higher proportion of large fires there compared to the Mojave (Fig. 1A). Lightning caused roughly 25% of all fires in both desert regions, with the remainder attributed to human activities (Table 2). Most fires occurred during the summer months of May through September, although this summer peak in fire activity was more pronounced in the Mojave than the Colorado Desert (Fig. 1B).

The annual number of fires increased significantly between 1980 and 1995 (Fig. 2A). The number of lightningcaused fires remained unchanged during this time interval (Fig. 2B), so increased fire frequency was partly due to an increased number of human-caused fires (Fig. 2C). Another possible reason for increased fire frequency between 1980 and 1995 in the California deserts is related to the period of above average rainfall that began at the end of the 1970s (Hereford and Webb, 2001). Increased rainfall likely increased fine fuel loads, especially those created by alien annual grasses, contributing to increased fire frequency.

Most fires in the Colorado Desert occurred along the northwestern ecotone with the Mojave Desert near Joshua Tree National Park and the San Gorgonio pass (Fig. 3; fire cluster 1). Fires in this area typically burn in creosote bush scrub, Joshua tree woodland, blackbrush, and piñon-juniper desert vegetation, but they also often spread up slope into chaparral and coniferous forests along the eastern slope of the San Jacinto and San Bernardino mountains.

There are a number of regional fire clusters in the Mojave Desert, mostly along the southwest and northeast ecotones with more mesic neighboring ecoregions (Fig. 3). Fire cluster 2 is in the Antelope Valley, at the ecotone with a region dominated by annual grasslands and blue oak

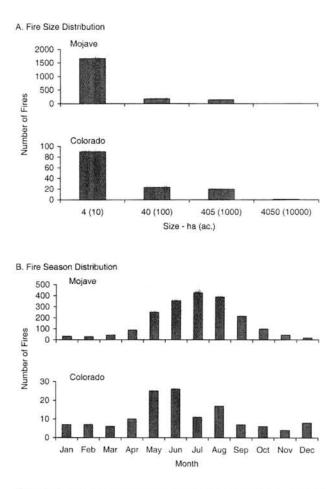


Figure 1. Frequency distributions of fires by (A) size and (B) seasonal occurrence in the Bureau of Land Management, California Desert District.

woodlands. Fire clusters 3, 4, and 5 are located within the Mojave Desert, in desert vegetation dominated by creosote bush. Fire cluster 6 is located in the Mojave National Preserve, in Joshua tree woodland, sagebrush, and piñonjuniper vegetation. Fire cluster 7 is in the Spring Mountains of Nevada, in creosote bush scrub, blackbrush, sagebrush, and piñon-juniper, and fires there often spread upslope into interior chaparral and coniferous forest. Fire cluster 8 is in the Black Mountains of Arizona, within creosote bush scrub and blackbrush vegetation. Fire cluster 9 extends from the Mormon Mountain and Tule desert region of southern Nevada to the Beaver Dam Slope of southwest Utah, and includes creosote bush scrub, Joshua tree woodland, blackbrush, piñon-juniper, and interior chaparral. Fire cluster 10 extends from the Virgin Mountains to the Grand Wash Cliffs of northwest Arizona, and includes creosote bush scrub, Joshua tree woodland, blackbrush, sagebrush, and piñon-juniper desert vegetation, with fires extending upslope into interior chaparral and coniferous forests.

Most of the smaller fires in the Mojave Desert are concentrated along major highways (Fig. 3). These small fires are mostly cause by human activity. In contrast, larger fires tend to be located in more remote wildland areas and are typically caused by lightning.

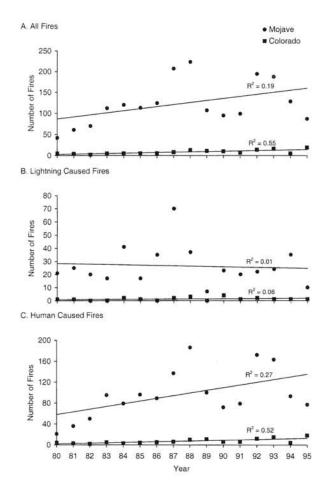


Figure 2. Change in the (A) total number of fires, (B) fires caused by humans, and (C) fires caused by lightning between 1980 and 1995 in the Bureau of Land Management, California Desert District.

Effects of Fire on the Desert Tortoise and its Habitat

Direct Effects.—Desert tortoises have been found dead or mortally injured immediately after fires (Woodbury and Hardy, 1948; Duck et al., 1997; Homer et al., 1998; Esque et al., 2002; Esque et al., in review). Fires can kill animals by incineration, elevating body temperature, poisoning by smoke, or asphyxiation (Whelan, 1995). Tortoises occupying underground cover sites such as burrows, caliche caves, rock shelters, and dens are less exposed to high temperature and smoke during fires. In general, deep cover sites provide more protection from fire than shallow ones. Because the desert tortoise cannot move quickly, its best chance to avoid the direct effects of fire is to already be in an underground cover site.

Early season fires are potentially more threatening than summer fires to the desert tortoise. During the spring, tortoises are active aboveground and therefore vulnerable to fire throughout their geographic range (Esque et al., in review). Although temperatures may be lower during early than late season fires (Brooks, 2002), they still appear to be high enough to kill tortoises located on the surface.

Years of high rainfall not only promote early season fires by stimulating growth of fire fuels, but also high rates

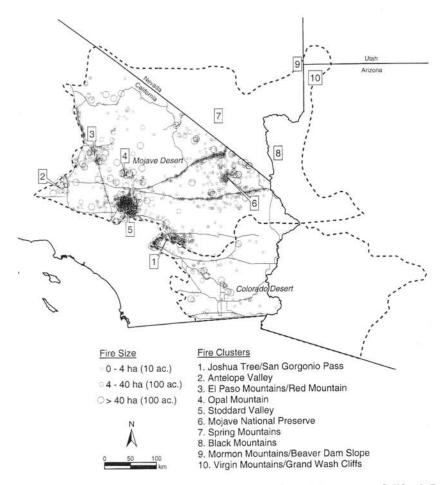


Figure 3. Spatial distributions of fires between 1980 and 1995 in the Bureau of Land Management, California Desert District, and clusters of fire activity since 1970s across the entire Mojave and Colorado deserts. Major roads are included as geographic reference points.

of desert tortoise reproduction (Turner et al., 1986). Small individuals such as hatchlings are more at risk from lethal heating than large ones, because they have a higher surface to volume ratio that allows heat to penetrate their vital organs relatively quickly. In the highly variable environment where desert tortoises live, recruitment during years of high rainfall may be very important. Unfortunately, tortoises are faced with a double-edged sword. High precipitation levels produce abundant food plants and drinking water, but also create abundant fuel loads that place tortoises at increased risk from fire.

Indirect Effects.—Fire can negatively affect desert tortoises by reducing plant cover. Perennial plants, especially woody shrubs, provide protection for desert tortoises from mortality due to predators or overheating from the sun (Woodbury and Hardy, 1948; Burge, 1978; Mushinsky and Gibson, 1991). Approximately 75% of all tortoise cover sites are located beneath shrub canopies in creosotebush/ bursage plant associations (Burge, 1977, 1978; Berry and Turner, 1986).

Reduced abundance and diversity of native annual plants caused by fire may deprive desert tortoises of important forage. Effects can include reduced availability of food plants, loss or reduction of available nutrients and trace elements, and change in seasonal availability of food plants (Nagy et al., 1998). The desert tortoise may selectively graze native forbs and herbaceous perennials, but they have also been shown to eat alien annual plants. In the western Mojave Desert native plants comprised 95% of the desert tortoise diet (Jennings, 1993), whereas in the northeastern Mojave Desert alien annual grasses comprised a significant part of their diet (Hansen et al., 1976; Esque, 1994).

Although single fires may not produce long-term reductions in the cover of perennial plants or biomass of native annual plants (O'Leary and Minnich, 1981), recurrent fire can convert native desertscrub to alien annual grassland (Brown and Minnich, 1986; Duck et al., 1997; Esque et al., in review). This new habitat is more prone to burning because alien annual grasses often increase in dominance after fire (D'Antonio and Vitousek, 1992). Alien annual grassland has little shrub cover or native annual plant biomass, and desert tortoises are very uncommon in such habitat (K. Berry and M. Brooks, *pers. obs.*). Areas of recurrent fire therefore appear to render habitat inhospitable for the desert tortoise.

FUTURE TRENDS

Rainfall patterns during the 1900s in the Mojave Desert suggest that we may be entering a 25–35 year drought period (Hereford and Webb, 2001). If this is true, then alien species that are sensitive to drought, such as *B. rubens*, may decrease in dominance at lower elevations, thereby reducing fuel loads and decreasing the frequency of fires. However, native shrub communities such as blackbrush and sagebrush, and piñon-juniper woodland, may become more prone to burning as their live fuel moisture levels decline in response to drought. Alien species that are adapted for arid conditions, such as *Schismus* spp., will likely remain abundant regardless of rainfall fluctuations.

Deposition of atmospheric nitrogen from air pollutants may reduce the spatial and temporal heterogeneity of soil nitrogen in the Mojave Desert and alter competitive hierarchies among native and alien species. Experimental addition of nitrogen (3.2 g NH₄NO₃/m²/yr) significantly increased density and biomass of alien species and decreased that of native species (Brooks, 1998, in press). Species richness of aliens was unaffected, but richness of natives decreased. Nitrogen deposition rates of 4.5 g/m²/yr have been recorded in the Los Angeles basin (Bytnerowicz and Fenn, 1996), and are associated with high dominance of alien annual grasses and the loss of native shrub communities there (Allen et al., 1998). Although current deposition rates are undoubtedly much lower in the Mojave Desert, future deposition rates will likely increase as human population and air pollution levels rise.

Changes in global climate may also encourage the invasions of alien annual species in the Mojave and Colorado deserts. Atmospheric concentrations of carbon dioxide have increased more than 25% since pre-industrial times, and carbon dioxide concentrations in the atmosphere are expected to double before the end of the 21st century (Gammon et al., 1985; Houghton et al., 1990). Increases in atmospheric carbon dioxide characteristic of the past century are known to enhance production of rapidly-growing, cool season species such as alien annual grasses and forbs (Poorter et al., 1996), and make communities generally more invasible (Dukes and Mooney, 1999). An increase in alien annual grass production may contribute to increased frequency and severity of wildfires in western North America (Mayeaux et al., 1994).

Urbanization will bring more invasive alien species into the region and increase ignition sources for fires. Increased amounts of landscaping with drought tolerant alien plants that may spread into wildlands, automobile travel within the region, locally produced air pollution, and recreational use of wildland areas will all increase the threat of plant invasions and fire.

MANAGEMENT RECOMMENDATIONS

Management of alien plants and fire should be closely integrated, because alien plants can create fuel conditions that promote fire in otherwise fire resistant landscapes that predominate in the Mojave and Colorado deserts. Although *B. rubens* is currently the primary cause of fire in this region, other alien species such as *Pennisetum setaceum* and *P.* *ciliare* create even greater fire hazards in the Sonoran Desert of Arizona and northern Mexico respectively (Búrquez et al., 2002; Esque et al., 2002). It is unknown if these species can become widespread and dominant in desert tortoise habitat, but their effects in similar ecosystems elsewhere should be a cause for concern.

Dominance of alien annual plants is often highest near roads (Brooks, 1998; Kemp and Brooks, 1998), so minimizing the number of paved and dirt roads and maintaining nonroaded wilderness areas may reduce the dominance of aliens. Other disturbances such as livestock grazing (Webb and Stielstra, 1979) and off-highway vehicle use (Davidson and Fox, 1974) also promote the dominance of alien annuals, but this effect can be reduced by fenced protection from these forms of disturbance (Brooks 1995, 2000d).

Invasions of new species often occur along roads and washes in the deserts of California (Brooks, 1998, 1999b; Kemp and Brooks, 1998), so efforts to monitor the arrival of new species and eradicate them should be focused in these areas. Early detection and eradication of potentially invasive species is the most cost-effective way of managing any plant invasion (Mack et al., 2000).

The best ways to reduce fire frequency are to reduce the number of fires started by humans and minimize the increases in fuel loads caused by alien plants. Reducing the number of fires started by humans may be accomplished by education and enforcing regulations limiting human activities that cause fires such as camping, target practice with firearms, and vehicle use. Unfortunately, increasing human populations within desert tortoise habitat, especially in the western and eastern parts of its range, will make enforcement more difficult and costly. A potentially more important approach to reducing fire frequency is to minimize the biomass of the alien species that fuel desert fires, and prevent the invasion of new species that may further increase fuel loads. Currently, methods used to reduce fuel loads include prescribed fire, mechanical removal, livestock grazing, and chemical treatments (Esque and Schwalbe, 2002), but large scale use of any of these methods is not currently consistent with competing management needs in the Mojave Desert.

Desert fires should be suppressed in most cases, because disturbances caused by fires are generally greater than those caused by appropriately planned fire suppression activities (Duck et al., 1997). Most large fires and areas of recurrent fire occur within mountainous areas designated as wilderness. The lack of motorized vehicle access in these areas can hinder fire suppression efforts, and managers should consider allowing motorized access by fire crews to control fires. Wilderness areas that are dominated by *B. rubens* and those experiencing recurrent fire and typeconversions to annual grassland would be prime candidates.

In some rare cases natural or prescribed fire may be a useful management tool. For example, fire early in the season may be used to temporarily reduce the dominance of alien annuals prior to revegetation of native plants. This would only be appropriate in habitat that is already typeconverted to alien annual grassland, where native plants and animals are relatively scarce, and the chance of recurrent fire is high. The few native plants and animals that may die in this depauparate habitat are potentially worth the possibility of restoring more diverse and less flammable native desertscrub. However, if alien annual grasses are abundant in these communities, fires should not be used because of the significant chance that the native shrubland will be replaced by alien annual grassland.

Research Needs

Much additional information is needed to effectively manage alien plants in the Mojave and Colorado deserts. We provide a list of species known to occur in this region and a preliminary assessment of their potential ecological threats (Table 1). Species on this list need to be prioritized for control using a method similar to the one developed by Hiebert (1997). This method includes two major components: 1) determining the significance of impact, requiring knowledge of both current and potential ecological effects; and 2) determining the feasibility of control and management, requiring information on abundance and geographic range, ease of control, side effects of control measures, effects of land uses, and biological control agents. Such a method is currently under development for use in California, Arizona, and Nevada by the California Exotic Pest Plant Council (www.caleppc.org) and the Southwest Vegetation Management Association (www.swvma.org). Most of the information needed to rank individual alien species for control is currently unknown for the Mojave and Colorado deserts, so future alien plant research should focus on providing this information.

Very little is known about historical fire regimes or the current effects of fire in desert tortoise habitat. Conditions before, during, and after fires need to be documented to develop predictive models. The mechanisms by which fire promotes dominance by alien annual grasses also need to be understood to develop methods to minimize their postfire dominance. Research is needed to understand the effects of fire on soils, plants, and animals. The quality of fire management planning will be limited until this information becomes available.

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