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Chapter 3:

Southwestern Grassland Ecology

Introduction

This chapter provides a brief overview, and selected in-depth coverage, of the factors and processes that have formed, and continue to shape, our Southwestern grasslands. In general, this chapter looks at how distributions of grasslands are regulated by soils and climate, and modified by disturbance (natural and/or anthropogenic). The attendant ecological components of grasslands will vary according to climate, soil, and other biotic factors including competition, predation, and mutualism. A shifting equilibrium typically exists between grasslands, deserts, and shrublands in the Southwest, such that changes in the severity or frequency of disturbance events (such as grazing, fire, or drought) can cause a change from one community type to another.

A problem of increasing importance to Southwestern land managers is that of exotic weed invasions. This chapter highlights the often-overlooked importance of fungi and soil crusts to grassland ecosystem function, and points out possible linkages to exotic weed invasions.

Grassland Evolution and Distribution

Humans have manipulated grassland vegetation for thousands of years through the use of fire, livestock

grazing, and other means. Therefore, it can be difficult at times to separate our influence from that of nature in the formation and maintenance of grassland ecosystems. The extensive North American grasslands evolved in the Miocene and Pliocene, during a period of global climate change (Axelrod 1958). In the late Miocene, C_4 dominated Southwestern grasslands expanded at the expense of C_3 vegetation. CO_2 levels had decreased prior to the Miocene, and C_4 plants were more tolerant of the lower CO_2 than C_3 plants. Periods of increased aridity, caused in part by the uplift of the Asian land mass and changes in seasonal precipitation patterns, facilitated the rapid expansion of drought-tolerant grasses and forbs, while restricting the growth of forests and woodlands (Jacobs and others 1999, Pagani and others 1999). Subsequently, natural and aborigine-caused fires swept across the grasslands at sufficient frequency to restrict the occurrence of trees and shrubs (Axelrod 1985, Dix 1964, Erickson 2001). Regional climate change and the Industrial Era increase in atmospheric CO_2 might have played a role in the current expansion of woody ecosystems into grasslands (Brown and others 1997).

Currently, fire helps to maintain the stability of grasslands by reducing the establishment of trees and shrubs. It also facilitates nutrient cycling by releasing nutrients from litter (Odum 1997) and accelerating the rate of decomposition in the soil. The reestablishment of periodic fire as a disturbance agent



Plains Mesa/Desert grassland ecotone, Sandoval County, New Mexico. (Photo by Rosemary Pendleton)

can be fundamental to the ecological restoration of Southwestern grasslands. However, prior to proceeding with large-scale fire reintroduction, appropriate fire frequencies and season need to be determined for each grassland type. In general, the response of grasslands to fire seems to depend primarily on pre- and postfire levels of precipitation (Ford 1999). Therefore, the use of fire as a management tool in a drought year should be carefully considered and aligned with management goals.

An excellent resource to find out more information about fire effects on vegetation and wildlife in Southwestern grasslands is the Fire Effects Information System (FEIS) <http://www.fs.fed.us/database/feis>. The FEIS database contains literature reviews taken from current English-language literature of almost 900 plant species, about 100 animal species, and 16 Kuchler plant communities found on the North American continent. The emphasis of each review is on fire and how it affects each species (FEIS 2004).

Central North American grasslands, including mixed-grass prairie, shortgrass steppe, and desert grasslands of the Southwestern United States and Mexico, are considered temperate grasslands. Temperate grasslands, broadly distributed between 30° and 60° latitude, are generally characterized by (1) rainfall intermediate between temperate forest and desert, (2) a long dry season, (3) seasonal extremes of temperature (alternating long warm summers and short cold winters), (4) dominance of grasses, and (5)

large grazing mammals and burrowing animals (Brown and Lomolino 1998, Lincoln and others 1998).

The periodic precipitation of temperate grasslands varies seasonally and annually. However, they generally average 250 to 750 mm of rain each year, though periods of drought are common and often prolonged. The rate of precipitation in temperate grasslands allows plants to release nutrients slowly into the ground over long periods. Dry temperate grasslands have maximum precipitation in the summer, and soil moisture is recharged by snowmelt in the spring. Precipitation in the arid and semiarid Southwestern grasslands is characterized by low rainfall, high evapotranspiration potential, low water yields (Branson and others 1981), and intermittent stream flow.

North American Plains grassland is represented mainly by mixed-grass prairie and shortgrass steppe in the Southwest. This largely midsummer flowering grassland extends from approximately 55° latitude in the Canadian Provinces of Alberta and Saskatchewan southward to below 30° latitude in Mexico, and once covered most of the American “Midwest” from the Eastern deciduous forest westward to the Rocky Mountains and beyond. More than 70 percent of the Plains grassland is now under cultivation (Garrison and others 1977). The plains grasslands developed under grazing by large herbivores and are generally tolerant of grazing (Engle and Bidwell 2000, Mack and Thompson 1982, Milchunas and others 1988).

Great Basin grassland merges with Plains grassland over a large transition area adjacent to the Rocky

Mountains in Montana, Wyoming, Colorado, New Mexico, and Arizona. Much of this grassland has been converted to cultivated cropland through irrigation, and most of the remainder has experienced a degree of shrub expansion due to grazing and fire suppression (Brown 1994). The spring-flowering Great Basin or Intermountain grassland is restricted to those areas west of the Rockies and east of the Sierra-Cascades that possess favorable soils, climate, and grazing history. Much of this grassland has been appropriately described as a shrub-steppe in that pure-grass landscapes without shrubs are limited (Franklin and Dyrness 1973).

In the Southwest, warm temperate grasslands are represented by a semidesert grassland with a more or less biseasonal to summer precipitation pattern. Since the 1970s, populations of woody plants, leaf succulents, and cacti have expanded, replacing perennial grass cover (Brown 1994). Factors attributed to changes in woody plant cover include regional climate shifts, increases in CO₂ concentrations, changes in fire frequency, and herbivory (Brown and others 1997, Detling 1988, Pagani and others 1999). Semidesert grassland adjoins and largely surrounds the Chihuahuan Desert, and with the possible exception of some Sonoran Desert areas in west central Arizona, it is largely a Chihuahuan, semidesert grassland. Extensive areas of this grassland occur in the Southwest in Chihuahua, western Coahuila, Trans-Pecos Texas, the southern half of New Mexico, southeast Arizona, and extreme northeastern Sonora (Brown 1994). Unlike the plains grasslands, desert grasslands were without megafaunal grazers for the last 10,000 to 11,000 years (Haynes 1991). Therefore the plant communities currently in place in the Southwest may be more susceptible to livestock grazing disturbance than other grasslands (Bock and Bock 1993, Loftin and others 2000, Mack and Thompson 1982). (For a comprehensive review of Southwestern grassland history and evolution see Van Devender 1995).

Soils and Climate

Precipitation and temperature are the main parameters of climate and are important properties that strongly influence both soil function and plant growth. Soil moisture and temperature directly affect the nature and development of soils. Grassland ecosystems are generally considered highly productive due to the hydrological, biological, and geochemical cycling between soil properties, and the resulting outputs of mass and energy. Soils vary considerably for grasslands in the Southwestern Region. The different grassland types in the Southwest result from unique combinations of climate, soil, topography, and parent materials. Given the wide geographic range of these

ecosystems, a high degree of inherent variability of climates, geology, landforms, and plant communities exists that directly influences rates of weathering, degree of stability, and site productivity.

Additions to, removals from, and vertical transfers and transformations within the soil are all basic kinds of soil-forming processes. These are, in turn, influenced by natural and anthropogenic disturbances, both at the soil surface and within the soil profile (Hendricks 1985). Historic and current disturbances have had an effect on the rates to which soil-forming processes have taken place. They also affect the degree to which the grassland system maintains its resiliency and ability to sustain soil functions that reflect stability and productivity.

Desert Grasslands

At lower elevations of the Southwest, grasslands encompass the Chihuahuan and Sonoran Deserts and are characterized by an arid climate with limited precipitation. The seasonal distribution of rainfall differs between these two desert environments. Chihuahuan Desert rainfall is unimodal and receives the majority of moisture within the summer months during the monsoon season. Sonoran Desert rainfall is bimodal with two distinct periods of precipitation. One period is during the winter months in which half or more of the annual precipitation is received. The remaining rainfall is received during the summer months.

Soil temperature is an important property that has a strong influence on plant growth and soil formation. Two soil temperature regimes are recognized in desert grasslands that include thermic and hyperthermic



Tulip prickly pear (*Opuntia phaeacantha*). (Photo by Rosemary Pendleton)

classes. Generally the hyperthermic temperature regime occurs in Arizona where precipitation is 250 mm or less, whereas the thermic temperature regime occurs in both Arizona and New Mexico desert grasslands where precipitation ranges from 250 to 410 mm (Hendricks 1985).

Landforms and parent materials of desert grasslands vary according to the degree of weathering, slope, relief, and mode of transportation of geologic materials. Soils of these landforms have evolved under paleoclimatic conditions and continue to change through the influences of today's climate and disturbances. Fluvial erosion, deposition, and volcanic activity are the primary geomorphic processes responsible for the origin and development of landforms supporting desert grasslands.

Desert grasslands characteristically occur on gently sloping floodplains, lower alluvial fans, concave playas, bajadas, and nearly level valley plains. Some remnant desert grasslands occur on isolated terraces, mesas, and sideslopes of moderately steep and steep hills. Minor patches of desert riparian vegetation with grassland affinities occur along drainage ways and dissected alluvial fans. Typically, these landforms contain both igneous and sedimentary lithologies of alluvial origin, although areas within desert grasslands and adjacent desert shrublands have areas of eolian, wind-deposited features that yield undulating dunes.



Black grama (*Bouteloua eriopoda*). (Photo by Rosemary Pendleton)

Dominant soils in desert grasslands are classified as Aridisols. Vertisols are of minor extent for those desert grasslands occurring within playas and closed basin topography. Entisols are characteristic of valley plains and drainages where active fluvial processes are taking place. A number of diagnostic soil properties help differentiate these soil orders and influence the kind and amount of desert grassland vegetation and its location (Robertson and others 2000). The physical and chemical weathering of soils along with the atmospheric deposition of dust yields soluble salts and carbonates. Reaction (pH) of soils generally ranges from neutral to alkaline.

The interconnections of soil, climate, and vegetation relationships in an ecological framework are described by Carleton and others (1991). For instance, it is recognized that mesquite (*Prosopis* spp.) will occur as a shrub throughout the Chihuahuan Desert but is confined to the upper Sonoran Desert. Mesquite does occur in the lower Sonoran Desert as a tree on certain alluvial soils as a result of fluctuating water tables. The hyperthermic/aridic soil climate causes a lack of perennial grasses in the lower Sonoran Desert. The high concentration of calcium carbonate favors calciphillic plants such as creosotebush (*Larrea tridentata* (Sessé & Moc. ex DC.) Coville) and crucifixion-thorn (*Canotia holacantha* Torr.) (Hendricks 1985). The presence of heavy clay surface horizons in playas supports rhizomatous plants such as tobosa (*Pleuraphis mutica* Buckl.), whereas loamy soil textures are suitable for black grama (*Bouteloua eriopoda* (Torr.) Torr.), and sand soil textures are dominated by sandhill muhly (*Muhlenbergia pungens* Thurb.).

Major disturbances include fire, livestock grazing, recreational activities, and the introduction of exotic species. Composition and successional sequence of some desert grassland plant communities have changed due to the introduction of livestock grazing and exotic, predominantly annual, plant species. Recreational activities such as off-road vehicle use have altered the soils hydrologic function in certain areas. Climate-induced disturbances include lengthy droughts and flash floods during torrential summer monsoons.

Great Basin Grasslands

Soils of Great Basin grasslands differ from other grassland soils because of their unique combination of climate, landform, and vegetation. The soil climate of Great Basin grasslands ranges from an aridic to ustic moisture regime, and a thermic to mesic temperature regime; with combinations of ustic/thermic classes in central and southern Arizona (Robertson and others 2000), and aridic/mesic classes in central and southern New Mexico.

The region typically receives less than 250 mm of precipitation per year. Mean monthly precipitation



Indian ricegrass (*Achnatherum hymenoides*).
(Photo by Rosemary Pendleton)



Blue grama (*Bouteloua gracilis*). (Photo by Rosemary Pendleton)



Needle-and-thread grass (*Hesperostipa comata*). (Photo by Rosemary Pendleton)

shows a strong winter-dominated pattern in the west, with a gradual shift eastward to more summer moisture, with less distinct wet and dry seasons compared with other deserts (Turner 1994). Air temperatures are cool in the winter months and hot during the summer months. The soil climate is quite variable and is dependent upon the fluctuations in weather patterns throughout the Southwest. With this degree of variability, the resulting genesis of geology, landform, and soils is complex. Yet, for this assessment, it is recognized that the geographic location of these grasslands is confined to the higher elevations of the Basin and Range physiographic province (Fenneman 1928): above desert grasslands and below or adjacent to pygmy conifer and evergreen oak woodlands, and therefore considered semiarid.

Volcanic and fluvial events are the primary geomorphic processes responsible for the origin and development of landforms supporting Great Basin grasslands. Landforms are typically nearly level elevated and lowland plains, gently sloping piedmont plains, and moderately steep uplands. These landforms vary in age and morphometric features, and they have experienced differing rates of erosion through anthropogenic and natural disturbances. These landforms also create a rainshadow effect along the frontal ranges of mountainous areas bordering basins and valley

floors (Dick-Peddie 1993). Parent materials are derived from igneous to sedimentary sources. Mixed alluvium occurs in fan and piedmont positions and valley plains, whereas colluvium and residuum parent materials are

dominant on elevated plains and upland landforms.

Soils are classified as Typic Haplustalfs, mesic or Typic Argiustolls, mesic for uplands (Carleton and others 1991). These soils are moderately deep to deep, with loam surfaces, and support blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths), New Mexico Feathergrass (*Hesperostipa neomexicana* (Thurb. ex Coult.) Barkworth), and Needle-and-Thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth). Aridic Haplustalfs, thermic, and Aridic Argiustolls, thermic, are slightly drier and warmer soils that support blue grama (*Bouteloua gracilis*), black grama (*Bouteloua eriopoda*), and Threeawns (*Aristida* spp.). Sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), which occur extensively throughout this grassland and can be in association with emory oak (*Quercus emoryi* Torr.) at adjacent ecotones in southern Arizona and gray oak (*Quercus grisea* Liebm.) in southern New Mexico. Some inclusions of Typic Ustipsamments with sandy surface textures support little bluestem (*Schizachyrium scoparium* (Michx.) Nash). Another

Great Basin grassland indicator is Soaptree yucca (*Yucca elata* (Engelm.) Engelm.) (Dick-Peddie 1993). Western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Löve) can occur on Vertic Haplustalfs and Vertic Argiustolls on nearly level lowlands and concave swales (Laing and others 1987).

The effects of grazing, in combination with changes in climate over time, and the absence of natural fire, have resulted in encroachment of woody shrubs and trees into the Great Basin grasslands. Other disturbances include the increase in abundance of exotic weed species and the resultant change in fire regimes.

Colorado Plateau Grassland

Soils of Colorado Plateau grasslands of this assessment are characterized by an ustic bordering on xeric soil moisture regime and a mesic soil temperature regime. Typically, over half the precipitation occurs during the winter months in the form of snow and rainfall. However, some areas receive more summer than winter moisture. Air temperature is generally cold during the winter and hot during the summer.

The geographic range of these grasslands is limited to the lower elevations of the Colorado Plateau and Southern Rocky Mountain physiographic provinces (Fenneman 1928, Laing and others 1987, Miller and others 1995). These grasslands are an integrate to adjacent cold desert sagebrush (*Artemisia* spp.) or four-wing saltbush (*Atriplex canescens* (Pursh) Nutt.) steppe communities and higher pinyon (*Pinus edulis* Engelm.) -juniper (*Juniperus* spp.) woodland ecosystems (Brewer and others 1991).

The primary geomorphic processes responsible for the origin and development of landforms of the Colorado Plateau grasslands are fluvial and volcanic. Landforms are nearly level to flat mesas, plateaus, and rolling elevated plains. Parent materials are dominated by basaltic igneous and limestone or sandstone sedimentary sources. Mixed alluvium parent materials support deep soils in narrow valley plains, whereas residuum from both igneous and sedimentary sources support shallow to moderately deep soils in steeper landscape positions.

Aridic Ustochrepts, mesic, calcareous are moderately deep soils with sandy loam surface horizons. Subsurface horizons are fine-loamy textured or skeletal and are generally calcareous in the lower part of the profile. These soils occur on upland plains derived from limestone and support stands of big sagebrush (*Artemisia tridentata* Nutt.), fourwing saltbush (*Atriplex canescens*), winterfat (*Krascheninnikovia lanata* (Pursh) A.D.J. Meeuse & Smit), Needle-and-thread (*Hesperostipa comata*), and Indian ricegrass (*Achnatherum hymenoides* (Roemer & J.A. Schultes) Barkworth). Typic and Pachic Argiustolls, mesic are deep soils with loam to clay loam surfaces that occur

on valley plains and lowlands derived from mixed alluvium. Dominant vegetation for these areas includes western wheatgrass (*Pascopyrum smithii*) and blue grama (*Bouteloua gracilis*).

The major disturbance of the Colorado Plateau grasslands is ungulate grazing. Composition and successional sequence of grassland plant communities have changed as a result of grazing. Climate induced disturbances include drought and flash floods during summer monsoon storms. Strong winds are common during the spring.

Plains Grasslands

The Plains Grasslands are within the Great Plains physiographic province (Fenneman 1928). Soils have ustic soil moisture regimes for shortgrass and midgrass communities and ustic bordering udic soil moisture regimes for tallgrass communities. Soil temperature is mesic for those areas of the plains that encompass the National Grasslands in eastern New Mexico, Oklahoma, and Texas. Climate ranges significantly in this region from semiarid to subhumid, which has a direct effect on the distribution of vegetation, along with the origin and genesis of the soils.

Pachic Argiustolls and Haplustolls occur on nearly level to gently sloping uplands and plains that are formed in alluvium, sandstone, and shale. These soils support mid- and tallgrass species. Typic Ustochrepts, Calcithodic Paleustolls, and Psammentic Haplustalfs occur on sandy and loamy, calcareous recent alluvium along stream terraces, outwash plains and eolian deposits (Burgess and others 1963, Murphy and others 1960). The depth to a calcareous substrate varies according to the degree of weathering and precipitation. Stands of tall- and midgrasses, shin oak (*Quercus havardii* Rydb.), and sand sagebrush (*Artemisia filifolia* Torr.) frequently occur on these soils. Typic Ustifluvents are located along drainage ways, flood plains, and stream courses that are derived from recent alluvium. Fluventic Haplustolls that support tallgrass species occur in association with riparian hardwoods and wetland plants. Historically, the plains grasslands have evolved over time with repeated ungulate grazing in combination with natural fire.

Montane Grasslands

Soils of Montane Grasslands have ustic to udic soil moisture regimes, and temperature regimes that include frigid, cryic and pergelic. The Montane Grassland assessment category includes those environments characterized by montane, subalpine, and alpine ecosystems. Climates are extreme with mean annual air temperature ranging from -3 to 7 °C; mean annual precipitation ranges from 56 to 76 cm, of which over 50 percent is received during the months October

through March. A significant portion of precipitation is snowfall.

The origin and development of landforms supporting montane grasslands are the result of glacial, fluvial, and volcanic geomorphic processes. Landforms associated with these grasslands include lowlands, upland plains, mountain slopes, and summit plains.

Typical Montane grasslands are characterized by Arizona fescue (*Festuca arizonica* Vasey) meadows on elevated plains of basaltic and sandstone residual, and alluvial parent materials that yield deep, clay loam, Typic, and Pachic Argiborolls (Brewer and others 1991, Laing and others 1987, Miller and others 1993, 1995). Other landform positions within this zone include valley plains of Kentucky bluegrass (*Poa pratensis* L.) supported by deep, loamy, Fluventic Haploborolls adjacent to riparian corridors of narrowleaf cottonwoods (*Populus angustifolia* James) growing in deep, sandy loam, Aquic Ustifluvents, frigid.

The Thurber fescue (*Festuca thurberi* Vasey) subalpine grasslands are higher in elevation than typical montane grasslands (Moir 1967). This environment is somewhat colder and wetter with a slightly shorter growing season. These grasslands are treeless expanses that border subalpine forests that are characterized by Subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and aspen (*Populus tremuloides* Michx.). These meadows and grasslands occur on mountain sideslopes, elevated plains and valley plains derived from dominantly igneous with inclusions of sedimentary parent materials. Argic Pachic Cryoborolls and Haploborolls are soils that contain deep, dark loamy surface horizons (Miller and others 1993). Surface rock varies; however, internal coarse fragments are numerous, thereby classifying these soils as skeletal.

Alpine tundra ecosystems are located above timberline, where a harsh climate of extreme cold and wet conditions creates wind-swept treeless expanses along mountaintop positions. These plant communities are limited in the Southwest and occur at elevations above 11,500 feet. The growing season for this environment is less than 90 days, approximately June through August. Strong winds, high intensity solar radiation and severe evapotranspiration are characteristic of alpine tundra environments. Soils are dominantly Pergelic Cryumbrepts, which contain dark surface layers that have a low base saturation that does not meet the mollic epipedon criteria (Miller and others 1993, 1995). Shallow to moderately deep with very cobbly sandy loam surface horizons, these soils are susceptible to erosion from wind and water, and human trampling. The landforms include nearly level to steep summit plains and mountain slopes.

Soil Biota

A variety of small organisms exist in grassland soils including bacteria, actinomycetes, fungi, algae, nematodes, micro- and macroarthropod invertebrates, and larvae. These soil organisms play a vital role in maintaining Southwestern grassland function. Although the majority of species involved remain undescribed, soil microflora and fauna have profound effects on essential ecosystem processes such as decomposition, nutrient cycling, and the maintenance of soil fertility (Adams and Wall 2000).

Soil microorganisms are essential components of the biogeochemical cycles that sustain life (Wolters and others 2000). Below- and aboveground communities are inextricably linked through complex interactions and feedback mechanisms. Any disturbance or change in the environment that affects aboveground vegetation will also affect the soil biota. The reverse is equally true. For example, an increase in CO₂ concentrations above North American grasslands could disproportionately increase photosynthesis relative to decomposition, resulting in a buildup of organic matter in grassland soils (Swift and others 1998). This buildup would, in turn, cause functional shifts in the soil community as nutrient turnover rates declined.

Changes in climate (precipitation patterns or temperature) directly affect soil processes. An environmentally induced decline in the types of organisms capable of degrading complex organic molecules such as lignin or chitin could result in a buildup of surface litter and a reduction in the nutrients available for plant growth, thus effecting changes in the surface vegetation (Schimel and Gullledge 1998). Fortunately, soil organisms have a high level of functional redundancy that could help buffer many of the effects of global change (Andren and others 1995). However, some key processes—including nitrogen transformations, nitrogen fixation, and the breakdown of recalcitrant molecules—are controlled by unique or specialized organisms (Wolters and others 2000). Changes affecting these taxa may have profound effects on ecosystem functioning.

Above- and belowground organisms interact in a variety of ways. For example, (1) microorganisms and soil invertebrates are responsible for the breakdown of complex organic material into plant-available nutrients; (2) cyanobacteria, actinomycetes, and other rhizobacteria fix atmospheric nitrogen, thereby increasing soil fertility; (3) cell material and excretions from soil microorganisms affect the formation and stability of soil aggregates that, in turn, affect water and air movement within the soil; and (4) mutualistic relationships formed with mycorrhizal fungi affect a plant's ability to grow and compete. Consequently,

changes that affect composition of the aboveground grassland community (that is, changes in climate, land use, atmospheric composition, or the introduction of invasive species) will likely affect the belowground community as well (Wolters and others 2000).

Bacteria, Actinomycetes, Fungi, and Algae

Bacteria are by far the most abundant group of soil microorganisms in terms of numbers, yet comprise less than half the microbial biomass because of their small size (Alexander 1977). Bacteria function in the decomposition of organic matter and in transformation and availability of many essential minerals. Several genera of free-living bacteria, such as *Azotobacter*, are capable of fixing atmospheric nitrogen. Vast communities of bacteria live on or near plant root surfaces where they feed on root secretions and dead cell material (Alexander 1977). Members of the genus *Rhizobium* form symbiotic relationships with roots of leguminous plants. Colonization by rhizobia results in the formation of root nodules, where they fix appreciable amounts of atmospheric nitrogen that is then available to the plant. Common legumes found on arid grasslands include the lupines (*Lupinus* spp.) and milkvetch or locoweed (*Astragalus* spp.). The woody mesquites (*Prosopis* spp.) also form nitrogen-fixing nodules (Geesing and others 2000).

Actinomycetes comprise the second most abundant class of soil microorganisms. They are extremely tolerant of desiccation and are found in large numbers in the grassland and steppe vegetation types common to the Southwest (Alexander 1977). Actinomycetes can utilize a variety of complex organic molecules including chitin and cellulose as energy sources. Many produce antibiotics and may be important in regulating the composition of the soil community. Members of the genus *Frankia* are capable of fixing nitrogen and form symbiotic root nodules with certain non-leguminous woody plants. Many of these species also form mycorrhizal associations (Rose 1980). These species are not common to grasslands, however.

Fungi account for large proportion of soil microbial biomass due to the extensive network of filaments (Alexander 1977). They function largely in the breakdown of complex organic molecules including lignin, a compound that is resistant to bacterial degradation. Some classes of fungi form specialized associations with plant roots. In addition to arbuscular mycorrhizal fungi, discussed in detail later in this chapter, Barrow and McCaslin (1996) observed two other major classes of fungi in roots of Southwestern grasses. Roots were commonly colonized by septate fungi that formed nondestructive interfaces within and among cortical cells, forming mycorrhizal-like associations. Chytridiomycete fungi were also commonly observed in plant roots. The function of chytrid fungi in the

soil ecosystem is unknown, but they may play a role in regulating mycorrhizal colonization and nutrient uptake (Barrow and McCaslin 1996).

Soil algae are found in every conceivable location throughout the world, from the arctic tundra to thermal springs to deep within commercial caves, anywhere that light is present. Algae are often the primary colonizers following volcanic eruptions (Alexander 1977). The role of green algae and cyanobacteria (blue-green algae) in fixing carbon compounds and stabilizing soils is addressed later in this chapter. Another algal group commonly found in soils is the diatoms. These algae have an outer wall that is highly silicified. Although small, the striking beauty of their regular geometric shapes makes them a fascinating group to study. As with other kinds of algae, most diatoms are obligate photoautotrophs (requiring light) and live in the upper soil surface where light can penetrate. They are most prevalent in neutral to alkaline soils (Alexander 1977).

Soil Invertebrates

Many macroarthropods spend part of their life cycle, usually as larvae, in the soil, and many microarthropods, such as mites (Acari) and springtails (Collembola), spend virtually all their lives there. Soil- and litter-inhabiting mites and nematodes (Zak and Freckman 1991) and collembolans (springtails) (Crawford 1990) occur in vast numbers and are species-rich in nearly all Southwestern habitats. The soil mites (Acari) are the smallest of the arachnids, the group that contains spiders and their relatives. Some mites are large enough to be visible to the unaided eye (about the size of grains of ground pepper), but not large enough to allow determination of their morphological characteristics. The mite fauna in desert grassland soils include more than 30 families and 100 species (Cepeda-Pizarro and Whitford 1989). The most abundant are the generalist microbe feeders such as the nanorchestid and tydeid mites. Some mite species feed on nematodes as well as fungi, yeasts, and bacteria. Included in this fauna are a variety of predators that capture and eat other mites and nematodes (Whitford and others 1995).

Nematodes represent another group of extremely abundant microscopic soil animals. There are approximately 100,000 bacteria feeders, 1,000 fungus feeders, 10,000 omnivore-predators, and 10 to 1,000 plant root feeders (root parasites) per square meter of soil (Freckman and others 1987). Nematodes are aquatic animals confined to single-molecule-thick water films surrounding soil particles, although they are well adapted to deal with dehydration. As the water films disappear in a drying soil, the nematodes enter an inactive state called anhydrobiosis, which is immediately reversible when the soil is wetted

(Whitford and others 1995). Studies have indicated that nematodes play a substantial role in the cycling of carbon and nitrogen in the soil environment (Bongers and Ferris 1999).

Protists (single-celled organisms that feed on bacteria and algae) populate the soil of all desert grasslands, but practically nothing is known of their distribution and biology. Naked amoebae predominate, along with smaller numbers of other orders. The abundance of protists in desert soils is astounding: there are 25,000 naked amoebae, 4,900 flagellates, and 700 ciliates in every gram of dry soil (Parker and others 1984). These numbers are deceiving, however, because most of the protists in dry soil are encysted (in an inactive physiological state; Whitford 1989). After a rain they quickly resume activity and remain active until the soil dries and they once again encyst (Whitford and others 1995). Grazing by protists on microbes stimulates the rate of decomposition of organic matter (Finlay 2001).

Grassland Invertebrates

Invertebrates perform vital ecological functions in grassland ecosystems. The scope of their contributions includes soil aeration, seed dispersal, and plant pollination and consumption, in addition to facilitating the decomposition of organic debris (such as dung and animal remains). Invertebrates also provide an important prey base for grassland fish and wildlife. (See volume 2 for more information on grassland wildlife, small mammals, birds, and fish.) This section gives a brief overview of the roles of some of the common invertebrates in Southwestern grasslands.

The importance of invertebrate animals to ecosystem properties and processes is frequently underemphasized (Whitford and others 1995). When the indirect effects of invertebrates on nutrient cycling processes and their direct and indirect effects on soil heterogeneity are considered, however, their importance becomes more evident. In fact, ecosystem properties such as resilience (the ability to recover following disturbance) are directly affected by the activities of key invertebrate species (Whitford and others 1995).

The invertebrate fauna of desert grasslands, and Southwestern rangelands in general, is incredibly diverse and includes several phyla (Parmenter and others 1995, Whitford and others 1995). While mammal, bird, reptile, and vascular plant species occur in the tens to hundreds, invertebrate species in desert grasslands number in the thousands or tens of thousands. Many of the less conspicuous species have never been described by taxonomists (Whitford and others 1995), and little is known about the diversity of arthropods on Southwestern rangelands. The available data indicate that species diversity for most groups of rangeland



Darkling beetle (*Eleodes longicollis*). (Photo by David C. Lightfoot)

arthropods is higher in the Southwest than in other parts of the country (Parmenter and others 1995).

Most of what we know about desert grassland invertebrates and their general life history characteristics is based on data from economically important species (Crawford 1981, Whitford and others 1995). Insects of the Southwestern rangelands are often thought of as agricultural pests because of the economically costly forage consumption by some species. Good reviews of important rangeland insect pests and research on those insects are found in Capinera (1987), Watts and others (1982, 1989), and Parmenter and others (1995). The pest species that are included in the above-cited literature represent only a small fraction of the insects and other arthropods that occur on Southwestern rangelands. Most species are not agricultural pests, many are rare, and many perform important functions in rangeland ecosystems (Crawford 1981, 1986, Lightfoot and Whitford 1990, MacKay 1991, Parmenter and others 1995, Walter 1987, Zak and Freckman 1991).

Grasshoppers (Orthoptera)

Many different species of plant-feeding insects occur on Southwestern rangelands (Crawford 1981, Watts and others 1989, Wisdom 1991). Of these, grasshoppers are among the most prevalent and conspicuous. A considerable amount of research has been conducted on grasshoppers throughout the Southwest, and more is known about the diversity and biology of grasshoppers than about other rangeland plant-feeding insects (Parmenter and others 1995). In North America, grasshopper species diversity is highest in the Southwest. Otte (1981) demonstrates that species densities of slant-faced grasshoppers (Gomphocerinae, primarily grass-inhabiting and -feeding grasshoppers) average



Regal grasshopper (*Melanoplus regalis*). (Photo by David C. Lightfoot)

around 30 species for locations in the Southwest, compared to five to 20 species for most of the rest of North America (Parmenter and others 1995).

Hewitt (1977) and Hewitt and others (1976) stated that grasshoppers compete with cattle for forage and that both herbivores have similar preferences in grass species. Estimates of the biomass consumption on rangelands in the Western United States by grasshopper herbivory have been difficult to calculate, but typically range from 6 to 12 percent of available forage, to as much as 50 percent in certain areas (Loftin and others 2000). In grassland at the San Carlos Indian Reservation in Arizona, Nerney (1961) found that grasshopper consumption ranged from 8 to 63 per-



Tarantula (*Aphonopelma* sp.). (Photo by David C. Lightfoot)

cent of the vegetation. However, Hewitt (1977) also reported a study from southeastern Arizona showing no correlation between grasshopper density and loss of forage. Quinn and others (1993) noted that as yet there is no measure of economic injury from grasshoppers that can be applied across all species or habitats (Loftin and others 2000).

Beetles (Coleoptera), Ants (Hymenoptera), Termites (Isoptera), and Spiders (Araneida)

The order Coleoptera contains a third of all known insects—approximately 300,000 species worldwide and approximately 30,000 species in North America (Milne and Milne 1996). Beetles are conspicuous components of the terrestrial invertebrate fauna of arid and semiarid ecosystems of North America (Allsopp 1980). They have an important role in the functioning of Southwestern grasslands, serving as predators, prey, scavengers, and parasites. In addition, many plant-feeding species attack plants and stored foods, while others pollinate flowers and eat plant pests.

Beetles appear to be relatively diverse in Southwestern grasslands. For example, the tiger beetle (*Cicindelidae*) is found worldwide, but in North America, the Rocky Mountains and the Great Plains contain the highest numbers of species, 15 to 20, compared with 10 for New England and 15 for the Middle Atlantic States (Parmenter and others 1995, Pearson and Cassola 1992). Ford (2001) found an average of eight beetle species per hectare on unburned, ungrazed shortgrass steppe in the southern Great Plains of New Mexico. Burned areas contained an average of 11 beetle species per hectare (Ford 2001). Darkling beetles (*Tenebrionidae*) are more diverse in Western arid lands than elsewhere in North America and are major detritivores in the Southwest (Crawford 1990).

African dung beetles have been recently introduced into grasslands throughout the United States to speed the decomposition of livestock fecal pats, primarily with the goal of reducing numbers of nuisance and disease-transmitting insects that breed in the dung (Dymock 1993; Hoebeke and Beucke 1997). While the grasslands of the Central and Southwestern United States contain fecal pats, the overall habitat conditions are too hot and dry to support these species (Loftin and others 2000).

Ants originated in tropical areas and spread into temperate habitats. Many of the species found in the Western United States are not unique to the region (Holldobler and Wilson 1990, Parmenter and others 1995). Ants are the dominant arthropod predators (on other arthropods and on plant seeds) in some ecosystems (Holldobler and Wilson 1990). In some areas of the Chihuahuan Desert there may be as many as 4,000 ant colonies per hectare. Arid regions of the Southwest

often contain a diverse ant fauna, with 23 to 60 species (MacKay 1991). For example, 23 to 50 species occur in the Chihuahuan Desert (Loftin and others 2000, MacKay 1991). Among the more conspicuous species are harvester ants in the genera *Pogonomyrmex* and *Aphaenogaster*. These species have large long-lived colonies (a decade or more) and contribute to soil mixing and aeration (MacKay 1991) and to seed dispersal (Loftin and others 2000).

Although termites occur primarily in the tropics, the species that are successful in temperate regions are of great importance in the recycling of nutrients in dead grass and wood (Loftin and others 2000, MacKay 1991, Schaefer and Whitford 1981). To avoid desiccation, temperate species are primarily subterranean, and their activity periods coincide with warm temperatures and an area's rainy season (Loftin and others 2000, MacKay and others 1989,).

Termites have low species richness (up to a dozen species in the Southwestern United States), but may be the greatest regional consumers of net primary production (MacKay 1991, Parmenter and others 1995). Bodine and Ueckert (1975) estimated that termites removed 20 to 50 percent of grass and plant litter from a grassland in Texas (Loftin and others 2000). Termites' positive contributions include nutrient cycling and nitrogen enrichment of the soils in arid and semiarid regions (Loftin and others 2000). Termites are known to consume cattle fecal pats (MacKay and others 1989).

Spiders form a major part of the arthropod fauna of the Southwest, but, as is the case with many other arthropod groups, the total number of species in the region is still unknown (Gertsh 1979). In a recent review of the status of arthropod systematics, Schaefer and Kosztarab (1991) estimate that most of the United States species of arachnids (and insects) that are still undescribed occur in the desert and montane Southwest and Great Basin areas (Parmenter and others 1995). Spiders serve as both predator and prey in Southwestern grassland ecosystems.

Mycorrhizal Fungi

The majority of plants in grassland ecosystems form some kind of mutualistic relationship with mycorrhizal fungi (Allen 1991, Miller 1987). In the relationship, soil resources are provided to the host plant root in exchange for energy-containing fixed-carbon compounds for the fungus. The fungus acts as an extension of the host root system. For example, 1 ml of soil may contain 2 to 4 cm of root, 1 to 2 cm of root hair, and 50 m of mycorrhizal fungal filaments, or hyphae (Allen 1991). Most external hyphae are concentrated near the plant root, but may extend 4 to 7 cm from the root surface (Read 1992, Rhodes and Gerdemann 1975). The small

diameter of the hyphae allows the fungus to penetrate small pores in the soil and efficiently extract mineral nutrients such as nitrogen, phosphorus, potassium, calcium, sulfur, copper, and zinc (Allen 1991, Stribley 1987).

In addition to uptake of minerals, mycorrhizae have been shown to improve plant water relations and soil structure (Allen and Allen 1986, Ames and Bethlenfalvay 1987, Mathur and Vyas 2000, Miller and Jastrow 1994, Thomas and others 1993), and to reduce susceptibility to pathogens and nematodes (Habte and others 1999, Newsham and others 1995). The result is an increased ability for the host plant to survive and grow under stressful environmental conditions.

Mycorrhizal relationships are classified according to the morphology of the root/fungus interface and vary depending on the species of plants and fungi involved. In grasslands, the vast majority of mycorrhizas are of the arbuscular mycorrhizal type, formed with fungi of the order Glomales (Allen 1991, Miller 1987). Arbuscular mycorrhizae are so named for the internal fungal structure where nutrient exchange takes place. Initial fungal colonization can occur through germination of soil-borne spores, or through pieces of hyphae or infected root fragments. A hyphal network then develops between cells of the root cortex. Hyphae enter the cell wall of some cortical cells and branch dichotomously to form a profusely branched surface, known as an arbuscule, surrounded by the host cell membrane. Nutrient exchange takes place across this interface (Allen 1991, Bonfante-Fasolo and Scannerini 1992, Bowen 1987).

Other types of mycorrhizal associations may be found in isolated patches within the grasslands, or at the ecotone between grasslands and other vegetation types (Allen 1991, Trappe 1987). Ectomycorrhizal associations, formed between coniferous plants and basidiomycete or ascomycete fungi, are found at the periphery of montane grasslands. Ericaceous plants (for example, *Vaccinium* and *Gaultheria*), which form their own kind of ectendomycorrhizae, are found in the understory of coniferous forests and on rocky uplands within or adjacent to montane meadows. Willows present within the meadow may form either ecto- or arbuscular mycorrhizas. Orchids and saprophytes, found in a wide variety of habitats, also form a unique type of mycorrhizae.

The boundary between arid grasslands and other vegetation types is less distinct in terms of mycorrhizal associations. Desert shrubland plants, including *Larrea* and *Prosopis*, are also primarily arbuscular mycorrhizal (Staffeldt and Vogt 1975, Titus and others 2001, Virginia and others 1986). Juniper species, found at the upper boundary of arid grasslands, also form arbuscular mycorrhizae (Klopatek and Klopatek 1997, Lindsey 1984), facilitating their expansion into

grass-dominated areas. Expansion of pinyon, which is ectomycorrhizal (Acsai 1989, Klopatek and Klopatek 1997), most likely depends upon the availability and dispersal of ectomycorrhizal inoculum.

Distribution and Occurrence

Arbuscular mycorrhizal fungi are found throughout the world, the same species often occurring on multiple continents. The fungi are grouped into three families and either five or six genera, based on wall characteristics of the soil-borne spores (Morton and Benny 1990). Associations between fungus and host plant appear to be nonspecific; a single root system may host associations with multiple species of fungi, and fungal networks may extend between adjacent mycotrophic plants. The fungi themselves are obligately mutualistic, and attempts to culture them separately have failed. Some species of fungi do appear to be habitat-specific, being associated with certain soil textures, nutrient levels, or extremes in pH (for example, *Glomus diaphanum* Morton & Walker and *G. spurcum* Walker & Pfeiffer), while others are common in a variety of habitats throughout the world (for example, *Glomus etunicatum* Becker & Gerdemann) (J. Morton, personal communication, Tatsuhiro and others 2000). Widespread or common fungal species may comprise different physiological ecotypes, however (Allen and others 1995).

Plant species differ in their ability to form mycorrhizal associations and in the amount of benefit derived. The degree of dependence on mycorrhizal fungi is correlated with the fineness of the plant root system and the number and length of root hairs per unit length (Baylis 1975, Hetrick and others 1992). Colonizing annuals in advanced families, such as the chenopod, mustard, and amaranth families, rarely form mycorrhizal associations and are referred to as “nonmycotrophic” (Allen 1991). Reeds and sedges in inundated soils also rarely form mycorrhizae; however, associations may form later in the season as soils dry out (Allen and others 1987, Miller and Sharitz 2000, Rickerl and others 1994).

Most grassland species are facultative mycotrophs and can survive with or without the association. They range from species that show no positive response to inoculation with mycorrhizal fungi, to those that show dramatic increases in growth and reproduction. The degree of response for any given plant depends on a number of factors, including the fungal species involved (fungal symbionts differ in their ability to acquire resources), soil texture and nutrient levels, environmental growing conditions such as temperature, precipitation, and light, and biotic factors such as competition and herbivory (Abbott and Gazey 1994, Cade-Menun and others 1991, Frey and Ellis 1997,

Hetrick and Bloom 1984, Hetrick and others 1986, Koide 1991, van der Heijden and others 1998).

In general, C₄ or warm-season grasses are more dependent on mycorrhizae than are C₃ or cool-season grasses (Hetrick and others 1990, VanAuken and Bloom 1998, Wilson and Hartnett 1998). Warm-season grasses alter their root morphology in response to colonization (Hetrick and others 1991, 1994), a trait associated with mycorrhizal dependency. Some grass species (such as *Andropogon gerardii* Vitman) are highly dependent on mycorrhizae for normal growth and reproduction (Hetrick and others 1989). There are some indications that perennial grass species may be more responsive to mycorrhizae than annuals (Boerner 1992). Grassland forbs and shrubs also vary in mycorrhizal dependence, with genera such as *Linum*, *Sphaeralcea*, and *Artemisia* consistently showing a positive response to mycorrhizal fungi (Lindsey 1984, R. Pendleton, data on file, Rocky Mountain Research Station, Albuquerque, NM). Few Southwestern grassland species could be considered truly obligately mycorrhizal, that is, unable to grow and reproduce without the symbiosis.

Community Interactions

Considerable recent work supports the idea that mycorrhizae are involved in regulating plant community interactions by (1) increasing the fitness of mycotrophic plant species, (2) affecting the outcome of competitive interactions among species, and (3) connecting plant root systems via hyphal networks.

Most studies on the beneficial effects of mycorrhizae measure plant growth or biomass as the dependent variable. Plant fitness, however, is measured by the number and quality of offspring produced. Production of biomass is important only as it contributes to the plant's ability to survive and reproduce. Therefore, although plant growth effects in field studies are often negligible, the true benefit of mycorrhizal fungi may rest in the enhanced ability of a plant to survive “ecological crunch” periods of acute stress (Allen and Allen 1986, Fitter 1986, 1989, Trent and others 1993). Such periods may include the vulnerable seedling stage, periods of short-term drought, or episodic outbreaks of insects or disease. The presence of mycorrhizal fungi has also been shown to affect the reproductive capacity of a plant, influencing the timing of reproduction, quantity of seed produced, and quality (size and competitive ability) of the resultant offspring (Koide and Lu 1992, Lewis and Koide 1990, Shumway and Koide 1995).

The presence of mycorrhizal fungi can alter the outcome of interspecies competition among plants. This has been demonstrated most conclusively in competition experiments between mycotrophic and nonmycotrophic plants. In the presence of mycorrhizal fungi, the mycotrophic grasses *Pascopyrum smithii*

and *Bouteloua gracilis* were able to outcompete non-mycotrophic *Salsola tragus* L., an exotic invasive of disturbed soils. In their absence, the reverse was true (Allen and Allen 1984). Similar changes in competitive outcome have been obtained using other grass-exotic weed, grass-grass, and grass-legume combinations that differed in their dependence on mycorrhizae (Benjamin and Allen 1987, Crush 1974, Fitter 1977, Goodwin 1992, Hall 1978, Hartnett and others 1993, Hetrick and others 1989, West 1996). Multispecies experiments have shown that the presence or absence of mycorrhizal fungi can alter species composition and diversity in grassland ecosystems (Grime and others 1987, Hartnett and Wilson 1999, van der Heijden and others 1998, Wilson and Hartnett 1997).

Species composition and diversity of the fungal community itself may affect plant community structure (van der Heijden and others 1998). Mycorrhizal fungal species differ in their ability to take up nutrients and promote growth (Haas and Krikun 1985, Jakobsen and others 1992, Stahl and Smith 1984, van der Heijden and others 1998, Wilson and Tommerup 1992). Fungal species are known to have a patchy distribution and may occur in specific microhabitats (Allen and MacMahon 1985, Johnson 1993). Therefore, individual plants may be colonized by the same fungal species, by different fungal species, or by multiple species of fungi (Rosendahl and others 1990, van der Heijden and others 1998).

The number and proportion of fungal symbionts can vary from plant to plant even within a relatively homogenous vegetation type. Differences among plants in their response to colonization, as well as in the complement of mycorrhizal fungi present on the root system, will differentially affect their ability to compete for soil resources (Streitwolf-Engel and others 1997, van der Heijden and others 1998).

Another factor affecting plant-plant interaction is that of interplant connections through a shared mycelial network. Studies have documented carbon and phosphorus transfer between plants connected by arbuscular mycorrhizal hyphae (Chiariello and others 1982, Francis and Read 1984, Newman and Ritz 1986, Whittingham and Read 1982). The ecological significance of these fungal connections is not well understood, however. Interplant connections may promote the transfer of nutrients from larger "source" plants to subordinate "sink" plants, thus allowing less competitive species to coexist with dominants (Allen 1991, Grime and others 1987). This scenario was invoked by Grime and others (1987) to explain why the addition of mycorrhizal fungi increased plant diversity in a microcosm experiment. Source to sink resource transfer may be of particular benefit to seedlings establishing in existing vegetation (Fitter 1989, Francis and Read 1984) and to plants growing in nutrient-poor soil patches (Allen and Allen 1990).

In contrast to the above theory, existing data from greenhouse competition experiments using mycotrophic species show an increase in competition in the presence of mycorrhizal fungi, rather than a cooperative interaction (Caldwell and others 1985, Hetrick and others 1989, Zobel and Moora 1995). There is great difficulty, however, in extrapolating data from greenhouse experiments with two species to actual field conditions, where the complexity of interaction is much greater. Zobel and Moora (1995) suggested that competition experiments might not include the critical stages of plant development (such as seedling and flowering stages) where source-sink transfer is thought to be most important.

Variation in precipitation patterns or patchiness in resource availability, factors rarely included in greenhouse experiments, can greatly affect mycorrhizal functioning and plant community composition (Allen 1991, Duke and others 1994, Hartnett and Wilson 1999, Pendleton and Smith 1983). Temporal and spatial niche partitioning due to differences in microhabitat requirements and in plant phenology limit the amount of actual competition experienced by a plant (Hetrick and others 1989). Certainly, extensive research is required before the role of mycorrhizae in regulating natural grassland communities can be well understood.

Disturbance and Succession

In grasslands, most arbuscular mycorrhizal (AM) hyphae and spores occur in the top 20 cm of the soil profile where the concentration of plant roots is the greatest (Allen 1991). Any disturbance resulting in the redistribution of these soils can affect the number and dispersion of mycorrhizal roots, hyphae, and spores. In most cases, soil disturbance leads to a reduction in the number of mycorrhizal propagules (Allen and others 1987, Jasper and others 1989, Moorman and Reeves 1979, Powell 1980). Small-scale natural disturbance such as gopher activity can create patches of low inoculum density as subsurface soils are brought to the surface (Koide and Mooney 1987). Inoculum density increases as hyphae from adjacent mycorrhizal plants slowly expand into sterile areas (Allen 1991). Spores may also be carried into these areas by crickets, grasshoppers, and other insects (Trappe 1981).

Large-scale disturbances such as surface mining, road construction, and watershed erosion can create extensive areas in which the amount of mycorrhizal inoculum is greatly reduced or eliminated (see for example Allen and Allen 1980). Mycorrhizal inoculum is introduced into these areas largely through wind-blown spores (Allen 1991). Consequently, the unaided restoration of mycorrhizal-dependent vegetation may require a long time (Miller 1987).

Changes in soil inoculum potential can affect a plant's ability to colonize disturbed areas. Many researchers have noted an increase in the abundance of mycotrophic species along a successional sequence (Allen 1991, Janos 1980, Miller 1987). Allen and Allen (1990) have proposed a successional model in which biomes are classified according to nutrient and moisture gradients. The degree of dependence on mycorrhizae increases with precipitation and decreases with enhanced soil fertility.

In arid grasslands, as in arid shrubland, early seral plant species are predicted to be largely nonmycotrophic, whereas late seral species are facultative in their dependence. These predictions are supported by numerous research reports. For example, Allen and Allen (1980) found five of seven annuals growing on strip-mined and disked prairie sites were nonmycorrhizal. Nonmycotrophic annuals predominated for up to 10 years on mined sites composed of sterile subsoil. Similarly, Pendleton and Smith (1983) found flat semi-arid disturbed sites to be dominated by nonmycorrhizal species. Cover of mycorrhizal species increased with water availability. Soil fumigation can delay succession, suggesting that soil biotic communities, including mycorrhizal fungi, have a significant impact on successional dynamics (Stevenson and others 2000).

Little is known about successional patterns in mesic and dry alpine grasslands. The successional model of Allen and Allen (1980) would predict that all seral stages comprise facultative species, with perhaps some obligate species in late seral stages. Allen and others (1987) found all surveyed species colonizing disturbed alpine ecosystems to be mycotrophic. No relationship between age since disturbance and degree of colonization or spore number was apparent.

Species of the fungal symbiont also appear to change with succession (Allen 1991). Fungal communities of late successional grasses apparently differ from those of early successional grass species (Johnson and others 1992). Others report an increase in diversity of VA fungal species with increasing seral stage (Allen and others 1987, Brundrett 1996, Nicolson and Johnston 1979).

Grazing

The response of mycorrhizae to aboveground herbivore grazing varies widely depending on the plant and fungal species involved, on the type and intensity of grazing, and on a number of abiotic factors. Some studies have shown a decrease in mycorrhizal colonization of forage grasses as a result of livestock grazing or defoliation (Allsopp 1998, Bethlenfalvay and Dakessian 1984, Bethlenfalvay and others 1985, Wallace 1981). Others report either no effect or an increase in mycorrhizal activity (Allen and others 1989, Davidson and Christensen 1977, Tisdall and Oades

1979, Wallace 1987). In some instances, colonization by mycorrhizal fungi has been shown to enhance tillering and a prostrate growth habit, thereby increasing the plant's ability to tolerate grazing (Bethlenfalvay and Dakessian 1984, Miller 1987, Wallace and others 1982). Allsopp (1998) found that the response to defoliation by three mycorrhizal forage grasses depended on the grazing tolerance of the host plant species.

The response of the mycorrhiza to grazing is likely related to the carbohydrate storage and photosynthetic capacity of the host plant at the time defoliation occurs. Regulation of the association seems to be a function of the host plant (Koide 1993). And, although generally considered beneficial to the host plant, the fungi can be parasitic if the net cost of the symbiosis exceeds the net benefit (Johnson and others 1997, Koide 1993). Plants benefit from the association when photosynthate is readily available or when the association increases the plant's ability to photosynthesize (Bethlenfalvay and Pacovsky 1983). Therefore, when soil resources are more limiting than photosynthetic leaf area, herbivory may have little effect on mycorrhizal functioning (Allen 1991).

Under conditions that severely limit the amount of carbon a plant is able to fix and store—such as extremely low nutrient availability, insufficient light, or prolonged drought—the fungus may constitute an excessive carbon drain on the plant (Johnson and others 1997). Herbivory under these conditions would likely be accompanied by a reduction in mycorrhizal function. For example, in a pinyon-juniper ecosystem, defoliation caused a decrease in mycorrhizal function for plants growing in nutrient- and water-stressed volcanic fields, but not for plants growing in a nearby sandy loam (Gehring and Whitham 1995).



Prescribed burn on the Kiowa National Grassland, Union County, New Mexico. (Photo by Mike Friggens)

Fire

Response of mycorrhizal fungi to fire is variable, with some studies reporting a decrease in mycorrhizal function, while others report no effect or an increase in function (Allen 1991, Eom and others 1999). Of those studies reporting a temporary decrease in mycorrhizal function, whether in soil propagule numbers or percent root colonization, most had recovered within 1 to 2 years (Dhillon and others 1988, Gurr and Wicklow-Howard 1994, Pendleton and Smith 1983, Rashid and others 1997). Recovery rates depended in part on fire intensity and on soil conditions at the time of burning (Klopatek and others 1987, Wicklow-Howard 1986). Klopatek and others (1987) reported moderate decreases in propagule numbers when soil temperatures reached 50 to 60 °C. Significantly greater propagule loss occurred at soil temperatures greater than 60 °C. Colonization of plant roots also decreased following fire; however, the decrease was less in wetter soils.

The observed response of mycorrhizal fungi to fire may be a reflection of fire effects on the plants themselves, rather than a direct effect upon the fungi (Dhillon and others 1988). Soil provides good insulation. Riechert and Reeder (1971) reported no increase in soil temperature at a depth of 1 cm, despite surface temperatures of 200 °C. Dhillon and co-workers (1988) attributed temporary decrease in root colonization to a fire-induced stimulation of root production that temporarily outstripped colonization by the fungi. Much of the research on fire effects on mycorrhizal fungi has been done in tallgrass prairie, however. Additional research on arid grasslands is needed. Recovery of vegetation in arid grasslands is highly dependent on postfire precipitation patterns and generally occurs at a slower rate than in more mesic grasslands. The response of mycorrhizal fungi to fire is most likely reflective of the vegetation response, generally proceeding at a slower pace in arid areas and depending on the same suite of factors that affect vegetation response.

The interaction between fire, watershed stability, and mycorrhizal fungi needs further research. However, one of the most important factors affecting mycorrhizal recovery following fire is that of soil erosion. In areas where postfire erosion is significant (such as steep slopes or high-intensity fires), loss of topsoil may delay the recovery of mycorrhizal function (O'Dea and others 2000). Eroding topsoil carries with it a large proportion of mycorrhizal propagules. Seedlings planted on eroded soils had significantly less colonization, growth, and survival than those with additions of captured eroded soil (Amaranthus and Trappe 1993).

Atmospheric Change

Disturbance in the form of increasing atmospheric CO₂ concentrations and anthropogenic nitrogen

deposition may also significantly affect mycorrhizal functioning within grassland communities (Egerton-Warburton and Allen 2000, Rillig and others 1999). Researchers are just beginning to explore these possibilities. McLendon and Redente (1991) reported a delay in successional change of plant species on fertilized plots. Early seral colonizers, nonmycotrophic *Salsola tragus* and *Bassia scoparia* (L.) A.J. Scott, still retained dominance of N-fertilized plots 2 years after control plots had changed to perennial (and mycotrophic) grasses, shrubs, and forbs.

Exotic Weeds

Noxious weeds compose a serious threat to the structure, organization, and function of ecological systems (Olsen 1999). Weeds prefer disturbed areas where resource availability is increased (Davis and others 2000). Of course, these are also areas where the mycorrhizal inoculum potential of the soil has been reduced. A healthy soil microflora can, in some cases, differentially enhance survival and production of native species over that of exotic weeds.

As mentioned previously, mycorrhizae generally enhance the competitive ability of those plants that are most responsive to the fungi. Many of the world's most aggressive weeds are either nonmycotrophic or facultatively mycotrophic (Trappe 1987). Invading annuals on arid grasslands are often nonmycotrophic weeds of the chenopod, mustard, and amaranth families (Allen 1991). Competition experiments between these species and native grasses have demonstrated enhanced competitive ability of native grass species in the presence of mycorrhizal fungi. Mycorrhizae contribute, therefore, to the resistance of these native communities to invasions of exotic weeds (Goodwin 1992).

Exotic grasses, on the other hand, are facultatively mycotrophic. Large areas in the Western United States are now dominated by exotic grasses such as cheatgrass (*Bromus tectorum* L.) in the Great Basin, Lehmann lovegrass (*Eragrostis lehmanniana* Nees) in the Southwest, and Mediterranean annual grasses in southern California (Allen 1995, McClaran 1995, Stylinski and Allen 1999). The role of mycorrhizal fungi in regulating competitive interactions between these exotic species and native vegetation is uncertain. It is likely, however, that competition between exotic and native grass species will be little altered by mycorrhizal fungi (Goodwin 1992).

In monoculture, cheatgrass shows no positive response to mycorrhizal fungi, although colonization levels can be quite high (Allen 1984, Benjamin and Allen 1987, Schwab and Loomis 1987). Cheatgrass may benefit, however, when the relative density of mycorrhizal competitors is high (Goodwin 1992, Schwab and Loomis 1987). Similarly, Nelson and Allen (1993) reported that the addition of mycorrhizae did not

enhance competitive ability of purple nodding tussock grass (*Nassella pulchra* (A.S. Hitchc.) Barkworth) in competition with annual slender oats (*Avena barbata* Pott ex Link).

Unfortunately, in some cases, invasive nonnative woody or herbaceous species are more responsive to mycorrhizae than are native grasses. In these instances, the presence of mycorrhizal fungi may actually enhance the competitive ability of the invading species. For example, Marler and others (1999) report that AM fungi strongly enhance the competitive ability of spotted knapweed (*Centaurea biebersteinii* DC.) grown in competition with Idaho fescue (*Festuca idahoensis* Elmer). Clearly, the problems stemming from invasive weeds will increasingly challenge the resourcefulness, skill, and ecological knowledge of all managers and researchers concerned with the health of our Southwestern landscapes.

Ecosystem Restoration

The establishment of mycorrhizal associations is an important consideration in the design of successful revegetation and restoration efforts of grasslands. Miller and Jastrow (1992) list eight site conditions under which management for mycorrhizae may be particularly important, nearly all of which are applicable to Southwestern grasslands. Mycorrhizae may aid in restoration attempts by enhancing plant survival, increasing soil stability, and through their effect on competitive interactions of successional plant species. Mycorrhizae are also important contributors to stable soil structure and the redevelopment of nutrient cycles (Miller and Jastrow 1992).

As discussed above, anthropogenic activities that remove, compact, or otherwise disturb soil can severely reduce or eliminate mycorrhizal propagules. This, in turn, affects the ability of mycotrophic plant species to colonize the site. In addition to aiding plant survival and establishment, the reintroduction of mycorrhizae may allow late or mid-seral species to perform better than nonmycotrophic early seral species, thereby speeding up the rate of succession (Allen and Allen 1988, Reeves and others 1979). Because of this, mycotrophy could be an important factor in determining of seed mixes for grassland rehabilitation.

Severely disturbed sites such as mine spoils are particularly difficult sites for plant establishment, combining adverse growing conditions with a lack of viable mycorrhizal inoculum. Inoculation with VA fungi can greatly improve survival and growth of desirable reclamation plants, particularly shrubs, grown on mine spoil material and other severely disturbed soils (Aldon 1975, Lindsey and others 1977, Smith and others 1998, Stahl and others 1988, Williams and Allen 1983). Transplants may then form islands of inoculum that can spread through root and

hyphal growth, as well as wind and animal dispersal (E.B. Allen 1984, M.F. Allen 1991). Reintroduction of mycorrhizae to severely disturbed sites may be enhanced through the use of soil amendments or redistribution of stockpiled topsoil, provided topsoil has been managed properly (Allen and Allen 1980, Allen 1984, Johnson 1998, Miller 1987, Pendleton 1981, Zak and Parkinson 1983).

Where severe soil disturbance makes it impractical to seed with mycorrhizal-dependent late-seral species, seeding with facultative midseral species such as cool-season grasses may help to increase soil inoculum to the point where more dependent warm-season grasses and shrubs can establish successfully (Noyd and others 1995). Johnson (1998) suggests that seeding of facultative mycotrophic species and manipulation of edaphic conditions to optimize mycotrophy may be a more cost effective method of rehabilitation than large-scale inoculation. The precise combination of techniques needed for successful rehabilitation will depend on soil conditions and the severity and scale of the disturbance, as well as management objectives (Allen 1995).

Biological Soil Crusts

Biological soil crusts are known by many names, including microphytic crusts, microfloral crusts, cryptogamic crusts, and cryptobiotic crusts (St. Clair and Johansen 1993). As the name implies, they are biological in nature, being composed of cyanobacteria, green algae, lichens, and mosses. Other bacteria and fungi (including mycorrhizal fungi) may also be present (Belnap and others 2001). It is important to distinguish biological soil crusts from inorganic soil crusts formed by chemical and physical means. Inorganic soil crusts reduce water infiltration and may hinder seedling emergence. In contrast, biological soil crusts play an important role in arid and semiarid lands by stabilizing soil surfaces, increasing soil fertility through the fixation of atmospheric nitrogen, and improving seedling establishment (Belnap and others 2001, Johnston 1997, St. Clair and Johansen 1993).

Biological soil crusts are formed by the interweaving of cyanobacterial and fungal strands within the upper soil surface. Gelatinous sheath material and other polysaccharides extruded by these organisms further help bind the soil particles together. The resulting crust may be anywhere from 1 mm to 10 cm thick (Belnap and Gardner 1993, Johnston 1997). The dominant photosynthetic organisms—cyanobacteria and green algae—require sunlight, and most of the living cells are found 0.2 to 0.5 mm below the surface (Belnap and others 2001). The polysaccharide sheaths of cyanobacteria expand when wet, pushing the interior bacterial filaments out across the soil surface. New

sheath material is produced by these filaments as they dry out. Old sheath material gradually becomes buried and, although no longer photosynthetic, continues to contribute to the thickness and water-holding capacity of the crust (Belnap and Gardner 1993).

Biological soil crusts are highly variable in appearance and may be grouped according to their morphology. They may be smooth or rough, flat or pedicelled, greenish or black, depending on the temperature regime of the area and the types of organisms involved (Belnap and others 2001). Simple algal and cyanobacterial crusts may be flat. Topography of these crusts increases as the more complex lichens and mosses colonize the site. Increased topography of crusts is also associated with frost heaving (Johnston 1997). Crust morphology in hot desert regions, including the Chihuahuan and Sonoran Deserts, is flat to slightly rough or rugose. Cool desert regions such as the Great Basin and Colorado Plateau are dominated by rolling or pinnacled crusts (Belnap and others 2001). Different morphotypes differ in their ecological function with regard to water retention and erodability (Eldridge and Rosentreter 1999).

Distribution and Occurrence

Biological soil crusts are found throughout the world, occurring on every continent and in multiple vegetation types. Although most well known from arid and semiarid regions, they also occur on shallow alpine soils and other areas where vascular plant cover is low. In the Southwestern United States, cyanobacteria, lichens, and mosses are the most important components of soil crusts (Ladyman and Muldavin 1996). Many of the most common organisms, such as *Microcoleus* spp., *Nostoc* spp., *Collema* spp., *Psora decipiens* (Hedwig) Hoffm., and *Catapyrenium lachneum* (Ach.) R. Sant., are cosmopolitan in nature, occurring in many geographic areas. Other species are endemic or have a much narrower geographic range (Belnap and others 2001, St. Clair and others 1993).

Regional trends in the timing and amount of precipitation greatly affect species composition of the crustal community. Regions in which precipitation falls mainly during the winter months have a diverse lichen community and a cyanobacterial community dominated primarily by *Microcoleus* (Belnap and others 2001). Great Basin areas are dominated by



Soil crust composed of algae, lichens, and mosses. (Photo by Rosemary Pendleton)

low-growing soil lichens such as *Collema tenax* (Swartz) Ach., *Catapyrenium lachneum*, and *Caloplaca tominii* (Savicz) Ahlner (St. Clair and others 1993). In contrast, crusts of the Great Plains are dominated by detached foliose (leaflike) or fruticose lichens (Belnap and others 2001). Crusts of the Colorado Plateau are dominated by the cyanobacteria *Microcoleus*, along with the lichen *Collema*. Upland areas of the Colorado Plateau have many species of the genus *Psora* (St. Clair and others 1993). In regions characterized by summer rainfall, the lichen community is small and the cyanobacterial community diverse. Common cyanobacterial genera in the Sonoran Desert include *Nostoc*, *Schizothrix*, and *Scytonema* (Belnap and others 2001).

On a local level, species composition is largely influenced by soil texture, soil chemistry, slope, and aspect (Belnap and others 2001, Ladyman and Muldavin 1996). In general, silty loams support a greater diversity of crust organisms than do sandy soils (Belnap and others 2001). Green algae are more common on acidic soils, while blue-green algae (cyanobacteria) are more common on alkaline soils (Ladyman and Muldavin 1996). Gypsiferous and calcareous soils often have extensive crusts with a high diversity of organisms (St. Clair and others 1993). Alpine sites have many unique lichen taxa, as well as some that are common to the region (Belnap and others 2001). In the arid Southwest, crust development is often noticeably greater on north-facing slopes and near ridge tops (Brotherson and Masslich 1985, Pendleton, personal observation).

Ecological Function

Biological soil crusts contribute to a variety of ecological functions, including soil stabilization, nitrogen fixation, nutrient availability, and vascular plant establishment. Of primary importance is the ability of biological crusts to reduce wind and water erosion of soil surfaces (Belnap 1993, Belnap and others 2001, Eldridge 1993, Johnston 1997, Ladyman and Muldavin 1996). Within the crust, filamentous cyanobacteria and green algae intertwine with soil particles, stabilizing soil surfaces. Fungal strands, or hyphae, further bind soil particles, as do the rhizoids of mosses. Polysaccharides exuded by cyanobacteria, algae, and some fungi (see mycorrhizal section) cement soil particles together into stable aggregates. The increased surface topography of later successional crusts also serves to protect the soil surface from wind and water erosion (Belnap and others 2001, Johnston 1997).

Several studies have shown that crusted soils require much higher wind velocities before soil movement will occur (Belnap and Gillette 1998, Mackenzie and Pearson 1979, Williams and others 1995). Eldridge (1993) found a significant increase in splash erosion when biological soil crust cover was less than 50 percent. Loss of soil fines—particles associated with soil nutrients—also increased with decreasing crust cover. Moss-dominated and some lichen-dominated crusts increase infiltration of surface water, thereby decreasing erosion potential (Ladyman and Muldavin 1996 and references therein). Other studies report reduced infiltration, particularly in crusts dominated by cyanobacteria (Ladyman and Muldavin 1996 and references therein). However, even when infiltration is not increased, sediment loss is still reduced when compared with disturbed soils where the crust layer has been completely lost.

Biological soil crusts contribute to the fertility of grassland soils by increasing soil nitrogen and carbon content. This may be particularly important in arid areas of the Southwest where vegetation is sparse. Carbon contributions are greater where crusts are dominated by lichens and mosses, whereas nitrogen gains are greater where cyanobacteria and cyanolichens predominate (Belnap and others 2001). Carbon inputs to the soil come from active secretion of fixed-carbon compounds, as well as through the destruction of cell membranes during wet-dry cycles and upon death of the organism (Ladyman and Muldavin 1996). The amount of biomass contributed may be substantial. Beymer and Klopatek (1991) estimated carbon contributions of up to 350 kg/ha/year by undisturbed soil crusts in northern Arizona. Harper and Pendleton (1993) reported higher levels of soil organic matter in crusted areas of southern Utah.

Crust organisms are metabolically active only when wet. However, even small amounts of liquid moisture can trigger a rapid induction of metabolic processes. Available evidence suggests that positive carbon gains require a prolonged wet period (Jeffries and others 1993). In the Colorado Plateau, most growth of biological soil crusts occurs during the spring (Belnap and others 2001). Similar studies in areas of high summer rainfall would help define seasonal growth patterns for these regions. Because organisms differ in the temperature and moisture contents needed for maximum photosynthetic efficiency, regional shifts in the timing and amount of precipitation received may result in a compositional change in the crust community.

The cyanobacterial component of soil crusts, whether free-living or part of a lichen symbiosis, is capable of fixing atmospheric nitrogen. This process takes place only under anaerobic conditions. Many cyanobacteria have specialized cells for this purpose, called heterocysts. Nonheterocystic cyanobacteria, such as *Microcoleus* create anaerobic conditions by the layering of their filaments beneath the soil surface (Belnap and others 2001). Estimates of the amount of nitrogen fixed by soil crusts range from 2 to 365 kg/ha/year (Belnap and others 2001, Johnston 1997, Ladyman and Muldavin 1996, Rychert and others 1978). Fixation rates depend on temperature and precipitation patterns, as well as the species composition of the soil crust.

Arid regions are generally low in nitrogen content compared to other regions, and arid regions have few nitrogen-fixing plant species (Farnsworth and others 1976, Wullstein 1989). Studies using stable isotopes demonstrate that much of the nitrogen used by higher plants in arid and semiarid regions was originally fixed by soil crust organisms (Belnap 1995, Evans and Ehleringer 1993). Other studies report that plants growing on crusted soils have higher tissue concentrations of nitrogen than plants growing in nearby disturbed areas (Belnap and Harper 1995, Harper and Pendleton 1993).

The presence of biological soil crusts can significantly affect germination and growth of vascular plant species. Small seeds can lodge in the cracks of the roughened crust surface. The dark surface of the soil crust can raise soil temperatures 5 °C or more, promoting earlier spring germination and growth (Harper and Marble 1988, Harper and Pendleton 1993). The greatest benefit may be to shallow-rooted annuals and to deeper-rooted perennials during the critical establishment phase following germination. Many studies have reported increased survival and nutrient content of young seedlings growing in crusted soils (Belnap and Harper 1995, Harper and Marble 1988, Harper and Pendleton 1993, Pendleton and Warren 1995).

Nutrients enhanced by the presence of soil crusts include nitrogen, mentioned previously, and also P, K, Ca, Mg, and Zn. Enhanced nutrient content may be due to the tendency of biological crusts to trap nutrient-rich soil fines (Belnap and Gardner 1993). Cyanobacterial sheaths also secrete chelating agents that increase the availability of essential nutrients (see references in Belnap and others 2001, Harper and Pendleton 1993, Ladyman and Muldavin 1996). Biological crusts interact with other soil microorganisms in promoting the establishment and growth of vascular plant species. Harper and Pendleton (1993) found increased colonization by several rhizosymbionts (mycorrhizal fungi, *Rhizobium*, and rhizosheath organisms) in plants growing on crusted soils.

There is no credible evidence that cover of vascular plant species and biological soil crusts are negatively related, as was suggested by Savory (1988). Cover of biological soil crusts has been positively correlated with diversity of plant species (Beymer and Klopatek 1992, Harper and Marble 1988). Numerous other studies report either a positive correlation or no correlation between plant cover and the cover of biological soil crusts (Belnap and others 2001).

Ladyman and others (1994) examined vegetative cover on three undisturbed mesas in New Mexico and found that the mesa with the highest crust cover also had the highest grass cover. Specifically, blue grama grass (*Bouteloua gracilis*) was positively associated with soil crust cover. In another comparison between two grassland communities, Kleiner and Harper (1977) found no competition between soil crust organisms and vascular plant species. Rather, grass cover and crust cover appeared to be independent of one another. Ladyman and Muldavin (1996) suggest that specific associations of vascular plants and crust organisms that appear to be negative, positive, or neutral, may be more a reflection of their particular habitat requirements rather than actual competition. Greenhouse experiments, however, seem to indicate some competition between soil microorganisms and plants, particularly when crust organisms are themselves becoming established (Harper and Pendleton 1993, Pendleton, unpublished data).

Disturbance and Succession

Disturbance of the soil crust through trampling, vehicular travel, or soil movement affects the functioning of biological soil crusts through changes in cover, composition, or by affecting rates of carbon and nitrogen fixation (Belnap and others 2001, Ladyman and Muldavin 1996). The impact of the disturbance depends on the severity and type of disturbance, the frequency of disturbance, soil texture, and climatic conditions. Disturbance that compacts the soil crust but leaves crust material in place is less severe than

disturbance that removes or kills crust organisms. Where the crust is destroyed, the loss of soil structure results in an unstable surface that is highly susceptible to erosion. Crusts formed on sandy soils are more easily damaged when dry, whereas crusts formed on clay soils are more vulnerable when wet. Lichens and mosses are more susceptible to disturbance than are cyanobacteria and green algae (Belnap and others 2001).

Repeated disturbance can result in a less complex (early successional) crust structure, or in the complete loss of the soil crust (Belnap and others 2001, Harper and Marble 1988). Estimates of recovery rates for soil crusts vary widely. Under optimal conditions visual recovery may occur within 1 to 5 years (Belnap 1993, Cole 1990, Johansen and Rushforth 1985). Recovery in terms of chlorophyll content, community composition, and organism density takes much longer. Belnap (1993) estimated recovery rates for Colorado Plateau crusts of 40 years for chlorophyll *a* content, 45 to 80 years for the lichen component, and 250 years or more for the moss component. Clearly, full recovery from severe disturbance can take a long time.

Crust development follows a definite successional pattern, with various organisms classed as either early or late successional species. Initial colonization of a site is usually accomplished by either cyanobacteria or green algae, depending on the acidity of the soils (Belnap and others 2001). A common colonizer of Southwestern soils is the large filamentous cyanobacteria, *Microcoleus*. These filaments help stabilize the soil surface, a function especially important for sandy soils, and allow colonization by other cyanobacteria and algae.

In hot deserts with summer monsoonal rainfall, different cyanobacteria, such as *Schizothrix* and *Nostoc* spp., may be more common (Johnston 1997). Once soils are stabilized, colonization by gelatinous nitrogen-fixing lichens, such as *Collema tenax*, can occur (Belnap and others 2001). Other early successional Southwestern species include the lichens *Cladonia chlorophaea* (Flk.) Spreng., *Endocarpon pusillum* Hedwig, and *Peltigera rufescens* (Weiss) Humb. Mid to late successional species include other lichen taxa (such as *Psora* spp.), mosses (*Grimmia* and *Tortula* spp.), and liverworts (*Riccia* spp.; Ladyman and Muldavin 1996). Because growth of crustal organisms can take place only when wet, succession occurs at a faster rate in years of high precipitation, on north-facing slopes, and on fine-textured soils that retain moisture longer (Belnap and others 2001, Ladyman and Muldavin 1996).

Monitoring of biological soil crusts has been suggested as a means of assessing ecosystem health. More recently, Eldridge and Rosentreter (1999) proposed

a system of monitoring using morphological groups rather than species. Crust morphology determines its functioning in terms of water retention, erodability, and resistance to disturbance (Belnap and others 2001, Eldridge and Rosentreter 1999). This system provides an easier and more accurate method for nonspecialists to use in monitoring the effects of different management practices on ecosystem health. Specific techniques for monitoring biological soil crusts are covered in Belnap and others (2001).

Grazing

Different regions of the Southwest have different grazing histories, soils, and precipitation patterns. With the exception of the short-grass steppe, most regions historically experienced minimal disturbance by large herds of grazing mammals and may therefore be more susceptible to damage from grazing animals (Belnap and others 2001, St. Clair and others 1993). The effect of livestock grazing on biological soil crusts is due primarily to trampling, or hoof action. Trampling breaks up the sheath and filament structure that binds the soil particles, leading to increased erosion and loss of soil fertility.

The destruction of the crust through hoof action, while advocated by some (Savory 1988), does not result in increased plant cover as had been surmised (Ladyman and Muldavin 1996 and references therein). The magnitude of the disturbance is proportional to the grazing pressure and is also dependent on the seasonality of grazing. As discussed previously, biological crusts on most soils of the Southwest are more tolerant of disturbance when soils are moist. On these soils, late fall/early winter grazing is least likely to cause damage to crusts (Anderson and others 1982, Belnap and others 2001, Marble and Harper 1989). Several researchers have suggested that periodic rest from grazing would benefit crust organisms and grasses alike (Brotherson and others 1983, Johansen 1986). Belnap and others (2001) recommend light to moderate grazing in the early to mid wet season. Low-elevation grazing during the winter months followed by grazing of high-elevation sites during the summer would more closely mimic grazing patterns of native ungulates.

Fire

Fire has historically been a common occurrence in grassland ecosystems. Evidence from other vegetation types suggests that fire can damage soil crusts, depending on the fire's intensity, frequency, and timing, and depending on soil moisture content during and immediately following the fire (Belnap and others 2001, Ladyman and Muldavin 1996). High intensity fires, followed by drought, can result in

substantial loss of the crust community, particularly lichens and mosses. Recovery may take many years. Unburned patches within the burned matrix can, however, provide propagules for reestablishment of soil crust organisms (Belnap and others 2001). Low intensity fires may allow for rapid regrowth of algae and cyanobacteria (Johansen and others 1993, Johnston 1997). Johansen and others (1993) theorized that recovery of the crust might be partially dependent on recovery of vascular plant cover. This suggests that recovery in fire-adapted grasslands may proceed at a faster pace. Adequate moisture during the postfire recovery period will further speed the recovery process.

Ford (2000) studied the effect of fire season on biological crusts in a short grass steppe. In the short term, growing-season fire appeared to reduce the impact of fire on microbiotic crusts ability to fix nitrogen, compared to dormant-season fire, due to the differences in the nature of the fire. Growing-season fires occurred when vegetation was green and moisture was high, whereas dormant-season fire occurred when moisture was low and fine fuel (vegetation) was dry. Again, adequate moisture appears to be the key component in crust recovery following fire and abundant precipitation will override any fire effects (Ford, personal communication).

Pollution

Many lichens are sensitive to common air pollutants and have been used as indicator species in other regions (Nash and Wirth 1988, St. Clair and others 1993). However, studies on Southwestern soil lichens found near pollution sources such as power plants have found no change in crust composition or cover (Belnap and others 2001, Ladyman and Muldavin 1996). It is thought that the low stature of soil lichens and the alkalinity of Western soils may ameliorate the effects of acidic sulfur emissions. Human-induced increases in atmospheric nitrogen deposition do have a negative effect on soil crusts, inhibiting natural fixation rates by soil microorganisms (Harper and Marble 1988). Fixation rates of cyanobacteria and cyanolichen crusts declined in the presence of power plant effluents (Belnap and others 2001). The effects of increasing atmospheric CO₂ levels have not yet been studied.

Exotic weeds

Little is known about the effects of exotic weed introductions on soil crust functioning. In areas where native bunchgrasses have been replaced by annual brome (such as *Bromus tectorum*), the soil crust consists of only a few species of annual mosses and cyanobacteria instead of the complex perennial crust community characteristic of undisturbed sites

(Kaltenecker 1997). This change in crust composition may be at least partially due to the drastic change in fire frequency that accompanies annual brome invasions. Similar studies are needed to determine the effects of lovegrass and other exotic weed invasions on composition and functioning of biological soil crusts in the Southwest.

Restoration

The use of soil inoculants may hasten recovery of soil crusts on severely disturbed sites. This would be particularly helpful for large-scale disturbances where nearby sources of naturally dispersed inocula are not available. Initial trials have been promising. St. Clair and others (1986) used a slurry of soil crust and water to inoculate pinyon-juniper and salt desert shrub communities following severe fire. Within 6 months, inoculated soils had greater numbers of algae and lichens. Belnap (1993) used crumbled dry crust material to inoculate scalped plots on four sites in the Colorado Plateau. Recovery of inoculated sites was significantly greater in terms of chlorophyll *a* content, crust cover, and species diversity 2 to 5 years following disturbance. These experiments relied on preexisting crust material taken from other locations. Johansen and others (1994) have developed techniques to culture nitrogen-fixing cyanobacterial species. Initial tests used intact or ground algininate pellets as the inoculum source (Buttars and others 1994, 1998, Johansen and others 1994). Currently, development of a more economically feasible delivery system is under way (Johansen, personal communication).

Invasive Weeds

For centuries weeds have been the focus of study for farmers and agronomists. Alien weeds have arrived in North America from a number of sources. Many species were introduced as contaminants of agricultural seed or as unnoticed hitchhikers that immigrated with people, household goods, and livestock to North America and subsequently moved with settlement across the continent. Other species were originally introduced as ornamental plants and subsequently escaped cultivation to become established in the native landscape. A third group of species are those intentionally introduced with the hope that they would fulfill a specific management objective, but that have since proliferated to the point where they now pose a serious problem (Brock 1998, Cousens and Mortimer 1995).

The invasion of alien species has been likened to a biological wildfire that is rapidly spreading at a rate of 200 acres/hour in the West (Lee 1999, Mitchell 2000). As the number of exotic species and acreage affected

has risen, so has the concern of environmentalists and managers. Exotic weed invasions now command the attention of scientists and conservationists from a variety of backgrounds (Cousens and Mortimer 1995).

At the Federal level, President Clinton (1999) established a cabinet-level Invasive Species Council, which is charged with providing leadership in the management of invasive species. Executive Order 13112 outlines a far-reaching program designed to “prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause.” The executive order was the impetus for the current Forest Service weed management program. As Sheley and Petroff (1999) stated, our “commitment to addressing the rapid invasion of noxious weeds has been revived and intensified.”

Among the definitions of a weed are the tried-and-true “a weed is a plant out of place” and “a weed is any plant that interferes with the management objectives of a site” (Lee 1999). Lee (1999) defines an *invasive* as a plant that is not native to a particular ecosystem, and an *invasive weed* as one that has or will have a negative impact on the environment. The terms “invasive” and “weed” are used with both native and nonnative species. While a species may be native to North America, it may become invasive in regions where it was not historically present.

The definitions used in this section are as follows. A *noxious weed* is a legal term that identifies an undesirable plant as one that is regulated in some way by law (Sheley and Petroff 1999). Executive Order 13112 (Clinton 1999) standardizes the terminology used by Federal land managers. *Alien species* are species not native to a particular ecosystem. *Invasive species* are alien species whose introduction causes or is likely to cause economic or environmental harm or harm to human health.

Problems stemming from invasive plant species are many. Biological invasions disrupt natural ecosystems, posing negative consequences for both ecological and socioeconomic systems (Davis and others 2000, Mitchell 2000). Invasive species displace desirable native species, reduce the quality of wildlife habitat, damage sensitive riparian and watershed areas, and increase erosion (Lee 1999, Masters and Sheley 2001). As native vegetation becomes displaced, opportunities for land use decline and land values drop. Improvement requires enormous inputs of time and money from managers and management agencies (Lee 1999). Less visible, but perhaps more important, are the alterations in ecological processes that accompany vegetation change (Masters and Sheley 2001). Changes in vegetation result in changes in the soil microflora, affecting nutrient

cycling and decomposition rates (Adams and Wall 2000) as discussed in a previous section.

One of the greatest challenges facing scientists and managers is the unpredictable nature of biological invasions—why certain species become problems and where these problems are likely to occur (Peterson and Vieglais 2001). Invasive species have a number of characteristic traits that have been identified (Mitchell 2000). They are generally fast growing, produce numerous small seeds, and are adapted to disturbance (Grime 1988). Some, however, appear to be extremely competitive and can invade under conditions of low stress and low disturbance (Mitchell 2000). The presence and spread of nonnative species is thought to be an indicator of ecosystem health (Mitchell 2000), but even communities in good condition can be susceptible to weed invasions (Sheley and Petroff 1999).

Several hypotheses have been proposed in an attempt to explain why invasions take place (see Masters and Sheley 2001 and references therein for a review). Invasions seldom occur as a moving front, but rather by the establishment of small satellite populations that are often some distance from previously known populations (Cousens and Mortimer 1995). Noble (1989) theorized that displacement of native vegetation could occur either because the invader is a superior competitor, or because the invader is adapted to novel conditions present at the time of the invasion. Climatic change (for example, global warming or increased CO₂ levels) may constitute such novel conditions and contribute to the spread of some invasive species (Brock 1998). Lonsdale (1999) lists three factors that affect the ability of an alien species to invade a new environment: (1) the number of propagules entering the new environment, (2) the physiology of the invading species, and (3) the invasibility of the environment.

Invasibility of a given environment depends on a multitude of factors, including degree of disturbance and the health and makeup of the resident community (Lonsdale 1999). Each community appears to have its own invasibility criteria. Davis and others (2000) recently proposed a general theory of invasibility. They hypothesize that resources required by an invading species are not uniformly available through time, but rather fluctuate. These fluctuations may be caused by meteorological events and/or site disturbances such as grazing, pests, or mechanical disturbance. Therefore, the degree to which a community is susceptible to invasion varies through time, and invasion events are episodic. A number of modeling studies have attempted to predict where invasions will occur geographically, some with a fair degree of success (Peterson and Vieglais 2001).

Management

No universal prescription exists for managing invasive weeds that grow on Forest Service grasslands. Management plans take into consideration the biology of the weed, the number of plants involved, and the condition of the plant community. A single weed that has not yet flowered can be eradicated using several methods. But if that individual plant is allowed to set seed, eradication becomes more complex and will likely require more than one treatment. Without treatment, those seeds will produce a population, and as the seed bank and number of plants increases, eradication becomes exponentially more difficult. At some point in the growth of the population, eradication becomes impossible and alternative management methods become necessary (Brock 1998).

To provide guidance for appropriate management and control strategies, weeds are assigned an A, B, or C classification (Lee 1999). These class assignments are based on the distribution and population size of an invasive weed within a State or other land management area. Class A species have limited distribution within a management unit. Preventing new outbreaks and eliminating existing populations is the primary focus of management plans for class A weeds. Invasive weeds that are not present within a management unit but are found in adjacent areas, and therefore pose an invasive threat, are also listed as class A weeds. Class B weeds have well-established populations, but these populations are found only in limited areas. Containment within the current population location and preventing the establishment of new populations is the management focus for class B weeds. Class C weeds are widespread throughout a State or management area. Class C weeds are candidates for long-term management and suppression programs (Lee 1999).

The 1970s saw an increase in concern about the presence, expansion, and difficulty in controlling noxious and invasive weeds. These concerns—coupled with the increased costs of weed control, concerns about herbicide use, and general complexity involved in trying to control weeds on public and private lands—led to a new concept for the management of weeds. Termed Integrated Weed Management (IWM), this concept incorporates multiple management techniques into an integrated and well-planned strategy for management and control of weeds (Sheley and others 1999).

Walker and Buchanan (1982) define IWM as the application of technologies in a mutually supportive manner and selected, integrated, and implemented with consideration of economic, ecological, and sociological consequences. IWM involves several components: (1) prevention, (2) early detection and eradication of new weed populations, (3) containment and treatment

of established invasive weed populations, and (4) revegetation and site rehabilitation. A successful IWM plan includes education, a constant sustained effort, evaluation of results, and improvement of management strategies as the plan is implemented (Lee 1999, Masters and Sheley 2001, Sheley and others 1999). Prior to the development of an IWM plan, survey and mapping of the management area must be done to identify existing invasive weed populations.

Prevention has two aspects. The first is to limit the movement of plant propagules to new locations. Some measures that limit propagule migration include the cleaning of seeds from equipment and vehicles, use of weed-free livestock feed, and efforts to prevent seed movement by other human activities. The second is the ongoing monitoring of the landscape so that new satellite populations are identified quickly and eradicated.

Management options for the treatment of existing weed populations fall into four basic categories: (1) chemical, (2) biological, (3) mechanical, and (4) cultural (Lee 1999, Masters and Sheley 2001, Sheley and others 1999). Chemical treatment involves the use of herbicides. A broad range of herbicides—registered for use on rangeland and grasslands—act upon various parts of the plant and at different life cycle stages of growth. It is extremely important to use the appropriate herbicide, one that has the maximum impact on the target species and minimizes impact on nontarget species (see Bussan and others 2001, Masters and Sheley 2001 for a review of herbicides and their uses).

Biological treatment uses living organisms to reduce weed populations. Alien plant species generally lack their complement of population-controlling insects and pathogens (Mitchell 2000). Biological control specialists collect potential control agents (insects or pathogens) from the country where the weed originated. After extensive testing, these are released into infested areas with the goal of suppressing the alien weed population. Eradication is not the goal of biological control, but rather the reduction of the population to more acceptable levels (Masters and Sheley 2001).

Mechanical (also called physical) treatment involves removal of aboveground plant parts and/or disruption of the root system such that the plant is killed or severely injured (Masters and Sheley 2001). Methods include hand pulling, tilling, plowing, and mowing. As with all forms of treatment, the method used must be appropriate to the biology of the target species. For example, tilling a weed that reproduces vegetatively will spread the infestation further, whereas tilling an annual weed prior to seed set may provide good control.

Cultural practices include all methods to promote the growth of desired vegetation. Healthy native plant communities are less susceptible to weed invasion. Cultural practices include fertilization, alteration of

grazing practices, reseeding, revegetation, and other practices that promote the growth of desirable plant species (Masters and Sheley 2001). Cultural practices go hand in hand with other forms of treatment. When invasive weeds are removed from a community, steps can be taken to facilitate the establishment of desirable vegetation and prevent weeds from filling the recently vacated niche in the plant community (Masters and Sheley 2001).

Fire, both wildfire and prescribed, can impact weed populations either positively or negatively. Although fire can reduce the population of some weed species, the disturbance caused by fire provides opportunities for weed population expansion (Crawford and others 2001). The effect of fire on invasive species populations in the Southwest is the subject of ongoing research.

USDA Forest Service Southwestern Region

The Southwestern Region (Region 3) of the USDA Forest Service has a variety of grassland communities—from National Grasslands to high elevation montane grassland and meadow communities, with a number of grassland community types in between. All grassland communities in the Region are subject to invasion by weeds. Presently, the primary weed management focus of Region 3 is the preparation of National Environmental Policy Act (NEPA) documents, which are required prior to the formulation of weed management plans (D. Parker, personal communication).

The Region currently lists 38 species on its noxious weed list (table 3-1); 23 are classified as class A, five as class B, and 10 as class C. The total of 15 B and C species is a relatively low number compared to the number of well-established invasive weed species in States adjacent to the Region (R. Lee, personal communication). This fact, coupled with the list of 23 class A species, illustrates that there is still an opportunity to prevent many species of weeds from becoming well established in the Region. Prevention is the least expensive and most efficient form of weed management. Cox (2001, also available at <http://web.nmsu.edu/~kallred/herbweb/newpage3.htm>) provides a detailed list of the alien plant species of New Mexico. In addition, the Cooperative Extension Services of Arizona and New Mexico maintain current State lists of invasive species that can be accessed online.

Summary

Distributions of grasslands are regulated by soils and climate and modified by disturbance. A shifting equilibrium typically exists between grasslands, deserts, and shrublands of the Southwest, such that changes in the severity or frequency of disturbance

Table 3-1. Noxious weed list, USDA Forest Service Southwestern Region (Region 3). Life cycle classification; A=annual, B=biennial, P=perennial. Class refers to Region 3 management priority classification (see text).

Scientific Name	Common Name	Origin	Life Cycle	Class
<i>Aegilops cylindrica</i> Host	Jointed Goatgrass	So. Europe	A	C
<i>Alhagi pseudalhagi</i> Medicus.	Camelthorn	Asia	A	C
<i>Asphodelous fistulosus</i> L.	Onion Weed	Mexico	P	A
<i>Cannabis sativa</i> L.	Marijuana	Asia	A	C
<i>Cardaria chalepensis</i> (L.) Hand. –Maz.	Lens-podded Hoary Cress	Eurasia	P	A
<i>Cardaria draba</i> (L.) Desv.	Whitetop/Hoary Cress	Eurasia	P	A
<i>Cardaria pubescens</i> (C.A. Mey.) Jarmolenko	Globe-potted Hoary Cress	Eurasia	P	A
<i>Carduus nutans</i> L.	Musk Thistle	So. Europe	B	B
<i>Centaurea calcitrapa</i> L.	Purple Starthistle	Europe	A	A
<i>Centaurea diffusa</i> Lam.	Diffused Knapweed	Eurasia	P	A
<i>Centaurea maculosa</i> auct. non Lam. ¹	Spotted Knapweed	Eurasia	P	A
<i>Centaurea melitensis</i> L.	Malta Starthistle	Europe	A	B
<i>Centaurea repens</i> L. ²	Russian Knapweed	Eurasia	P	A
<i>Centaurea solstitialis</i> L.	Yellow Starthistle	Europe	A	A
<i>Cirsium arvense</i> (L.) Scop.	Canada Thistle	Eurasia	P	A
<i>Cirsium vulgare</i> (Savi) Ten.	Bull Thistle	Eurasia	B	C
<i>Convolvulus arvensis</i> L.	Field Bindweed	Europe	P	C
<i>Dipsacus sylvestris</i> Huds. ³	Teasel	Eurasia	B	A
<i>Drymaria arenarioides</i> Will.	Alfombrilla	Mexico	P	A
<i>Eichhornia azurea</i> (Sw.) Kunth	Anchored Waterhyacinth	Brazil	P	A
<i>Euphorbia esula</i> L.	Leafy Spurge	Eurasia	P	A
<i>Halogeton glomeratus</i> (Bieb.) C.A. Mey.	Halogeton	Asia	A	B
<i>Hydrilla verticillata</i> (L.F.) Royle	Hydrilla	So. Africa	P	A
<i>Hyoscyamus niger</i> L.	Black Henbane	Europe	B	A
<i>Isatis tinctoria</i> L.	Dyer's Woad	Europe	B	A
<i>Kochia scoparia</i> (L.) Schrad. ⁴	Kochia	Asia	A	A
<i>Linaria dalmatica</i> (L.) P. Mill.	Dalmation Toadflax	Europe	P	A
<i>Linaria vulgaris</i> P. Mill.	Yellow Toadflax	Eurasia	P	A
<i>Lythrum salicaria</i> L.	Purple Loosestrife	Europe	P	A
<i>Onopordum acanthium</i> L.	Scotch Thistle	Europe	B	A
<i>Peganum harmala</i> L.	African Rue	No. Africa	P	B
<i>Rorippa austriaca</i> (Crantz) Bess.	Austrian Field Cress	Eurasia	P	B
<i>Salsola iberica</i> (Sennen & Pau) Botsch. ex Czerepanov ⁵	Russian Thistle	Russia	A	C
<i>Sonchus arvensis</i> L.	Perennial Sowthistle	Eurasia	P	A
<i>Sorghum halepense</i> (L.) Pers.	Johnson Grass	Mediterranean	P	C
<i>Tamarix ramosissima</i>	Salt Cedar	Eurasia	P	C
<i>Tribulus terrestris</i> L.	Puncture-vine	So. Europe	A	C
<i>Verbascum thapsus</i> L.	Mullein	Asia	B	C

¹= *C. biebersteinii* DC.

²= *Acroptilon repens* (L.) DC.

³= *D. fullonum* L.

⁴= *Bassia scoparia* (L.) A.J. Scott

⁵= *S. tragus* L.

events (such as grazing, fire, or drought) can cause a change from one vegetation type to another. Humans have manipulated grassland vegetation for thousands of years through the use of fire, livestock grazing, and other means. It is therefore difficult to separate human influence from that of climate and other factors in the formation and maintenance of these ecosystems.

Southwestern grasslands are generally characterized by low to intermediate rainfall, a long dry season, seasonal extremes of temperature, dominance of grasses, and large grazing mammals and burrowing animals. Because some Southwestern grasslands developed under grazing by large herbivores, they are generally tolerant of grazing. Other Southwestern grasslands are thought not to have had a long evolutionary history of grazing and might be more susceptible to grazing disturbance.

Soils vary considerably for grasslands in the Southwestern Region because of different climate, vegetation, topography, and parent materials. Small organisms that exist in grassland soils include bacteria, fungi, algae, and nematodes. These soil organisms have a profound effect on essential ecosystem processes such as decomposition, nutrient cycling, and maintenance of soil fertility. Arthropods also perform vital ecological functions in grassland ecosystems. Some of their contributions include soil aeration, seed dispersal, and plant pollination, in addition to facilitating the decomposition of organic debris. Invertebrates also provide an important prey base for wildlife.

The majority of plants in Southwestern grasslands form some kind of mutualistic relationship with mycorrhizal fungi. These range from plant species that show a negative response to inoculation with mycorrhizal fungi, to those that show dramatic increases in growth and reproduction. Because of this differential response, the quantity and type of mycorrhizal fungi present in the soil can affect plant community interactions by influencing the relative fitness and competitive ability of mycotrophic plant species. Biological soil crusts also play an important role in the Southwest. They stabilize soil surfaces, increase soil fertility through the fixation of atmospheric nitrogen, and improve seedling establishment. The cover of biological soil crusts has been positively correlated with diversity of plant species. There is no credible evidence that plant cover and biological soil crusts are negatively related.

Biological invasions disrupt natural ecosystems, posing negative consequences for both ecological and socioeconomic systems. They displace desirable native species, reduce the quality of wildlife habitat, damage sensitive riparian and watershed areas, and increase erosion. As native vegetation becomes displaced, alterations in ecological processes occur including changes in vegetation, soil microflora, nutrient cycling, and decomposition rates.

No universal prescription exists for the management of invasive weeds growing on Forest Service grasslands. Weed management plans currently being written by the Forests of the Southwestern Region will provide guidelines for addressing the complex problem of invasive weeds.

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