# INVASIVE PLANTS AND FIRE IN THE DESERTS OF NORTH AMERICA

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## ABSTRACT

Invasive plants and fire create substantial challenges for land managers in the deserts of North America. Invasive plants can compete with native plants, alter wildlife habitat, and promote the spread of fire where it was historically infrequent. Increased fire frequency in the Mojave and Sonoran deserts has converted native shrublands to alien annual grasslands. Fire suppression and overgrazing of livestock has allowed native woody shrubs, such as mesquite (*Prosopis* spp.) and creosotebush (*Larrea tridentata*), to invade perennial grasslands in the Chihuahuan Desert, and native trees, such as juniper (*Juniperus* spp.) and pinyon (*Pinus* spp.), to invade sagebrush (*Artemisia* spp.) steppe in the Great Basin. The reintroduction of fire can be complicated by the positive effect of fire on alien invasive plants, and the subsequent effects of invasives on post-fire establishment by native species.

Invasive alien grasses especially benefit from fire, and promote recurrent fire, in many cases to the point where native species cannot persist and native plant assemblages are converted to alien-invaded annual grasslands. This vegetation type-conversion can affect wildlife ranging from herbivores to carnivores and reduce overall biodiversity. The effective management of many wildlife species can depend on the control of invasive plants and the maintenance of appropriate fire regimes.

Fire can be used to either control invasive species or to restore historical fire regimes. However, the decision to use fire as a management tool must consider the potential interrelationships between fire and invasive species. Historical fire regimes did not occur in the presence of many invasive plants that are currently widespread, and the use of fire may not be a feasible or appropriate management action if fire-tolerant invasive plants are present. The management of fire and invasive plants must be closely integrated for each to be managed effectively.

*keywords:* desert, disturbance, fire, invasive plants, land management, North America.

*Citation:* Brooks, M.L., and D.A. Pyke. 2001. Invasive plants and fire in the deserts of North America. Pages 1–14 *in* K.E.M. Galley and T.P. Wilson (eds.). Proceedings of the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, FL.

## INTRODUCTION

Invasive species rank second only to habitat destruction in causing species endangerment across the United States. About 42% of federally threatened or endangered species are listed because of threats from invasive species (The Nature Conservancy 1996, Babbitt 1998, Wilcove et al. 1998). In the Mojave Desert, the desert tortoise (*Gopherus agassizii*) is a federally threatened species due partly to the negative effects of invasive plants and fire (M.L. Brooks, unpublished data). Invasive plants negatively affect other sensitive desert species, such as the sage grouse (*Centrocercus urophasianus*; Fischer et al. 1996) and cause changes in ecosystem processes (D'Antonio and Vitousek 1992). Accordingly, the management of invasive plants is now a top priority for land managers in the deserts of North America.

The Federal Wildland Fire Management Policy defines fire as a critical natural process that should be reintroduced where it has been historically suppressed (Glickman and Babbitt 1995). This policy also recognizes that fire hazards develop as fuels accumulate over time and recommends that fire be used to prevent high fuel loads. However, it does not consider interactions involving fire and invasive species or that the reintroduction of historical fire regimes may create new and potentially unknown changes in ecosystem processes and fire hazards.

Fundamental ecosystem changes have occurred in the deserts of North America during the 1900s, resulting from separate and interactive effects of invasive species and fire, and from land use activities. Problems with invasive species and fire may get worse, since recent Census 2000 data show that increases in human populations in the desert southwest currently exceed the national average (U.S. Census Bureau 2001). In this paper, we describe the factors that promote plant invasions and alter fire regimes, discuss the ecological changes that result, review the use of fire and other methods to control invasive plants, and summarize the information needed by managers to prevent further changes and restore ecosystem integrity in areas that have been altered in North American deserts.

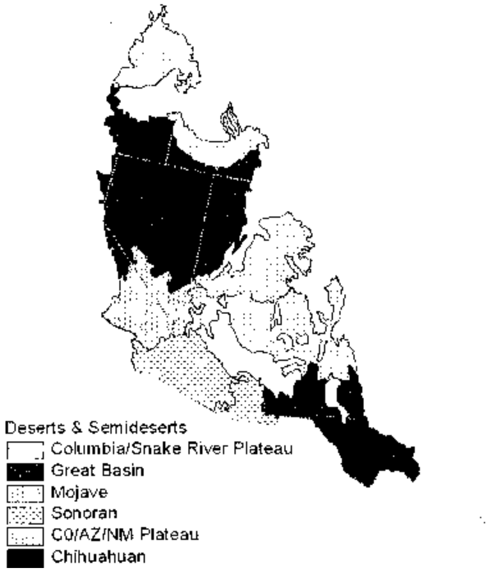

Fig. 1. Map of the western United States with an overlay of the desert and semi-desert ecological regions. (Data source: Common Ecological Regions of the Conterminous United States. A draft prepared by the National Interagency Technical Team.)

## DESERT REGIONS

The arid and semi-arid deserts of North America are generally distinguished by 2 regions: (1) the contiguous Great Basin, Mojave, and Sonoran deserts; and (2) the more disjunct Chihuahuan Desert (Figure 1). (The Arctic is sometimes considered a North American desert, but it is not included in this review.)

The Great Basin Desert is the coldest and northernmost desert in southwestern North America, constituting 32% (409,000 km$^2$) of the total North American desert area (MacMahon 1979). Typical vegetation at low elevations includes sagebrush-dominated communities, sagebrush steppe that includes codominance of perennial grasses, and salt desert shrublands dominated by saltbush (*Atriplex* spp.). At higher elevations, pinyon–juniper woodlands are composed mostly of *Pinus* spp. and *Juniperus* spp. (Fowler and Koch 1982, West and Young 2000). Precipitation occurs mostly as snow during the winter, and hard frosts limit the northern distributions of many dominant plant species common to other deserts. The Columbia and Snake River plateaus to the north and the Colorado, Arizona, and New Mexico plateaus to the southeast are floristically similar to the Great Basin, but differ hydrologically because they do not occur in closed hydrologic basins. However, issues related to fire and invasive plants are similar, and therefore the Plateau regions are included in this review.

The Mojave Desert is transitional between the Great Basin Desert to the north and the Sonoran Desert to the south and constitutes 11% (140,000 km$^2$) of the total desert area in North America (MacMahon 1979). Typical vegetation includes creosotebush scrub and saltbush scrub at low elevations, and shadscale (*Atriplex confertifolia*) scrub, blackbrush (*Coleogyne ramosissima*) scrub, Joshua tree (*Yucca brevifolia*) woodland, and pinyon–juniper woodland at progressively higher elevations. Creosotebush and burrobush (*Ambrosia dumosa*) are most common and widespread, dominating 70% of the region (Shreve 1942). Rainfall occurs mostly during winter, but summer rainfall approaches 50% of the annual total in the central and eastern Mojave (Rowlands et al. 1982). Moderate frosts limit the number of cacti species that occur here.

The Sonoran Desert constitutes 22% (275,000 km$^2$) of the total desert area, >50% of which lies in Mexico (MacMahon 1979). Two of 6 subdivisions of this desert occur in the United States (Turner and Brown 1982). The Lower Colorado River Valley subdivision includes the most xeric regions of the Sonoran Desert with creosote bush and burrobush dominating most of the region. The Arizona Upland subdivision is less xeric and includes one of the most floristically diverse areas of all the North American deserts, containing many species of cacti, subtrees, shrubs, and perennial grasses. Annual rainfall is bimodal over a spatial gradient from dominant winter rainfall at the western margin to dominant summer rainfall at the eastern margin, and frosts are infrequent (MacMahon and Wagner 1985).

The Chihuahuan Desert is the largest of the North American deserts, constituting 36% (453,000 km$^2$) of the total desert area, with >85% occurring in Mexico (MacMahon 1979). Within the United States, grasses in the genera *Hilaria, Bouteloua, Oryzopsis, Sporobolus,* and *Muhlenbergia* dominate extensive perennial grasslands, while creosotebush, tarbush (*Flourensia cernua*), and mesquite dominate microphyll brushwood (Medellín-Leal 1982). Rainfall occurs primarily during the summer. Frosts are infrequent.

## PLANT INVASIONS

### General Processes

A successful species invasion comprises 3 phases: introduction, colonization, and naturalization (Groves 1986). Humans are a primary vector for long-distance dispersal and thus are largely responsible for initial introductions. Individual plants typically succumb to the vagaries of the environment as they arrive at a new site and nascent populations often die within a few generations, thus never successfully naturalizing and producing self-perpetuating populations (Mack 1995). However, the constant flood of new propagules into desert regions, especially near urbanized areas, increases the probability that new populations will establish. These populations often remain restricted to urban areas, but some spread outward into wildlands and cause ecological problems. One of the biggest challenges for land managers is to identify these problematic species and control them before they establish and spread in wildland areas.

The spread of invasive plants into wildlands may be facilitated if open ecological niches exist for invaders to establish (compare Elton 1958, Simberloff 1995). Some scientists believe that maintenance of high species diversity is sufficient for restricting invasion success (Tilman 1997). However, in a case from the Mojave Desert, native species richness was not significantly correlated with species richness or biomass of invasive annual plants (Brooks 1998). Others have proposed models for weed management that rely on optimizing the range of structural, functional, and life history types within plant communities to minimize the number of open niches (Sheley et al. 1996, Maxwell and Sheley 1997). Major disturbances such as fire can reduce community complexity and may provide opportunities for new plant species to invade. Restricting human impacts and maintaining a wide range of species within the community may not be sufficient to block invasions into isolated, undisturbed environments, but it may be enough to hinder the spread and rise to dominance of some species (Svejcar and Tausch 1991, Kindschy 1994).

Nitrogen and phosphorous are generally the most important nutrients limiting the productivity of plant communities, second only to water in areas with limited rainfall (Tilman 1982, 1989, McLendon and Redente 1994). Annual plants often respond more rapidly than perennial plants to increased levels of nutrients, and native plants that grow well on infertile soils generally have lower maximal growth rates and respond less to increased nutrient levels than generalist weedy species or those that thrive on fertile soils (Grime 1977, Chapin et al. 1986). In particular, invasive annual grasses respond positively to increased levels of nitrogen and phosphorus, especially in low-nutrient ecosystems (Gutiérrez et al. 1988, Hobbs et al. 1988, Huenneke et al. 1990, Gutiérrez et al. 1992, Brooks 1998, Young et al. 1999).

The relative importance of nitrogen and phosphorus varies depending on concentrations of soil carbonates (e.g., $CaCO_3$) that are often common in desert soils (Cooke et al. 1993). Where soil carbonates are high, they bind to and reduce the availability of phosphorus (Lajtha and Schlesinger 1988), thereby making phosphorus the primary limiting mineral nutrient for plant growth. Where carbonates are low, available phosphorus is higher and available nitrogen can become the primary limiting nutrient.

New populations of invasive species often remain undetected or spread very slowly during an initial lag phase. They often establish where soil nutrient and moisture levels are relatively high in washes, roadsides, the areas beneath shrub canopies, and where the desert borders more mesic ecosystems (Brooks 1999*a*, Brooks and Berry 1999). Species may be restricted to these sites until they reach a critical mass that can take advantage of years of high rainfall which create more mesic conditions across desert landscapes. This invasion sequence was observed for Sahara mustard (*Brassica tournefortii*) during the 1960s to 1970s in the Sonoran desert (Sanders and Minnich 2000) and the 1980s to 1990s in the Mojave Desert (M.L. Brooks, personal observation). Similar sequences have been noted in other North American desert regions (Mack 1981, 1986).

The evolutionary histories of invasive species influence their ability to establish in desert regions. Species that evolved in arid regions may be predisposed to successful establishment in the deserts of North America, whereas species that evolved in more mesic regions may be more constrained by low levels of soil moisture and mineral nutrients. For example, Mediterranean grass (*Schismus* spp.) evolved in the most arid regions of the Middle East and has established in the most arid regions and microhabitats of the North American deserts (Brooks 2000*a*). In contrast, red brome (*Bromus madritensis* ssp. *rubens*) evolved in mesic to semi-arid regions of the Mediterranean and its dominance is limited by available soil moisture and mineral nutrients in arid regions and microhabitats in the North American deserts (Brooks 2000*b*).

Periods of high rainfall provide opportunities for mesic-adapted invasive plants to invade. Hunter (1991) documented an increase in red brome density following a series of wet years beginning in 1976 at a site bordering the Mojave Desert and the Great Basin; this species has remained dominant at that site ever since. Biomass of invasive annual grasses can be positively correlated with years of high rainfall (Rogers and Vint 1987) and regions of high rainfall (M.L. Brooks, unpublished data).

Recent evidence suggests that the next 25–35 years may bring below-average rainfall to the southern deserts of North America (Dettinger et al. 2001). If rainfall decreases, then many invasive plant species will likely decline in dominance, especially those that evolved in mesic regions. Some of these species may become locally extirpated from arid low elevation sites, but they will likely persist in more mesic refugia at higher elevations and near urbanized areas. However, the drought stress experienced by native plant communities may reduce their biomass and species diversity, potentially making them more susceptible to plant invasions when the climate shifts back to normal or above-average rainfall.

Atmospheric levels of carbon dioxide ($CO_2$) are expected to double before the end of the 21st century (Houghton et al. 1990), which may increase the dominance of invasive grasses (Smith et al. 1987, Poorter et al. 1996) and increase fire frequency and severity across western North America (Mayeaux et al. 1994). In addition, atmospheric nitrogen deposition from air pollutants will likely increase as human populations continue to grow in desert regions, possibly increasing the amount and spatial homogeneity of soil nitrogen and the dominance of invasive species.

Yields of invasive grasses increased in response to experimental additions of nitrogen in the Columbia Plateau and Great Basin (Wilson et al. 1966, Young et al. 1999), and addition of nitrogen at a rate of 3.2 g $NH_4NO_3/m^2/yr$ significantly increased density and biomass of invasives and decreased that of native annuals in the Mojave Desert (Brooks 1998). Conversely, invasive annual grass productivity can be decreased by adding carbon (sugar or sawdust) to the soil which increases the mineralization of nitrogen by microbes, thereby decreasing nitrogen availability to plants (Young et al. 1999). Nitrogen deposition rates of 4.5

g/m$^2$/yr have been recorded in the Los Angeles Basin (Bytnerowicz and Fenn 1996), and were associated with high dominance of alien annual grasses and the loss of native shrub communities (Allen et al. 1998). The effects of changing carbon dioxide and nitrogen levels in the atmosphere are beyond the control of local land managers, but there are many other factors discussed below that managers can control to potentially reduce the ecological impacts of invasive plants.

## Effects of Land Use Practices

Humans have a long history of manipulating desert ecosystems in North America, and many of these activities have facilitated plant invasions. Prehistoric humans may have created vegetation clearings and water diversions for crops in the Southwest (Betancourt and Van Devender 1981, Riley 1995). During the late 1500s, the Spanish introduced nonindigenous plants and animals including livestock into the region, but grazing impacts were probably restricted to areas near towns and presidios (Bahre 1995). Europeans brought familiar plants with them to their settlements, many of which have become our most problematic invasive weeds (Mack et al. 2000). Current human activities, such as livestock grazing, water diversion, mineral and gas extraction, military training, and recreational activities are all implicated in the decline of ecological integrity in desert regions (Bogan et al. 1998, Brussard et al. 1998, Smith and Collopy 1998, Lovich and Bainbridge 1999).

Livestock grazing is the most pervasive land use throughout the arid and semiarid ecosystems of North America. With the exception of bison (*Bison bison*) that occasionally migrated into northern portions of Chihuahuan desert grasslands, arid and semiarid ecosystems evolved during the Holocene without the influence of sizeable herds of large grazing mammals (Mack and Thompson 1982). By the late 1800s and continuing throughout the 1900s, all desert ecosystems experienced unsustainable levels or inappropriate seasons of livestock grazing (Archer 1994, Miller et al. 1994, Bahre 1995). Overstocking and grazing during seasons of rapid growth and reproduction threatened populations of desirable forage plants (Stoddard 1946), which, when coupled with drought, can reduce plant growth and competitive ability (Caldwell et al. 1981, Busso et al. 1989). Currently, many areas grazed by livestock have higher densities of invasive annual plants than ungrazed areas (Webb and Stielstra 1979, Brooks 1995, 1999*a*, 2000*c*). Areas of intensive grazing near watering tanks can also support large populations of invasive annuals (Andrew 1988, M.L. Brooks, unpublished data).

Desert soil surfaces are often populated by biological crusts, which consist of non-vascular plants and microbes including lichens, mosses, and cyanobacteria. These organisms play a major role in soil stabilization of interspaces between vascular plants, and invasive plants generally do not become established where crusts are abundant (Harper and Marble 1988, Kaltenecker et al. 1999). Many soil crust species are reduced by repeated disturbances from hoofs, human feet, and vehicles (Belnap 1995). Fire decreases the number of soil algae by 1 order of magnitude, although species composition may not change during the first 2 years post-fire (Johansen et al. 1993). After disturbances, soil particles are more likely to dislodge and erode via wind (Williams et al. 1995, Belnap and Gillette 1997, 1998) or water (Harper and Marble 1988). Recovery time depends on the ecosystem, species composition, and soil type, but can range from 14 to 250 years (Belnap and Eldridge 2000).

Besides livestock grazing, several other land uses disturb soils and potentially increase ecosystem vulnerability to plant invasions. Military training facilities are scattered throughout the region (U.S. Department of the Interior 1996, Lovich 1998). Vehicle maneuvers, campsites, and live-ammunition training disturb and compact soils while also burning and uprooting plants. These disturbances lead to recovery times that range from tens to hundreds of years (Lovich 1998, Lovich and Bainbridge 1999) and may influence not only plants, but also associated foodwebs (U.S. Department of the Interior 1996).

Recreational vehicle use (off-highway vehicle or OHV) has increased throughout the region and causes similar impacts as military training activities. Vegetation cover can be reduced by OHV activity on most soils, except barren sands and dry salt or clay flats where vegetation cover was initially low (Vollmer et al. 1976, Webb and Wilshire 1983). Invasive annuals can be more abundant in areas of high compared with low OHV use (Davidson and Fox 1974, Brooks 1995, 1999*a*, 2000*c*), and fire frequency can be high in areas of high OHV use (M.L. Brooks, personal observation).

Mineral and energy exploitation—ranging from historical placer mining along rivers to subsurface and surface mining to fossil fuel extraction—is common in some desert regions. Each type of extraction has different regulations relating to the restoration of the environment, but all extractions result in severe disturbances to plants and soils (MacDonnell 1993).

Water diversions and ground water extractions for irrigation and flood control have lowered water tables in many southwestern deserts (Bogan et al. 1998, Brussard et al. 1998). Lowered water tables can enhance the establishment of phreatophytic invasive species, such as saltcedar (*Tamarix* spp.), while potentially weakening the xerophytic upland plant communities. Increased urban growth in these water sensitive ecosystems will likely continue to impact plant communities as demands for water increase.

Human activities require access corridors (e.g., roads, utility right-of-ways, and irrigation channels) that also provide conduits for the spread of invasive species. Construction of these corridors reduces native plant cover (Vasek et al. 1975*a, b*, Johnson et al. 1983) and increases invasive species numbers and cover dominance (Frenkel 1970, Johnson et al. 1975, Lathrop and Archibald 1980*a, b*, Zink et al. 1995, Brooks 1998). The redirection of overland water flow along linear corridors can create localized areas where water becomes concentrated (Schlesinger et al. 1989), benefiting invasive plants (M.L. Brooks, personal observation).

Transportation routes are major vectors for long distance dispersal of invasive plants (e.g., Wilcox 1989), and during the early 1900s, railroads fostered invasions for many weedy species, such as cheatgrass and Russian thistle (*Salsola iberica*; Mack 1981, Yensen 1981). Roads continue to facilitate dispersal of invasive plant seeds (Trombulak and Frissell 2000) and can lead to locally high levels of OHV use, livestock grazing, fire, and other human-related activities that promote the dominance of invasives.

## FIRE REGIMES

### Shrublands

### *Historical Fire Regimes*

Fire was historically infrequent in most desert shrublands, especially those dominated by creosote bush and saltbush in the Mojave, Sonoran, and parts of the Great Basin deserts. These plant communities historically lacked a large grass component (Hastings and Turner 1965, Humphrey 1974, 1987), and the native annual plants that still dominate these regions (MacMahon 2000) generally do not provide fuels sufficient to carry fire (Brooks 1999*b*). Thus, bare interspaces between widely spaced shrubs and low fuel loads prevented fires from spreading far beyond points of ignition.

Some desert plant assemblages occurring at high elevations and latitudes may occasionally fuel large fires, especially in the Great Basin (Rogers and Steele 1980, Bahre and Shelton 1993). Communities dominated by sagebrush or blackbrush have relatively high shrub cover and a flammable shrub architecture that can allow fire to spread (Bowns 1973, Sapsis and Boone 1991). Pinyon–juniper woodlands can also carry large crown fires, but it can take hundreds of years for the necessary conditions to develop. In the Mojave and Sonoran deserts, these plant communities occur in relatively small relictual islands at high elevations, whereas in the Great Basin Desert they occur in more contiguous expanses covering much of the region.

In contrast to shrublands of the Mojave and Sonoran deserts where fires were extremely rare, native plant assemblages dominated by sagebrush in the Great Basin experienced historical fires every 30 to 100 years (Wright and Bailey 1982). This pattern changed during the 1800s when human-induced fire suppression and fuel reductions by livestock grazing reduced fire frequency and allowed pinyon–juniper woodlands to encroach into areas previously dominated by sagebrush (Miller et al. 1994, Miller and Rose 1999, Miller and Tausch *this volume*). As these expanding woodland plant communities matured in the absence of fire, they became susceptible to high intensity crown fires that were often followed by increased dominance of alien invasive plants, such as cheatgrass, medusahead (*Taeniatherum caput-medusae*), starthistle (*Centaurea* spp.), and Canada thistle (*Cirsium arvense*). These invasives can hinder the reestablishment of native shrubs by competing with them for soil resources or by promoting frequent fires that native shrub species cannot survive. Thus, fire may be an important natural ecosystem component in the Great Basin, but its reintroduction by land managers is complicated by the presence of invasive plants.

### *Recent Changes in Fire Regimes*

Old-world invasive grasses now dominate many shrublands in the Great Basin, Mojave, and Sonoran deserts. Such grasses include the annuals cheatgrass, red brome, Mediterranean grass, and medusahead, and the perennials bufflegrass (*Pennisetum ciliare*), fountain grass (*Pennisetum setaceum*), natal grass (*Rhynchelytrum repens*), and Lehmann lovegrass (*Eragrostis lehmanniana*). These species have increased the biomass and continuity of fine fuels, allowing fire to spread across the landscape where it was previously restricted to isolated patches (Humphrey 1974, Brooks and Esque 2000). Fire return intervals have shortened from a range of 30 to 100 years to 5 years in some areas of the Great Basin (Whisenant 1990). Changing fire regimes in the Mojave and Sonoran deserts are only beginning to appear, but similar shifts toward short return intervals are emerging in these regions as well (M.L. Brooks, unpublished data).

Invasive grasses thrive in post-fire landscapes, partly due to temporary increases in the availability of soil nutrients after desert fires (Figure 2a; Stubbs 2000, Brooks in press). The post-fire dominance of invasive grasses promotes recurrent fire that converts high diversity native shrubland to low diversity alien grassland. This grass–fire cycle is recognized in many ecosystems worldwide (D'Antonio and Vitousek 1992), and has been documented in the Great Basin since the 1930s (Pickford 1932, Piemeisel 1951, Young and Evans 1978, Whisenant 1990), but has only been reported in the Mojave and Sonoran deserts beginning in the early 1980s (M.L. Brooks, unpublished data). The recent spread of invasives and increased fire frequency in the Mojave Desert was correlated with above average rainfall and increases in the number of fires caused by humans since the late 1970s (M.L. Brooks, unpublished data).

In the desert shrublands of North America, recurrent fire and vegetation type-conversion to grassland may be accompanied by a homogenization of soil nutrients on the landscape that can complicate restoration efforts. Mojave desert landscapes homogenized by agriculture are very slow to recover, but this involves significant soil disturbances that are not typical of fires (Carpenter et al. 1986, Goldberg and Turner 1986). The use of herbicides or fire creates minimal soil disturbances, and they were used in recent studies to remove *Artemisia* spp., but had minimal effects on soil resource heterogeneity after 14 years (Burke et al. 1987) and 45 years (Schlesinger et al. 1996). Although individual fires may not have significant effects, recurrent fires may lead to resource homogenization. Preliminary data suggest that soil nutrients can become spread out across the landscape in areas that have

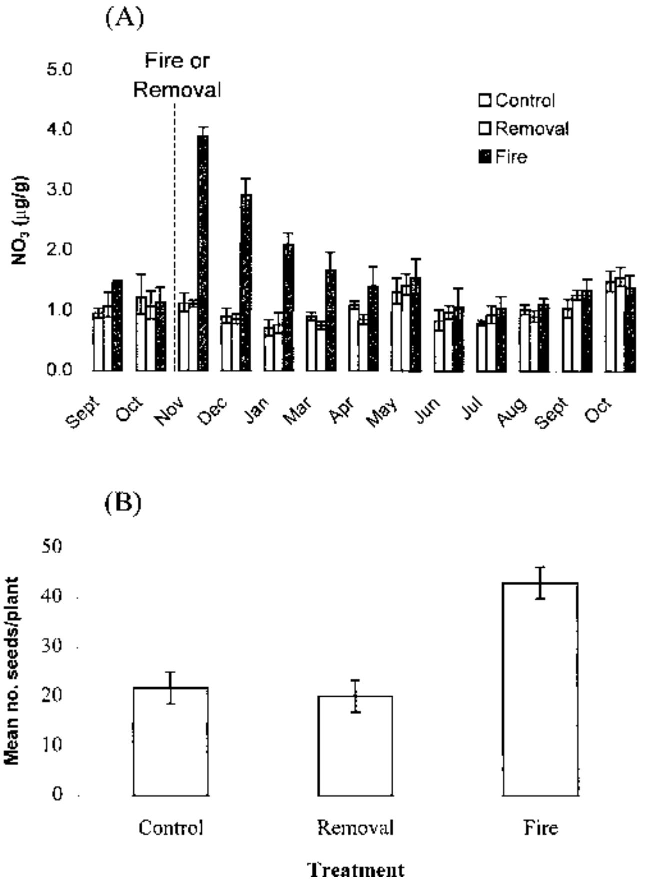

Fig. 2. (A) The median available NO$_3$ in soils (± 1 SE) from the same treatments described in the part B of this figure. (B) The mean number of medusahead seeds (± 1 SE) from plants growing where western juniper remained (control) and where cutting (removal) and burning (fire) killed the juniper in early November 1997 (from Stubbs 2000).

burned 2 or 3 times during a 15-year period in the Mojave Desert (M.L. Brooks, unpublished data). Additional research is needed to determine how widespread this process is and to develop management tools to mitigate its effects.

### Perennial Grasslands

Native perennial grasslands of the Chihuahuan and Sonoran deserts have been converted to shrublands more typical of those found in other North American deserts. These type-conversions are linked to historic overgrazing by livestock and fire suppression by humans that have reduced fine fuel loads and increased fire return intervals from historical estimates of 10 years (Humphrey 1958, 1963, 1987, McPherson 1995). In the absence of frequent fire, and due partly to the dissemination of seeds by livestock, fire-sensitive shrub species, such as mesquite and creosotebush, have invaded from their adjacent native ranges. The mechanism promoting this type-conversion may be partly related to the spatial redistribution and altered availability of soil nutrients. Conversion of grassland to shrubland is associated with a shift from homogeneous to heterogeneous distributions of soil nutrients concentrated beneath shrubs, and a decrease in the relative amounts that are available for plant growth (Schlesinger et al. 1990). Reduced fire frequency, concentration of nutrients under shrubs, and decreased availability of nutrients favor shrubs over perennial grasses.

The heterogenization of soil nutrients that occurs during the conversion of perennial grasslands to shrublands, and the possible homogenization of nutrients in the conversion of shrubland to invasive annual grasslands, may involve the same process operating in opposite directions. The ecological effects of these changes on patch and landscape dynamics, and the tools to mitigate these effects, may be similarly related. Future research should investigate the bidirectionality of this process in contrasting desert systems.

## EFFECTS OF PLANT INVASIONS AND CHANGING FIRE REGIMES

### Direct Effects

Invasive plants can out-compete native annual (Inouye et al. 1980, Pake 1993, Brooks 2000*d*) and perennial plants (Young et al. 1976, Eissenstat and Caldwell 1988, Melgoza and Nowak 1991). For example, red brome can deplete soil water faster and at greater soil depths than native annual species (L. DeFalco, U.S. Geological Survey, unpublished data), and along with cheatgrass effectively compete with native species for water (Eissenstat and Caldwell 1988, Melgoza and Nowak 1991). Red brome, Mediterranean grass, and red-stemmed filaree (*Erodium cicutarium*) can utilize increased levels of soil nitrogen faster than native species and thus reduce the growth rate of natives, possibly due to their increased consumption of soil water (Brooks 1998). These 3 species can significantly reduce native seedling biomass and species richness (Brooks 2000*d*). Although cases of invasive plants displacing natives have not been documented, the native annual grass six-week fescue (*Vulpia octoflora*) became uncommon after the invasion of an ecologically similar invasive annual grass (Mediterranean grass) in coastal and desert regions of southern California during the 1940s (O. Clarke, University of California-Riverside [retired], personal observation).

Densely packed stands of invasive annual plants may reduce the germination rates of native annuals. High densities of native annual plant seedlings can inhibit the germination rate of seeds remaining in the soil (Inouye 1980, 1991), and it seems plausible that high densities of invasive annual plant seedlings should have similar effects. Plant litter created by invasive grasses may also impede germination of native annuals 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).

Perennial grasses and annuals typically survive fire because their perennating buds or seeds are at or below the soil surface (Whelan 1995). In contrast, woody shrubs and cacti are often killed by fire (Wright

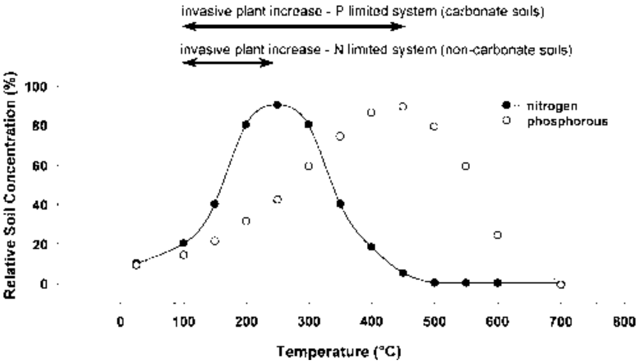

Fig. 3. Theoretical effects of soil heating during fires on the availability (%) of nitrogen and phosphorus and the resulting effects on the growth rate and yield of invasive plants.

and Bailey 1982), and those that are only damaged are vulnerable to recurrent fire. Resprouting plants translocate resources from roots into new shoot tissue, and when these resources are lost during a second fire, the plants appear to have little left to establish new shoot material. Fires that occur when woody shrubs are actively growing and have limited carbohydrate reserves in their root tissue may have similar effects as recurrent fire. Herbivory of resprouting tissue may have similar effects as recurrent fire, but they may not become apparent until 5 to 10 years post-fire when burnt plants finally die (M.L. Brooks, personal observation).

Fire can either increase or decrease soil nutrient availability, which should affect the relative productivity of invasive annual grasses in ecosystems with naturally low soil nutrient levels (Figure 3). Invasive grasses respond positively to increased levels of nitrogen and phosphorous in desert regions (Wilson et al. 1966, DeLucia et al. 1989, Brooks 1998). There are theoretical temperature thresholds above which these mineral nutrients should become less abundant, and below which soil nutrients should be unaffected (Figure 3). Between these temperature thresholds, there exist theoretical zones within which the availability of soil nutrients and the productivity of invasive plants should increase. As simple as this may seem, temperature thresholds of nutrient transformations can vary widely. Soil properties (e.g., texture, chemistry, moisture) and the amount and duration of soil heating strongly influence nutrient availability, but how these factors interact to affect soil nutrients and the subsequent productivity of invasive annual grasses is unknown. Current studies are underway to determine these relationships.

## Higher-Order Effects

The impacts of fire and invasive plants do not stop at the boundaries of the plant kingdom, but have repercussions on higher-order organisms in foodwebs. A classic example exists at the Snake River Birds of Prey National Conservation Area (NCA) south of Boise, Idaho. The NCA is a mixture of Intermountain sagebrush steppe and salt desert shrub communities. Without cheatgrass in these communities to provide a continuous source of fuel, they would be a mixture of perennial shrubs, such as Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) or shadscale, and scattered native perennial bunchgrasses. Fires would typically burn only small stands creating mosaics of perennial grass-dominated and shrub-dominated patches across the landscape, similar to those anticipated when prescribed fires are applied to these native ecosystems (Bunting et al. 1987).

The incorporation of cheatgrass into the interspaces of plant communities at the NCA makes them vulnerable to larger, more frequent fires. Between 1980 and 1988, almost half of the 200,000 ha of the NCA were converted from shrub steppe to invasive grasslands by a series of over 200 fires (Smith and Collopy 1998). This large-scale change in the structure of the plant community caused reductions in suitable habitat and concomitant shifts in the abundance of some species of passerine birds (Knick and Rotenberry 1995).

Conversions of sagebrush steppe to invasive annual grasslands may also relate to the recent decline in sage grouse populations. Sage grouse have become restricted to a small range in the northern Intermountain West (Crawford and Lutz 1985). Sage grouse successfully nest in habitat with shrubs and tall residual grass cover ($>$20 cm), and chicks feed on native forbs (Gregg et al. 1994, DeLong et al. 1995, Sveum et al. 1998). The large-scale loss of the shrub structure following fires (Fischer et al. 1996), and the replacement of tall perennial bunchgrasses and native forbs with shorter invasive annual grasses, may lead to further declines in their populations.

Sagebrush steppe also provides important habitat for jackrabbits (*Lepus* spp.; Knick and Dyer 1997). The loss of this habitat due to fire is associated with a decline in their densities during the last 3 jackrabbit cycles between 1971 and 1992 at the NCA (USDI 1996). Jackrabbits are the primary prey of golden eagles (*Aquila chrysaetos*) during their nesting season in the Great Basin. Kochert et al. (1999) documented that radio-tagged golden eagles avoided previously burned areas and that eagle fledging success declined as the extent of burned area increased in their territory. Thus, the loss of native vegetation to recurrent fire has affected first- and second-order consumers in the Great Basin.

In the Sonoran Desert, South African lovegrasses (*Eragrostis lehmanniana* and *E. curvula*) were introduced to revegetate degraded lands and provide livestock forage (Cox et al. 1984). The invasive nature of Lehmann lovegrass has been well documented (Cox and Ruyle 1986, Anable et al. 1992), and native plant communities converted to Lehmann lovegrass experience reduced faunal diversity. At a Sonoran Desert site, Bock et al. (1986) found that conversion to Lehmann lovegrass communities reduced species numbers of birds (7 of 9 species), rodents (3 of 7 species), and grasshoppers (8 of 13 species). Only 1 species each within these 3 taxa increased due to conversion.

Lovegrasses tend to tolerate or establish and potentially increase following fires (Ruyle et al. 1988, Anable 1990, Bock and Bock 1992; see Cable 1965 for an exception) while many native plants decline with fire in the same ecosystem (Cable 1965, Martin 1983). Anable et al. (1992) speculated that the greater productivity of Lehmann lovegrass compared with the native species (Cox et al. 1990) may increase fire frequencies in Sonoran ecosystems creating positive feedbacks that will enhance its dominance in the Southwest similar to cheatgrass in the Great Basin. Bock and Bock (1990:60) believe that fires may be ''more destructive than beneficial to wildlife and wildlife habitat in (1) Sonoran and Mojave Desert scrub, (2) black grama ranges in the lower parts of the Chihuahuan shrub steppe, and (3) riparian woodlands.'' If increased fire frequencies in these desert ecosystems cause further shifts to invasive plant communities, then the abundance and diversity of wildlife species may decline.

Buffelgrass and fountain grass can also promote fires where they were historically infrequent and may threaten biodiversity in desert regions (Williams and Baruch 2000, Brooks and Esque in press). These species are currently invading the Sonoran and Mojave deserts, and the potential geographic and ecological range that they may ultimately reach is largely unknown.

The invasion of riparian areas by the invasive saltcedar has caused water tables to drop due to its very high rate of evapotranspiration (Sala et al. 1996, Lovich 2000). As water tables drop, the availability of surface water declines and native riparian plants begin to senesce. With the loss of native riparian plants and surface water, native wildlife generally decline as well (Lovich and de Gouvenain 1998), such as desert bighorn sheep that depend so critically on sources of perennial water. The accumulation of dead plant material promotes fires, from which saltcedar can recover with vigorous sprouting (Busch 1995). Although the high water and salt content of saltcedar foliage make it difficult to burn, the rapid buildup of dry plant litter in saltcedar stands promotes recurrent fire which favors saltcedar over native plants.

The desert tortoise is both directly and indirectly affected by invasive plants and the fires that they cause. Direct mortality from fire can be catastrophic for a species already in decline. Long-term habitat changes are especially threatening (M.L. Brooks, unpublished data), and desert tortoises are virtually absent from areas of recurrent fire (M.L. Brooks, personal observation). Loss of important cover sites (Woodbury and Hardy 1948, Mushinsky and Gibson 1991) and changes in species composition of their forage plants (Jennings 1993, Nagy et al. 1998) may cause more subtle, but potentially critical impacts. Increased stress imposed by invasive plants and fire may increase the susceptibility of desert tortoises to disease (K. Berry, U.S. Geological Survey, personal communication). Concern is so great that members of the multiagency Desert Tortoise Management Oversight Group ranked invasive species and fire second only to disease as major threats to the survival of this species (annual meeting, 29 March 2000). The recovery of the desert tortoise may require a rangewide effort to mitigate the effects of invasive species and fire.

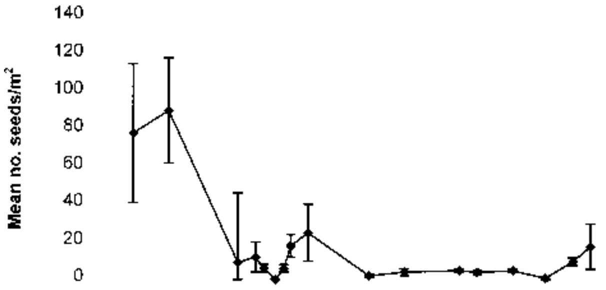

Fig. 4. The number of cheatgrass seeds (± 1 SE) in the seed bank at a site near Snowville, UT over 2 years (from Pyke 1994).

## MANAGEMENT ISSUES

### Management of Invasive Species

The interactive effects of invasive plants and fire are generally negative, but when incorporated into management plans fire and some alien plants can become positive tools. Fires control some invasive plants, while some alien plants may provide fire resistant fuel breaks that control the spread of fire. Fire is an effective tool for controlling invasive plants provided it kills all adult plants, their perennating buds, or eliminates seed banks (Whelan 1995). For example, invasive annuals with short-lived seed banks may be amenable to control using fire. One such species is cheatgrass, which has a soil seedbank that can approach zero density before seeds contained within inflorescences disperse to the ground (Figure 4; Pyke 1994). With most of the next generation's seed suspended above-ground, this alien annual is susceptible to local extirpation or significant population reductions immediately following fire.

Although fire may be used to control invasive annual grasses, its effectiveness is often partial or temporary. For example, fire was initially proposed as a method to control medusahead (Furbish 1953, Murphy and Turner 1959, Murphy and Lusk 1961), but later studies indicated that its effectiveness was incomplete (Sharp et al. 1957, Torell et al. 1961). Follow-up treatments with herbicides or propane weed flamers may be necessary to kill individuals that escape initial fire treatments (Turner et al. 1963). The Bureau of Land Management (BLM) is using this technique in north-central Oregon for medusahead control and to prepare sites for revegetation (S. Cook and D. Zalunardo, Prineville District BLM, personal communication). The BLM is also considering this technique along with grazing and herbicide applications in their restoration activities in the Great Basin (Rasmussen 1994). M.L. Brooks and T. Esque of the U.S. Geological Survey are testing the use of fire and herbicides to control red brome and buffelgrass at BLM and National Park Service units in the Mojave and Sonoran deserts.

Predicting which species may be controlled by fire requires information on a plant's (1) life history, (2) location of perennating buds relative to lethal fire temperatures, and (3) seed dispersal and longevity. Seed longevity is a particularly critical factor when evaluating fire's effectiveness in controlling annual plants. The lack of information regarding seed longevity may lead to conflicting management recommendations. One example is the literature on the ecology and management of yellow starthistle (*Centaurea solstitialis*). Yellow starthistle seed is reported to remain viable in the soil seed bank for up to 10 years (Callihan et al. 1993), suggesting that fire would be an ineffective control tool, yet prescribed fire can reduce the dominance of this invasive annual (Di'Tomaso et al. 1999). These conclusions appear contradictory. However, it is possible that yellow starthistle has evolved genetic strains that vary in seed dormancy, or that only fires with sufficient intensity and duration are capable of generating lethal temperatures within the soil seedbank. Detailed studies of regional variation in seedbank longevity and fire behavior are needed to evaluate the potential use of fire to control yellow starthistle and other invasive annual plants.

Land managers must be cautious when using fire to control invasives because it may promote the establishment of other fire-tolerant invasive species. For example, forage kochia (*Kochia prostrata*) is being promoted in the Intermountain West as a living fuel break. It tolerates fire and competes successfully with cheatgrass (Monsen 1994), indicating that this species may spread to adjacent areas where cheatgrass is being managed using fire. In another example, prescribed fire is used to remove invading junipers from sagebrush plant communities (Miller and Tausch *this volume*), but this tool may promote the dominance of invasive annual grasses. Prescribed fires during autumn to reduce western juniper in northcentral Oregon raised levels of available nitrogen for 4 months following the fire, which may explain why seeds of medusahead were 200% higher in burned than unburned sites (Figure 2b). Stubbs (2000) recommended cutting juniper on sites where medusahead is a potential invader to reduce the threat of medusahead increase.

Even the mechanical removal of invasives may create opportunities for other species to dominate. For example, when the biomass of red brome was experimentally reduced, biomass of red-stemmed filaree subsequently increased in the Mojave Desert (Brooks 2000*d*). In this case, the reduction of red brome may reduce fire hazards even if red-stemmed filaree replaces this species because the latter species creates less flammable fuel (Brooks 1999*b*). In all cases where invasive species are targeted for control, the potential for other invasive species to fill their void must be considered.

### Management of Fire

Fire resistant plants can be used as living firebreaks or greenstrips that will slow or stop wildfires from spreading (Pellant 1990, 1994). Effective plants for this type of fire management must achieve some or all of the following criteria: (1) disrupt fuel continuity, (2) reduce fuel accumulations and volatility, and (3) increase the density of plants with high moisture content. Native plants in the Great Basin, where greenstripping was developed and tested, generally do not meet the firebreak criteria. This is understandable because native species that are capable of surviving fires in this ecosystem evolved fire-tolerance rather than fire-avoidance mechanisms. Consequently, introduced species, such as crested wheatgrass (*Agropyron desertorum* or *A. cristatum*), have been used because they retain high amounts of moisture late into the season (Pellant 1994, Monsen 1994). Additionally, greenstrip species must be highly competitive with the alien annuals to disrupt fuel continuity in cheatgrass-dominated sites.

Managers in desert ecosystems are often faced with a dilemma regarding revegetation after wildfires. The emergency fire rehabilitation (EFR) program funds the revegetation of plants to protect either soils from erosion or ecosystems from weedy plant invasions (USDI–BLM 1999). The EFR policy strongly advocates seeding in a timely fashion to maximize establishment and minimize the potential for erosion or weed invasion. However, the availability of native seeds for revegetation is limited. Therefore, introduced plants are typically used in EFR seed mixtures in the Great Basin (Richards et al. 1998).

The identification and use of competitive native perennial plants for aridland rehabilitation has become a priority for managers and researchers (Pyke and Borman 1993, Monsen 1994, Shaw and Roundy 1997, USDI–BLM 1999). Early seral species, such as bottlebrush squirreltail (*Elymus elymoides*), may provide managers with native plant materials that can successfully germinate and establish in the presence of invasive annuals (Jones 1998). Restoration projects that involve mixing of native species to provide a variety of above and below ground growth forms and sowing at high densities may increase establishment of desirable plants while also providing adequate competition against invasive plants (Pyke and Archer 1991).

Reducing levels of available nitrogen immediately after fire may increase the rate of establishment by native plants and reduce the dominance of invasive annuals. Sucrose has been used experimentally to reduce nitrogen by increasing soil microbial biomass. Such treatments have reduced the growth of invasive plants while enhancing the establishment and composition of late-seral native plants in a semiarid ecosystem (McLendon and Redente 1994). More research is needed to identify cost-effective techniques for reducing available nitrogen and enhancing the success of the native plants.

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