Anthropogenic Degradation of the Southern California Desert Ecosystem and Prospects for Natural Recovery and Restoration

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ABSTRACT / Large areas of the southern California desert ecosystem have been negatively affected by off-highway vehicle use, overgrazing by domestic livestock, agriculture, urbanization, construction of roads and utility corridors, air pollution, military training exercises, and other activities. Secondary contributions to degradation include the proliferation of exotic plant species and a higher frequency of an-

thropogenic fire. Effects of these impacts include alteration or destruction of macro- and micro-vegetation elements, establishment of annual plant communities dominated by exotic species, destruction of soil stabilizers, soil compaction, and increased erosion. Published estimates of recovery time are based on return to predisturbance levels of biomass, cover, density, community structure, or soil characteristics. Natural recovery rates depend on the nature and severity of the impact but are generally very slow. Recovery to predisturbance plant cover and biomass may take 50-300 years, while complete ecosystem recovery may require over 3000 years. Restorative intervention can be used to enhance the success and rate of recovery, but the costs are high and the probability for long-term success is low to moderate. Given the sensitivity of desert habitats to disturbance and the slow rate of natural recovery, the best management option is to limit the extent and intensity of impacts as much as possible.

We've mined it, dammed it, irrigated it, developed it, and subjected it to nuclear assault, yet the desert, somehow both fragile and tough, manages to endure, a rugged old touchstone for us to measure ourselves against.

Malcolm Jones, Jr., 1996

The landscape and native vegetation of the southern California deserts have been significantly altered during the last century by a variety of factors including: livestock grazing (Bentley 1898, Humphrey 1958), introduction of exotic species (Mooney and others 1986, Rejmánek and Randall 1994), off-road vehicle use (see reviews in Webb and Wilshire 1983), urbanization and its attendant effects (Reible and others 1982, Walsh and Hoffer 1991), and military activities (Lathrop 1983a, Prose and others 1987). Extreme temperatures, intense sun, high winds, limited moisture and the low fertility of desert soils make natural recovery of the desert very slow after disturbance (Bainbridge and Virginia 1990). Conditions suitable for plant establishment occur only infrequently and irregularly, and it may take hundreds of years for full recovery to take place without active

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intervention. Many of the actions of desert development and utilization have profound effects on ecosystem stability, diversity, and productivity (Rundel and Gibson 1996).

The literature on human impacts to the biotic and physical components of the Mojave Desert is large and diffuse. In this paper we review the major human-induced impacts on the California desert, and the prospects for natural recovery and restoration, by characterizing the effects of past actions on the Mojave Desert ecosystem and other arid lands. In addition, we briefly suggest practical strategies and methods for planning and implementing desert restoration projects and improving recovery of these areas by soil management, transplanting, direct seeding, and other techniques.

Area of Study

Our review focuses on the Mojave and Colorado Deserts of southern California, an area of approximately 10 million ha. The Mojave Desert occupies portions of Inyo, Kern, Los Angeles, Riverside, and San Bernardino counties in California. The geographical and ecological boundaries of the Mojave Desert are discussed in detail by Vasek and Barbour (1977) and Hickman (1993). The modern plant community of the Mojave has been characterized as "desert scrub" (Turner 1982, Hickman 1993), even though it is composed of several recognizable community types including: creosote bush scrub, saltbush scrub, shadscale scrub, blackbush scrub, and Joshua tree woodland (Vasek and Barbour 1977). Perennial plant diversity is low compared to the Colorado Desert: areas dominated by Larrea tridentata and Ambrosia dumosa occupy about 70% of the Mojave (Lathrop and Rowlands 1983). More than 250 species of annual plants are found in the Mojave, including 80-90 species that are endemic (Turner 1982). In Death Valley and the Salton Sink, annuals account for 42% and 47% of the local flora, respectively (Johnson and others 1978). Overall plant diversity is low below 1000 m, but increases to levels approaching more temperate habitats at higher elevations (Cody 1986).

The Colorado Desert is that part of the Sonoran Desert found mostly in Imperial and Riverside counties, California (Burk 1977). The Colorado Desert is generally separated from the Mojave Desert to the north by the Little San Bernardino, Cottonwood, and Eagle Mountains. The boundary between the two desert ecosystems is poorly defined to the east of these mountain ranges (Vasek and Barbour 1977). A bimodal rainfall pattern composed of winter frontal systems and summer convectional storms distinguishes the Colorado Desert from the western Mojave Desert (Burk 1977), where most precipitation comes from winter rains. In addition, the region is generally lower, flatter, hotter in the summer and warmer in the winter, and hosts a slightly different flora than the Mojave Desert (Hickman 1993). Dominant vegetation in the Colorado Desert is "Sonoran creosote-bush scrub" (Hickman 1993). Plant communities recognized by Burk (1977) include creosote bush scrub, cactus scrub, wash woodland, palm oasis, saltbush scrub, and alkali scrub. There is broad overlap of plant species between the Mojave and Colorado Deserts, but there are a significant number of freeze-sensitive arboreal species that are found only in the Colorado Desert.

Both deserts are characterized by dominant perennial plant species that are long-lived (Bowers and others 1995), some exceptionally so (Vasek 1980). Density and cover of long-lived species increases with age of the site surface (Webb and others 1987, 1988, Bowers and others 1997).

While our focus is specifically directed to the problems of desert lands in California (most of our experience is in the Colorado Desert), we believe our review will prove useful for desert management in other parts of the Southwest, northern Mexico, and in other drylands around the world.

Factors Contributing to Habitat Degradation

The following sections summarize major anthropogenic degradation factors in the southern California desert ecosystem other than agricultural development and urbanization. An understanding of the nature and the effect of disturbances is useful in estimating recovery times or determining what course of action may be required to restore a habitat. Table 1 summarizes the estimated time intervals required for affected plant communities to fully or partially recover from human-induced disturbances.

Impacts on the desert can be loosely divided into historic and current impacts. There is rarely a complete distinction between the two but, in general, the historic impacts include such things as overgrazing, aqueduct building, and the operation of the Desert Training Center in World War II. Grazing still continues, but the major impacts from grazing occurred in the mid to late 1800s. A very rough estimate of the magnitude and extent of these different activities is shown in Table 2. The following factors are not presented in order of importance.

Livestock and Grazing

Cattle and sheep have grazed almost continuously through large areas of the region from the mid-1800s to the present, although the numbers have dropped off in recent years. The establishment of ranching fostered the development of a major industry in the western United States that prospered until droughts, harsh winters, and overgrazing caused a series of dramatic herd declines in the late 1800s. Populations of sheep (60,000) and cattle (67,000) peaked in Imperial County in 1920. In 1968 there were 25,000 cattle and 138,000 sheep grazing on Bureau of Land Management (BLM) and National Monument desert lands in California, predominantly in the Mojave (Ruch 1968). In 1979, 1.8 million ha of public lands administered by the BLM in the California desert were grazed by 75,000 sheep and 14,000 cattle (Bureau of Land Management 1980). Excellent histories of grazing in the desert southwest are provided by Humphrey (1958, 1987).

No published studies have yet fully documented the impact of grazing by livestock in the California desert or estimated the time required for heavily grazed areas to recover to pregrazing levels of plant diversity, density, and cover (Oldemeyer 1994). The rarity of undisturbed reference sites and long-term studies makes it difficult to quantify the effects of grazing, but it is possible to

Table 1. Estimated natural recovery times in years for California desert plant communities subjected to various anthropogenic impacts

Impact	Location	$T_{ m recovery}$	Reference
Tank tracks (military)	eastern Mojave	65, ^a 76 ^b	Lathrop (1983a)
Tent areas (military)	eastern Mojave	45, ^a 58 ^b	Lathrop (1983a)
Dirt roadways (military)	eastern Mojave	112, ^a 212 ^b	Lathrop (1983a)
Tent sites (military)	eastern Mojave	8-112 ^c	Prose and Metzger (1985)
Tent roads (military)	eastern Mojave	$57-440^{\circ}$	Prose and Metzger (1985)
Parking lots (military)	eastern Mojave	$35-440^{\circ}$	Prose and Metzger (1985)
Main roads (military)	eastern Mojave	100–infinity ^c	Prose and Metzger (1985)
Military	eastern Mojave	1500-3000 ^d	Prose and Metzger (1985)
Townsites	northern Mojave	80-110, e $20-50$, b $1000+f$	Webb and Newman (1982)
Pipeline	southern Mojave	centuries ^g	Vasek et al. (1975a)
Powerline	southern Mojave	$33^{ m h}$	Vasek et al. (1975b)
Fire	western Colorado Desert	$5^{ m b,i}$	O'Leary and Minnich (1981)
Off-road vehicle use	western Mojave	probably centuries	Webb et al. (1983)
Pipeline (berm and trench)	Mojave Desert	100 ^j	Lathrop and Archbold (1980b)
Pipeline (road edge)	Mojave Desert	98 ^j	Lathrop and Archbold (1980b)
Powerline pylons and road edges	Mojave Desert	100 ^j	Lathrop and Archbold (1980b)
Under powerline wires	Mojave Desert	20 ^j	Lathrop and Archbold (1980b)

^aRecovery time to control density.

^jBiomass recovery assuming that successional vegetative growth is approximated by a straight line. Recovery of long-lived species is estimated to take at least three times longer than indicated.

Table 2. Adverse impacts on California desert, their relative intensity and historical occurrence

Intensity	Current/historic
moderate	primarily historic
moderate	historic
moderate/severe	historic/current
severe	current
severe	current
severe	current
severe	both
severe	both
locally severe	both
locally severe	current
	moderate moderate/severe severe severe severe severe severe severe locally severe

describe the nature of these impacts and their probable extent. Consequently, conclusions about the effects of grazing on arid ecosystems have been contradictory and controversial (Anonymous 1991, Borman and Johnson 1990, Coe 1990, Field 1990, General Accounting Office 1992, Gillis 1991, Poling 1991). Some argue that grazing is beneficial to rangelands, suggesting that the act of grazing stimulates new plant growth (Savory 1988).

Other putative positive benefits include the dispersal of seeds, production of fertilizer in the form of excrement, and churning of soil generated by moving hooves (but see Balph and Malecheck 1985). Others point to negative impacts of grazing including: soil compaction and increased erosion, trampling of plants, and overcropping. Grazing effects on arid ecosystems are reviewed in detail by Archer and Smeins (1991).

The effects of overgrazing are far less controversial. As early as the late 1800s there was recognition of dramatic range deterioration in the United States as a result of overstocking of cattle (Bentley 1898). In his report, Bentley concluded that "The ranges have been almost ruined, and if not renewed will soon be past all hope of permanent improvement." In spite of early recognition of a problem, solutions have still not been satisfactorily implemented (General Accounting Office 1992).

The impacts of grazing, whether positive or negative, may be extensive. In a recent biological assessment in the western Mojave Desert of California, 100% of a 234-square-km area was impacted to some extent by

^bRecovery time to control cover.

^cEstimated recovery time for Larrea tridentata to reach control densities.

dEstimated recovery time ("if at all") for recovery to original vegetative structure assuming establishment of control densities.

^eCompaction recovery time.

^fTotal estimated recovery time.

g30-40 years assuming linear rates of succession; 3000 years until formation of large creosote clonal rings.

hIncomplete recovery time in areas of high impact.

Time for appearance of perennial seedlings. See Brown and Minnich (1986) in section on fire.

sheep grazing (Tierra Madre Consultants 1991). In a detailed analysis of the effects of sheep grazing on 2.6 square km of desert tortoise habitat, Nicholson and Humphreys (1981) observed soil disturbances in 80% of the area used by sheep. Thirty-three percent of the plot was heavily used by sheep.

Livestock grazing, by its very nature, causes a decrease in plant cover and biomass, at least initially. Decreases in cover have been shown to be associated with a decrease in the diversity and abundance of lizards and other wildlife species in arid ecosystems (Busack and Bury 1974, Germano and Hungerford 1981, Germano and others 1983, Germano and Lawhead 1986). In the Mojave Desert Nicholson and Humphreys (1981) observed large decreases in plant cover in areas grazed by sheep. Similar results were reported by Webb and Stielstra (1979) in the Mojave. In addition, they observed a 60% reduction in above-ground biomass on plots grazed by sheep. Other studies, in American deserts outside of the Mojave Desert, have not detected appreciable differences between grazed and ungrazed plots (Heske and Campbell 1991, Rice and Westoby 1978), but most sites had been grazed before the studies were initiated. An important point to make is that the response of plants to grazing varies according to species, season, plant phenology (Genin and Badan-Dangon 1991), local conditions (drought, edaphic factors, etc.), and past historical use.

Direct effects of grazing on desert animals such as the desert tortoise (*Gopherus agassizii*) are not well documented. Grazing sheep can damage tortoise burrows. Nicholson and Humphreys (1981) reported that of 164 tortoise burrows on a 2.6-square-km study site, 10% were damaged and 4% were destroyed. Most burrows were well protected since they were generally located under shrub cover. Damage was considered to be insignificant since tortoises were often observed digging new burrows in late spring regardless of the availability of existing burrows. Others have gone so far as to suggest that cattle dung actually serves as an important food supply for desert tortoises (Bostick 1990), although this has never been rigorously substantiated (Hal Avery personal communication).

Webb and Stielstra (1979) observed that soils in the Mojave Desert exhibited greater surface strength in areas where sheep bedded and grazed relative to control areas. The greatest compaction occurred in the upper 10 cm but compaction was also observed at lower depths. At the surface, soils are trampled by grazing, often obliterating cryptobiotic soil crusts leading to increased erosional potential. Erosion is of special concern for desert soils because the nutrient capital is often concentrated in the surface soil. Gross disorgani-

zation of community structure is possible with the loss of only a few centimeters of soil (Charley and Cowling 1968).

Even limited grazing can cause significant shifts in vegetation and damage to soil crusts. Kleiner and Harper (1977) found that seven plant species that were common in the ungrazed area were absent or insignificant in a comparable grazed section of Canyonlands National Park. They attributed this in part to changes in cryptobiotic soil crust, which decreased from 38% cover in the ungrazed area to 5% in the lightly grazed area. Grazing also increases the spatial and temporal heterogeneity of water, nitrogen, and other soil resources, fostering increased desertification of productive arid lands (Schlesinger and others 1990).

As stated above, the rate of natural recovery of habitats exposed to grazing depends on the intensity of past grazing and local conditions. In a blackbrush (Coleogyne ramosissima) association in Utah and Arizona, shrub cover is greater in areas that have never been grazed than in grazed areas. In the same area, plots protected from grazing for ten years showed no difference from heavily grazed areas indicating slow rates of recovery (Jeffries and Klopatek 1987). Exclusion of grazing for 14-19 years did not allow recovery of native perennial grasses in southeastern Arizona (Roundy and Jordan 1988). In the deserts of Kuwait land degradation does not necessarily stop following protection from grazing (Omar 1991). Drought, erosion, and sand encroachment continue to degrade land in the absence of grazing. Human activities and grazing may hasten degradation, but in concert with drought the three can be devastating.

In a recent review of the effects of grazing on public land in the hot deserts (Chihuahuan, Mojave, and Sonoran) of the American Southwest, the General Accounting Office (1992) concluded that a high environmental cost has been exacted on these fragile ecosystems and that land degradation due to grazing is continuing. The report concluded by noting that the high environmental risks, budgetary costs, low economic benefits, and management problems associated with livestock grazing on hot desert public lands merits Congressional consideration. Recommended options included raising grazing fees or appropriating additional funds to offset costs of administration and monitoring, and discontinuing livestock grazing altogether in hot desert areas.

Different plant communities respond to grazing in a variety of ways related to a complexity of factors. Results for the Mojave Desert suggest that livestock grazing can have locally significant effects on the plants (Figure 1) and ultimately on desert wildlife. Efforts to restore

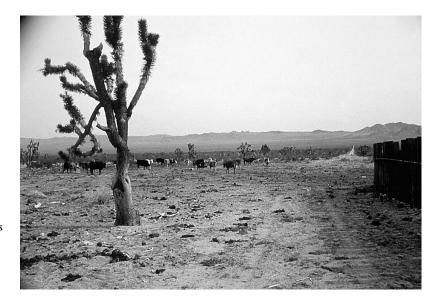


Figure 1. Cattle grazing can have locally significant effects on vegetation and soils, as shown in this photo of a cattle watering area and corral in what is now the Mojave National Preserve, California. Note the almost total destruction of perennial plants in the immediate area. The visual effect is greatly diminished as distance from the watering area increases. Photo by Jeff Lovich.

degraded rangeland in the Mojave should start by considering the effects of grazing and the potential impacts of soil compaction, erosion, and plant community alteration.

Linear Corridors

Roads, railways, powerlines, and pipelines, some of the most conspicuous elements of the modern Mojave Desert landscape, are all characterized by long and relatively narrow corridors of disturbance. The fact that most linear corridors are narrow does not necessarily imply that their impacts are minimal. According to Brum and others (1983), over 8000 km of overhead power transmission lines were present in the California desert in 1980, impacting more than 28,000 ha of land. An additional 50,000 ha of land will be impacted by the year 2000 if the projected threefold increase in power demand is accurate. Information summarized in the California Desert Conservation Area Plan (Bureau of Land Management 1980) suggests that an additional 2000 km of energy production and utility corridors are needed to meet the needs of southern California to the year 2000.

The immediate effect of linear corridor construction on soil conditions and plant cover is one of nearly complete destruction (Vasek and others 1975a). In some cases recovery is retarded due to operation and maintenance of corridors (Artz 1989). Other negative secondary effects of corridors include mortality of animals along roadways (Rosen and Lowe 1994, Boarman and Sazaki 1996), habitat fragmentation and restriction of movements and gene flow, increased access to remote areas for illegal collection and vandalism of plants and animals (Nicholson 1978, Garland

and Bradley 1984, Boarman and Sazaki 1996, Jennings 1991), and increased erosion (Wilshire and Prose 1987). The steel towers associated with many electrical energy transmission corridors provide nest sites and hunting perches for ravens (Corvus corax), a native predator that has increased dramatically in recent years due to human subsidy. The towers may allow ravens to hunt more effectively for the federally threatened desert tortoise (Gopherus agassizii) and other desert wildlife (Boarman 1993). Corridors can also serve as a source of exotic invasive plants brought in on construction equipment (Zink and others 1995). Invasive plants prosper in the disturbed conditions and contribute to an increased likelihood of fire. The construction of pipelines for gas, oil, and water and much more destructive than overhead lines because extensive trenching is usually required. This traditionally has led to severe soil impacts (leaving subsoil on the surface), disturbing stabilized crusts and rock surfaces, and concentrating runoff and erosion. More recent pipelines have incorporated some environmental protection and some rehabilitation but the low value of the desert land, the high cost of revegetation, and the lack of money for enforcement and supervision has often led to neglect and minimal treatment.

The impacts of linear structures can extend far beyond the boundaries of the immediate disturbance. Schlesinger and others (1989) studied the effects of diversion structures (earthen dikes) along the Colorado River Aqueduct on plants and soil. The structures were constructed to prevent runoff due to precipitation from washing sediments into open portions of the canal. Large areas downslope of the diversion structures received only incident precipitation, with essentially no runoff from the extensive drainages in the uplands

above the diversion structures. As a result, large areas of desert habitat on the downslope side of the diversion structures had a lower biomass of perennial and annual plants in comparison to adjacent areas with no diversion structures.

Garland and Bradley (1984) observed that some species of rodents in the Mojave of Nevada are more abundant near highways, while others are not. However, reduced abundance may have been an artifact of natural habitat heterogeneity since no mortality was observed during the 11-month study. Another effect of roads is edge enhancement in which perennial shrubs along roadsides are denser, larger, more vigorous, and support greater numbers of foliage arthropods than those away from roadsides (Vasek and others 1975b, Lightfoot and Whitford 1991). Johnson and others (1975) noted that primary productivity, as measured by standing crop, at study sites in the Mojave Desert of California increased about 17 times on the basis of vegetated area alone and 6 times when the area of the bare road surface was included as part of the productive unit. Unpaved roads showed increases of 6 and 3 times, respectively, in each category. Increased water availability from pavement runoff and increased retention of moisture under the pavement are probably responsible for the observed increase in plant vigor, although removal of competing plants that formerly occupied the roadway may confer an advantage to plants along the berm (Vasek and others 1975a). The increase in vigor attracts herbivorous insects (Lightfoot and Whitford 1991).

The effects and recovery of linear corridor construction in deserts have been studied by several researchers. The process of natural recovery, following powerline construction in the Sonoran Desert starts immediately with invasion by pioneering annual species, but perennial species may not return for over five years. The density and diversity of annual species may increase in comparison with undisturbed sites, perhaps due to the removal of large woody species (Hessing and Johnson 1982). An effect that is apparently linked to changes in plant abundance and composition is a reduction in the density, but not the community composition, of arthropods following establishment of access roads for power-line construction (Johnson and others 1983).

In the Mojave Desert, plant cover also increases following powerline construction. The rate of increase and composition of colonizing species varies considerably, confounding the ability to predict succession relative to adjacent undisturbed areas. Ground cover of short-lived perennial species increases in areas of severe disturbance, under the central wires, and along the edge of maintenance roads. After 33 years there was a

noticeable, but not complete, recovery of predisturbance vegetation (Vasek and others 1975b). Natural revegetation (0–41% ground cover) by long-lived perennials has been observed 12 years after construction of a pipeline by trenching, piling, and refilling (Vasek and others 1975a). Disturbed and control areas appear to have similar cover, biomass, and densities of vegetation following partial recovery, but similarities disappear when the proportions of long-lived and dominant species are compared (Lathrop and Archbold 1980a,b). Species with these characteristics are not well represented on disturbed sites.

Management strategies for minimizing the effects of linear corridor construction include: placement of power poles closer to existing access roads, modifying construction techniques for buried pipelines, less frequent road grading, and limiting the width of motorcycle race corridors along powerlines (Artz 1989). Lathrop and Archbold (1980b) proposed several recommendations for routing corridors to minimize environmental impacts including: (1) routing them through gently sloping areas to minimize erosion, (2) routing them through areas occupied by colonizing species such as cheesebush (Hymenoclea salsola), (3) avoiding areas dominated by high nitrogen fixation communities such as cat's claw acacia (Acacia greggii), and (4) avoidance of undue soil compaction with implementation of soil loosening efforts to aid natural revegetation. Revegetation of linear corridors was evaluated by Kay (1979, 1988), Graves and others (1978), and Brum and others (1983).

The slow recovery of the desert to linear corridor impacts is perhaps best demonstrated by the visibility of many of the old Native American trade routes. Long-term use by foot traffic alone was sufficient to compact the soil and recovery after several hundred years has not been enough to hide these trails (personal observation).

Mining

Mining has been an important activity in the California desert since the late 1880s. Mining communities such as Kokoweef, Hart Mountain, Boron, Johannesburg, and many others have had mostly localized impacts on the desert. The most obvious forms of degradation are pits, ore dumps, and tailings, but the once-great demand for fuel and timber, grazing, and road building associated with mines was unquestionably more important in the past. Fugitive dust and toxic tailings are a more recent concern from some of these mining areas.

The Bureau of Land Management (1980) estimated that 12,545 ha in the California Desert Conservation

Area had been affected by major mining operations. If the many small prospects and adits are included, the area affected by mining would certainly be larger. The brine evaporation and dry lake mine operations are extensive and lead to substantial wind erosion (Wilshire 1983). Another problem is animal mortality at poorly managed cyanide extraction gold mines in the Mojave Desert (Clark and Hothem 1991, Henny and others 1994).

Military Training Operations

Large areas of the California desert have been impacted by temporary and ongoing military activities. Major training exercises included activities by General Patton in the early 1940s, the Desert Strike operation in 1964, and Bold Eagle in 1976. Between 1942 and 1944 more than a million soldiers passed through these training facilities, which covered more than 46,800 square km (Bureau of Land Management, 1990). The camps were effectively small cities, up to 2800 ha in size (e.g., Camp Granite) (Prose and Metzger 1985). Continuing impacts are generated by active military bases including the National Training Center (at Fort Irwin, the Marine Corps Air Ground Combat Center at Twentynine Palms, China Lake Naval Air Weapons Station, and the Chocolate Mountain Aerial Gunnery Range (Lathrop 1983a). Military operations cause intensive damage in many areas but also provide protection of thousands of hectares from other sources of disturbance by prohibiting public access. At Fort Irwin alone, the area in need of remediation is estimated to exceed 50,000 ha.

The recovery of large areas of the eastern Mojave Desert subjected to military training exercises almost 36 years earlier was studied by Lathrop (1983b). Impacted areas included tent sites, roads, and tank tracks. All impacted areas exhibited significant reductions in plant density and cover relative to control areas. Reductions of cover and density were greatest in tank tracks and least in tent areas. Recovery to predisturbance levels of cover and density varied according to disturbance type. Tent areas showed the greatest recovery, and roadways showed the least, reflecting the intensity of disturbance. Recovery in tank tracks was intermediate. Diversity of dominant perennials also varied between disturbed and nondisturbed areas but results were clouded by low species richness at the study sites and small sample sizes of the subdominants. However, diversity in disturbed transects at the Camp Ibis study site was low relative to control sites. Species similarity decreased between control and disturbed transects with increased disturbance and use intensity.

Similar observations and conclusions were reached by Prose and Metzger (1985) and Prose and others (1987) at abandoned military camps in the eastern Mojave. Long-lived species such as *Larrea tridentata* were dominant in all control areas but percentage cover and density were reduced in impacted areas. Dominant plants in disturbed areas included pioneer species such as *Ambrosia dumosa* and *Hymenoclea salsola*. Percentage cover values for pioneer species in disturbed areas were equal to or greater than control values.

Differences in vegetative structure between control and impacted plots were due to soil compaction, changes in soil texture, removal of the top layer of soil, and alteration of drainage channel density (Prose and others 1987). Penetrometer measurements show that a single pass by a "medium" tank can increase average soil resistance values by 50% relative to adjacent untracked soil in the upper 20 cm, but values of up to 73% were recorded. Dirt roadways could not be penetrated with a penetrometer below 5–10 cm due to extreme compaction. Physical modifications to the soil beneath tank tracks extended vertically to a depth of 25 cm and outward from the track edge to 50 cm (Prose 1985).

Recovery times to predisturbance levels of density and cover were estimated by Lathrop (1983b) assuming linear rates (Table 1). Recovery to predisturbance species composition would require much longer, if it were to occur at all. Areas receiving the greatest amount of soil compaction, such as roadways, require the longest recovery times. Tank tracks and tent areas recover in a shorter amount of time. Overall, recovery in plant density is slow relative to increases in cover. In other words, the number of individuals changes little following recovery from disturbance, but surviving individuals cover larger areas. A major conclusion from Lathrop's study was that recovery to some original level of community composition and stability may not occur in the foreseeable future. However, recovery of comparable disturbed areas has been excellent on restoration test plots at the Marine Corps Air Ground Combat Center near Twentynine Palms, California (Zink personal communication).

Off-Road Vehicles

Off-road vehicle (OHV) use is one of the major recreational activities in the deserts of California. The Motorcycle Industry Council estimated that 4.7 million motorcycles were used by 11.7 million people in 1978 for off-highway recreation in the United States, a figure that does not include dune buggies and four-wheel drive vehicles (Kockelman 1983).

The impacts of OHVs have been well documented (Webb and Wilshire 1983) and include destruction of soil stabilizers (see section on biotic components of soil), soil compaction, reduced rates of water infiltra-

tion, increased wind and water erosion, noise, decreased abundance of lizard populations (Busack and Bury 1974), and destruction of vegetation (Vollmer and others 1976). Compaction of a desert soil reduces the root growth of desert plants and makes it much harder for seedlings to survive (Bainbridge and Virginia 1990, Bainbridge and others 1995a). An excellent review of the effects of OHVs in the Mojave and other deserts is contained in Webb and Wilshire (1983) and the reader is referred to that document for information beyond that presented herein.

Soil compaction is a common effect of any compressive action on most soils. Compaction results from a variety of factors other than OHV use, including trampling by grazers, human trampling (Liddle 1991, 1997), and even raindrops (see review in Webb 1982). In the case of OHVs, compaction occurs at shallow depths related to the geometry of the contact surface between the tire and the soil interface. In one study the greatest increase in soil density occurred at a depth of 30-60 cm after being compacted by a motorcycle (Webb 1983). Soil density increases as a function of the number of vehicle passes, while soil infiltration rate decreases. Soils that are most susceptible to compaction are loamy sands and coarse gravelly soils with variable particle sizes. Wet soils are more susceptible to compaction than dry soil. Soils that are least affected include sands and clays.

Another by-product of heavy OHV use is increased wind and water erosion. The degree of erosion experienced in an area exposed to OHV use is affected by two main factors. First, increased water erosion is partially attributable to decreased infiltration rates due to compaction. Second, OHVs destroy surface stabilizers (see section on biotic components of soil), making soils more susceptible to erosion (Hinkley and others 1983). The enormity of the problem in the Mojave Desert is underscored by the fact that satellite photos revealed six dust plumes covering over 1700 square km of the western Mojave on 1 January 1973 that were attributed to surface destabilization primarily by OHVs (Nakata and others 1976, Gill 1996).

As shown in numerous photographs in Webb and Wilshire (1983), the effects of erosion can have indirect effects, since debris flows (Nakata 1983) can bury plants at some distance from the impacted area. Areas that are least susceptible to water and wind erosion following OHV use are dunes, playas, and areas with abundant coarse surface material (Gillette and Adams 1983, Hinckley and others 1983). Restoration of OHV areas affected by erosion requires actions to not only stop continuing erosion (Harding 1990, Heede 1983, Middleton 1990), but also action to restore past damage.

Desert soils vary in their susceptibility to OHV

damage. Susceptibility is generally high in all areas except barren sand dunes (but see Bury and Luckenbach 1983), and the clay flats of playas. Soil damage caused by OHVs is environmentally significant due to the fact that desert soils may take 10,000 years to develop (Dregne 1983). From this estimate, Dregne concluded that it was futile to speak of disturbed soil recovery in time frames related to human occupancy.

Another major effect of OHV use is the destruction of plants. Lathrop (1983a) examined aerial photographs of nine disturbed and undisturbed areas in the Mojave Desert to assess the effects of OHV usage. Perennial plant density and cover were dramatically reduced in OHV areas. The percentage of cover and/or density in OHV-impacted areas relative to control areas was less than 15% in three of the sites examined. Destruction of plants resulted not only from crushing stems and foliage, the extensive root systems that fill the intershrub spaces, and germinating seeds, but also from the superstructure of the vehicle. The latter factor is important since it is responsible for plant destruction in an area wider than the track width of the vehicle. The wheel tracks of a full-size off-road vehicle operating in an undisturbed area can damage almost 0.5 ha of land with every 6.44 km traveled. Support vehicles, including very large and heavy motor homes, are very destructive, and camping areas are especially hard hit.

An easily detected but poorly understood effect of OHVs is noise. Noise from certain types of OHVs can reach 110 decibels, which is near the threshold of human pain. Brattstrom and Bondello (1983) demonstrated that OHV use in the Mojave Desert caused noise levels that caused hearing loss in animals such as kangaroo rats, desert iguanas, and fringe-toed lizards; interfered with the ability of kangaroo rats to detect predators such as rattlesnakes; and caused unnatural emergence of spadefoot toads that were estivating until the arrival of rain for breeding, a situation that could result in death. The authors noted that although OHVs are not the loudest source of human-generated sound in the Mojave, they occur more frequently than any other high-intensity sound source. In their report, Brattstrom and Bondello recommended that OHV areas be located away from the ranges of "all undisturbed desert habitats, critical habitats, and all ranges of threatened, endangered, or otherwise protected desert species."

The impact of OHV use on desert tortoises in the Mojave Desert of California was examined by Bury and Luckenbach (1986) in an unpublished report. Significantly more tortoises and active burrows were found on a 25-ha control plot than on a similar plot exposed to OHV use. In addition, subadult and adult tortoises on

the control plot exhibited larger body mass than those on the OHV plot.

Impacts related to OHV use present a serious challenge to desert restoration projects for three reasons: (1) the potentially severe impact of OHV use in desert ecosystems, (2) the widespread nature of the OHV impacts in the California desert, and (3) the fact that OHV areas are often located in or near environmentally sensitive habitats. Areas targeted for restoration should be closed to OHV use prior to initiating procedures to ameliorate past damages.

Invasive Plants

Invasive exotic plants have had a significant impact on the natural communities of California (Mooney and others 1986, Rejmánek and Randall 1994), including the southern California desert ecosystem. Invasion has been facilitated by habitat disturbances that allow exotic species to colonize habitats once dominated by native species (Hunter and others 1987). Once established, exotic plants may diminish the abundance of native species due to competitive interactions or by disruption of natural processes such as fire frequency and intensity.

Some of the more important exotic plants in the southern California desert are saltcedar (*Tamarix ramosissima*), also known as tamarisk (Lovich and de Gouvenain 1998), Russian thistle (*Salsola iberica*) (Young 1991), filaree (*Erodium cicutarium*), and several grass species including split grass (*Schismus* spp.) and bromes (*Bromus* spp.) (Brown and Minnich 1986, Hunter 1991). Immense areas of desert are colonized by these species. Although other exotic plants are present in the Mojave Desert, these are important because of their ubiquity.

Exotic plants present two major problems to the integrity of the desert ecosystem. First exotic annuals increase the fuel load and frequency of fire in a community that is poorly adapted to fire. Second, some exotic plants exhibit allelopathic effects that negatively affect native species, especially annuals. Negative interactions have been demonstrated between Russian thistle and other species in the laboratory (Allen 1982a, Lodhi 1979). In addition, competition of Russian thistle with native perennial grasses increases under drought conditions (Allen 1982b), furthering establishment of the exotic. Fortunately, Russian thistle competes poorly with established vegetation and rarely supplants wellestablished native populations. Unfortunately, once the soil is disturbed and native plants are eliminated, Russian thistle gains a strong foothold (Young 1991). General reviews of the threats posed by exotic species invasions in native ecosystems are summarized by Cheater (1992) and D'Antonio and Dudley (1993).

Air Pollution

One of southern California's most famous exports is smog. While most noticeable in the inland valleys of the state, smog is often transported via atmospheric processes into the Mojave Desert (Pryor and Hoffer 1991). Anthropogenic pollutants include ozone, sulfur dioxide, and various particulates. Atmospheric tracer experiments have shown that pollutants released in the San Fernando Valley impact the southern Mojave Desert towns of Adelanto and Palmdale, while those released in the southern San Joaquin Valley impact the northern Mojave Desert towns of Mojave and China Lake (Reible and others 1982). Experimental tracers used in atmospheric transport studies are diluted by factors of only 2-3 during passage between source and receptor areas. Impacts are maximized during evening and nighttime hours, independent of the time of release in the San Joaquin Valley, because of the diurnal mountain-valley wind cycle. Ozone levels in the Mojave Desert can exceed 100 parts per billion (ppb) or more when offshore wind transports atmospheric pollutants from the Los Angeles Basin (Thompson and others 1984a). By comparison, ozone levels in remote areas range from 20 to 40 ppb.

The most obvious effect of smog in the Mojave Desert has been visibility degradation in an area historically distinguished by extraordinary visibility (Walsh and Hoffer 1991). Median visibility is 48–88 km in large urban areas and 104–128 km in nonurban locations. Visibility has decreased 10%–30% from the middle of the 1950s to the early 1970s at many recording stations (Trijonis 1979).

Much of the visibility loss is related to particulates, including nitrogen-rich compounds. Dryfall of these compounds from air pollution can be a major source of supplemental N for plants. This favors many exotic plant species over native annuals and perennials. Wedin and Tilman (1996) found that half the native plant species in a Minnesota grassland were lost from the community at supplemental N levels mimicking dryfall deposition rates.

A less obvious effect is damage to plants. Stolte (1991) observed injurious effects to desert plants exposed to ozone and sulfur dioxide in laboratory experiments. Annual plant species of the genera *Camissonia* and *Cryptantha* exhibit high sensitivity to both gases. The grass *Oryzopsis hymenoides* exhibits high sensitivity to sulfur dioxide, as do some types of cryptogamic soils. Responses of cryptogamic soils include increased electrolyte leakage, chlorophyll degradation, and reduced nitrogen fixation (Belnap 1991).

Studies of plants from the Mojave and Colorado Deserts show that perennial species vary in their re-



Figure 2. The effects of fire in the desert are obvious in this photo taken near Palm Springs, California, about five years after the blaze. Note the almost complete elimination of perennial shrubs in the burned area to the left. Perennial plant species in the Mojave and Colorado Deserts are long-lived and very sensitive to fire, traits that collectively contribute to the long recovery times typical of many desert plant communities after fire. Photo by Jeff Lovich.

sponse to SO₂ and NO₂. Larrea tridentata is sensitive to fumigation by these pollutants under experimental conditions, displaying extensive leaf injury and reduced growth or dry weight. Encelia farinosa and Ambrosia dumosa show intermediate responses, while Atriplex canescens appears to be resistant (Thompson and others 1980). Sensitivity also varies among native annual plants, with Camisonia claviformis, C. hirtella, and Cryptantha nevadensis exhibiting leaf injury at low concentrations of SO₂ and O₃ (Thompson and others 1984b).

Fisher (1978) suggested that high rates of mortality in desert holly (*Atriplex hymenelytra*) in the northern Mojave Desert (Death Valley) were related to elevated ozone levels. During the summer months he recorded ozone levels that were twice the national standard of 0.08 ppm. Photosynthesis and water use was significantly reduced in greenhouse experiments where seedlings were exposed to 0.15–0.18 ppm ozone for 3 h. Ozone-induced reduction in water-use efficiency was postulated to be the cause of declining *Atriplex* populations in Death Valley.

Additional summaries of the impacts of air pollution in the Mojave and Colorado Deserts are provided by Mangis and others (1991), Thompson (1995), and VanCuren (1995).

Anthropogenic Fire

Fire was not an important factor in shaping the prehistoric structure and dynamics of plant communities in the California desert. The infrequency of fire in the prehuman landscape of the desert was due to limited biomass, large intershrub spacing, low combustibility of some native plants, sparse groundcover to support and propagate combustion, and the absence of human-mediated fire suppression activities (Humphrey

1974, O'Leary and Minnich 1981, Minnich 1983, Brown and Minnich 1986). Such is not the case in other desert and semidesert areas of the American Southwest, including parts of the Sonoran and Chihuahuan deserts, where fire was an important prehistoric agent in maintaining grassland seral stages (Humphrey 1958, 1963, 1987, Reynolds and Bohning 1956).

The proliferation of exotic annual plant species such as Bromus, Schismus, and Salsola has dramatically increased the fuel load and frequency of fires in many ecosystems around the world (D'Antonio and Vitousek 1992), including parts of the California desert (O'Leary and Minnich 1981, Brown and Minnich 1986), in recent years. The frequency of fires in the Colorado Desert of California is further enhanced by the proximity of previously burned areas (Chou and others 1990). Native perennial shrubs are poorly adapted to relatively low-intensity fires as evidenced by low rates of recovery (Figure 2). In the upper Coachella Valley on the east scarp of the San Jacinto Mountains near Palm Springs, California, burned creosote bush scrub is replaced by open stands of Encelia farinosa, native ephemerals, and exotic species such as Schismus and Bromus (Brown and

Postfire vegetational recovery along a chaparral-desert ecotone including parts of Anza-Borrego Desert State Park in San Diego County, California was examined by Tratz and Vogl (1977). They observed high recovery (as measured by speed of resprouting) in chaparral shrubs and desert-wash plants, but low recovery in cacti. Herbivorous mammals present before the burn were also present afterwards, since rapid recovery of shrubs provided adequate food supplies for wildlife, even in the first months after the fire. If California desert perennial plant communities are not well adapted

to fires, animals that coevolved in the ecosystem should not be expected to respond favorably to fire either.

According to fire personnel at the California Desert District (CDD) Office of the Bureau of Land Management (BLM), the CDD (including the Mojave and Colorado Deserts) had a ten-year average of 175 fires per year prior to 1992 (range 100–475) that affect an average of 10,927 ha annually (range 607–34,400 ha). The CDD estimates include a very small amount of BLM land outside the desert.

Impacts on Biotic Components of Soil: The Invisible Component of Biodiversity

Although emphasis is often placed on the physical and chemical properties of various soils, they contain important biotic components as well including: soil surface stabilizers such as algae and lichens, nematodes and other metazoans, various bacteria, and mycorrhizae. Odum (1994) referred to these organisms as the invisible component of biodiversity. While not as conspicuous as macrofloral elements, biotic components of soil are important symbionts that are easily destroyed by certain human activities.

Undisturbed desert areas are characterized by the presence of soil stabilizers, including lichen, fungal, bacterial, and algal crusts; desert pavement; mechanical crusts; and chemical crusts. The biotic components of these stabilizers are collectively referred to as cryptobiotic soil. Mineral-derived crusts form under a variety of physical and chemical conditions that may actually be facilitated by biotic components (Elvidge and Iverson 1983, Taylor-George and others 1983). Soil stabilizers are important agents in preventing erosion but are easily disturbed since they occur at the surface. Stabilization mechanisms include binding soil particles with thallial filaments in the case of biotic stabilizers, armoring the surface, and increasing surface roughness. Crusts also provide germination sites for vascular plants (but see Wood and others 1982), and conserve water (see review in Cole 1990). The susceptibility of crusts to damage varies according to the composition of the underlying soil. In soils subjected to large shear stresses, a single pass by a vehicle is capable of destroying well-developed crust. When the forces are mainly compressive, crusts can survive a single pass in a slightly modified form; however, OHV use is capable of quickly eliminating crusts in an impact area (Wilshire 1983).

Considerable research has been conducted on the impacts of grazing and other agents of trampling on cryptobiotic soil crusts. These crusts are very important not only because of the soil-stabilization functions mentioned above, but because they facilitate the accu-

mulation of organic material and soil nutrients, particularly nitrogen in the upper layers of soil (Kleiner and Harper 1977, Johansen 1993), and enhance soil moisture retention (Belnap and Gardner 1993). Research in desert and semidesert areas in Utah and Arizona has consistently shown that cryptobiotic soil is heavily impacted by grazing, even light winter grazing (Kleiner and Harper 1977, Anderson and others 1982, Brotherson and others 1983). Impacts include the destruction of surface pinnacles associated with development of cryptogamic soils (Anderson and others 1982) and the virtual obliteration of biotic elements (Cole 1990). Lichens and mosses are most sensitive to disturbance, with algal components being more resilient (Brotherson and others 1983).

Cole (1990) conducted an interesting experiment at Grand Canyon National Park to examine the effect of trampling by hikers wearing lug-soled boots. Only 15 passes were required to destroy crusts. Visual evidence of biotic components was reduced to near zero after 50 passes. The results of Cole's experiment clearly illustrate the fragility of crusts to trampling.

Cryptobiotic soil recovery may require long time intervals without intervention. Following exclusion of grazing in a Utah semidesert study site, cryptobiotic cover increased from 4%-15% in 14-18 years, but only 1% per year for the next 20 years (Anderson and others 1982). Cole (1990) observed partial recovery from human trampling in one to three years and extensive recovery after five years. However, surface irregularities associated with well-developed cryptogamic cover remained low even after five years, suggesting that recovery was incomplete. Belnap (1993) noted that over 250 years may be required for full recovery on the Colorado Plateau. Recovery was improved but was still very slow when scalped experimental plots were inoculated with crusts from surrounding areas. In the northern Mojave Desert, lichen crusts may not reoccupy heavily disturbed areas even after 63 years (Wilshire 1983). Details of the formation and recovery of chemical and mechanical crusts are discussed in detail by Wilshire (1983). The nitrogen-fixation capabilities of damaged soil may take over 50 years to recover (Belnap 1995).

Important symbiotic relationships have developed between certain species of vascular plants and vesicular-arbuscular mycorrhizal (VAM) fungi and rhizobia. The small-diameter hyphae of symbiotic fungi serve as energy efficient root hairs, enabling the host plant to better absorb nutrients, particularly phosphorus (Bloss 1985) and water (Bethlenfalvay and others 1984). Rhizobia are bacteria capable of fixing atmospheric nitrogen for use by plants. The importance of VAM fungi in desert plant communities is underscored by the fact

that in a recent survey of 38 plant species (19 families) in Anza-Borrego Desert State Park in the Colorado Desert of California all were colonized by VAM species (Bethlenfalvay and others 1984). Plants naturally associated with VAM that are also found in the western Mojave Desert include *Hymenoclea, Ambrosia, Opuntia,* and *Larrea.* Bloss (1985) reported numerous plant associations in the Sonoran Desert of Arizona as well.

Previous studies have demonstrated the importance of maintaining and enhancing soil microbes in restoration projects (St. John 1984, Bainbridge 1990). Establishing plants in disturbed areas with marginal soils may be difficult or impossible without the presence of a vigorous population of microbial symbionts. These symbionts are adversely affected by soil compaction. Studies have shown 1–2 m of hyphae per gram of soil in Mojave and Sonoran soils, yet virtually none in disturbed areas (Zink personal communication). Restoration is complicated by the fact that fertilizers can inhibit mycorrhizae growth.

Can the Desert Be Restored?

Plant growth and establishment are naturally slow under the extreme conditions of the desert, and disturbance makes these conditions even more severe (Bainbridge 1990). Disturbance typically reduces both the infiltration of water into the soil and the moisture-holding capacity of the soil (Bainbridge and Virginia 1990). This increases the value of rapid deep root growth, which is made more difficult by increases in soil strength from compaction and reduced soil moisture. These synergistic effects make plant establishment much more difficult after disturbance. Revegetation and restoration work can help mitigate many of these impacts and speed recovery, but the severe conditions and unpredictable rainfall still make restoration of these sites very challenging.

A brief history of revegetation studies in the deserts of California was provided by Kay and Graves (1983). Studies in the Mojave Desert are few and relatively recent. One of the earliest studies evaluated the success of revegetation efforts along the second Los Angeles Aqueduct (Kay 1979, 1988). Construction involved stripping the vegetation from an area 200 km long \times 60 m between 1968 and 1970. The seeds of seven species of native plants were distributed at six 2- to 15-ha sites on the aqueduct. The seeds of all but one species, *Atriplex polycarpa*, were from local stock. Surface preparation involved ripping the soil to 25 cm on 60-cm centers to relieve compaction. A rangeland drill was used to set the seeds at a depth of about 1 cm. Success varied among plant species. *Ambrosia dumosa* exhibited good establish-

ment on three of six sites, but only one site had numbers approaching that of adjacent undisturbed areas. Larrea tridentata exhibited similar results. The other species, including Atriplex polycarpa, Ephedra nevadensis, Hymenoclea salsola, and Lepidospartum squamatum, were totally unsuccessful. Atriplex canescens suffered as a result of heavy grazing. The most abundant shrub along the aqueduct, Chrysothamnus nauseosus, established itself naturally, although it was uncommon in adjacent undisturbed areas. Kay (1988) concluded that natural revegetation is good in many years and poor in others, while artificial seeding did not consistently hasten or improve plant recovery.

In another experiment along the aqueduct, Graves and others (1978) tested the effects of a single irrigation and the success of direct seeding versus transplanting. The two methods of establishment exhibited widely variable success rates from site to site and according to species, but were not enhanced by irrigation. Substrate characteristics may influence the success of irrigation as measured by the appearance of native winter annuals (Johnson and others 1978).

The overall success of the revegetation attempt along the aqueduct was low. The vast majority of the aqueduct was still a highly visible scar in the early 1980s (Kay and Graves 1983), but recovery was inhibited by grazing and OHV use. Conclusions from the study were that more attention should be focused on establishment of visually dominant species such as *Larrea tridentata*, seeding should take place as soon after disturbance as possible, areas should be protected from grazing and OHV use, and local seed stock should be utilized for all species.

Highway revegetation studies were also reviewed by Kay and Graves (1983). Survival of container-grown shrubs planted in October 1973 and February 1974 at a site in Mojave, California, was 90% in May 1974. The roots of the transplants were exposed after a heavy rain in December 1974, and all plants were dead by October 1975. Atriplex spp., Chrysothamnus spp., and Ephedra spp. exhibited the greatest survival. Success was limited by rabbit overgrazing and competition from Russian thistle (Salsola). Container plantings were more successful when planted in the late winter or early spring. Application of fertilizer encouraged both the invasion of native woody shrubs and the nonnative annual grass Schismus arabicus.

Others have experienced similar success in revegetation. Brum and others (1983) observed low, long-term seedling establishment for a variety of species under several irrigation treatments along a powerline transmission corridor. The overall germination–establishment rate for seedling and postseeding irrigation success was 0.3%, and 26% for transplanted seedlings. *Larrea* exhib-

ited poor germination under field conditions and responded poorly to all revegetation attempts.

More successful revegetation has been achieved at the Nevada Test Site in the northern Mojave Desert (Romney and others 1990). Greater than 80% survival of transplanted native shrubs and grasses was achieved when plants were protected from jackrabbits and irrigation was provided periodically.

Restoration efforts in the Colorado Desert of California were reviewed by Bainbridge and Virginia (1990). Although the plant communities differ somewhat between the Colorado and Mojave Deserts, both ecosystems pose similar challenges to restoration attempts: high temperatures, intense sunlight, limited moisture availability, high levels of herbivory by rodents and rabbits, and low soil fertility. Much of the success in revegetation experiments in the Colorado Desert is due to efforts to protect plants from herbivores and the use of buried water reservoirs for irrigation. Direct seeding attempts have generally been unsuccessful relative to transplants. *Larrea tridentata*, in particular, responded well to transplanting, especially if pruned prior to planting to increase the root-to-shoot ratio.

Assessing the nature and magnitude of humaninduced disturbances makes restoration planning more efficient by enabling limited resources to be directed at critical problems. Ongoing studies (Bainbridge and others 1995a,b) of the effectiveness of desert restoration techniques are steadily advancing our ability to rehabilitate degraded arid lands in the southwestern United States, and the reader is referred to these references for details beyond the brief overview given in this section.

Plant recovery usually requires container-planting activities as well as site improvement. The most common method of direct seeding is simple hand seeding, which allows species to be matched to specific site conditions, appropriate planting depths, and results in a more natural appearance than machine planting. However, limited rainfall and removal of seeds by rodents and harvester ants may severely limit seedling establishment during typical years.

Transplanting is increasingly being used to provide nurse and seed plants for the disturbed areas (Bainbridge and others 1995b). The dominant shrubs and trees of the Colorado Desert are relatively easy to grow in a nursery or maintained landscape setting, and they are well adapted to transplanting with after-care. They are more challenging to establish in the field in a low-or no-maintenance situation, although once established, growth rates can be high. Reestablishment of annuals has been more difficult. New containers and soil mixes have improved plant survival. Deep pipe and buried pot

irrigation and hand watering have also been effective. Tree shelters to limit herbivory and wind damage are also important.

A full appreciation of the ecological setting and adaptation of desert plants can make establishment less costly and more successful, but it is still expensive. The cost of restoring road edge areas in Joshua Tree National Park is fairly well established (after almost 10 years of work) and runs up to \$15,000 per ha to establish large potted perennials in areas that are easily accessed. The cost of duplicating this type of work at remote sites would be much higher. Research conducted by colleagues at San Diego State University has emphasized lower-cost, less-intensive restoration, but the costs (excluding research) are still on the order of \$12,000–25,000/ha. Even these high project costs provide no guarantee of success.

Conclusions

Desert areas disturbed by human activities may take centuries to recover without active intervention. Undisturbed desert soils are often in a relatively stable equilibrium developed over hundreds or thousands of years. Removal of vegetation and disturbance of soil crusts or soil structure can destroy this equilibrium, leading to wind and water erosion that are very difficult or impossible to control without very high investments in material and labor.

One of the key lessons of our research in the Mojave and Sonoran deserts is the critical importance of minimizing the intensity, frequency, and area of disturbance. Past research summarized in this paper has identified the wide range of effects from human disturbance and the difficulty and the high cost of mitigating damage. While recovery rates can be increased with modest expenditures, a major restoration program to improve recovery for just the OHV-damaged areas in the California desert region could exceed one billion dollars. Available funding will permit only a limited restoration for selected sites, even with continuing generous contributions of volunteer labor. Fences, signs, and enforcement to prevent further damage may often be a better investment than intensive restoration.

Recent research in the Mojave Desert demonstrates the benefits that protection can impart, even to previously disturbed areas. Brooks (1995) conducted a comparison between the Desert Tortoise Research Natural Area (DTNA) and unprotected land immediately adjacent. The DTNA was fenced to prohibit both OHV use and sheep grazing between 1978 and 1979. By the time of his study in 1990–1992, Brooks demonstrated that aboveground live annual biomass was generally greater

inside than outside the fenced area, with the exception that the exotic annual grass *Schismus barbatus* produced more biomass outside the fenced area. Percent cover of perennial shrubs, seed biomass, and rodent density and diversity were also greater inside the fenced area.

To be successful, revegetation and restoration require careful attention to ecological relationships, both above and below ground, herbivory, soil characteristics, microclimate, and patterns of moisture availability (Bainbridge 1990, Bainbridge and others 1995a). Undoing the damage done to the soil system by disturbance is a critical step toward recovery and restoration. In general, strategies that recreate or mimic natural conditions are most likely to speed recovery of the entire ecosystem.

Research conducted in the Mojave and Colorado desert ecosystem has important applications for the American Southwest and throughout the world's arid zones. These areas have deteriorated rapidly under pressure from overgrazing, poor farming, and removal of trees and shrubs for fuelwood. The lessons learned in the desert ecosystem of southern California may help people living in these areas to protect or restore the productivity of their lands, and improve their lives.

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