

Chapter 9

Belowground Ecosystems

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INTRODUCTION

The USDA Forest Service defined ecosystem management as "an ecological approach to achieve multiple-use management of national forests and grasslands by blending the needs of people and environmental values in such a way that national forests and grasslands represent diverse, healthy, productive, and sustainable ecosystems" (June 4, 1992, letter from Chief FS). This approach spans many different scales, both in time and space. It also implies that we need to carefully analyze and evaluate interactions between different parts of the ecosystem, including how humans interact and impact ecosystems.

The belowground component is essential for all terrestrial ecosystems and harbors many of the fundamental mechanisms underlying large-scale ecosystem behavior. The soil, with its chemical and biological properties, is responsible for important processes such as biogeochemical cycling. Soils contain a wide array of organisms ranging from microflora and fauna (nematodes, fungi, cyanobacteria) to macroorganisms (earthworms, ants, termites). They also provide a nutrient and hydrologic reservoir crucial for organism survival both below and above the ground. Thus, soil systems are much more complex than above-ground systems.

One way to promote sustainable ecosystems is to develop and apply ecological theory to managing ecological systems (Lubchenco et al. 1991). Most individuals think of ecological processes operating in relation to land surface, i.e., two-dimensionally. However, soil organisms exist and operate in three dimensions—numbers and processes are usually expressed as a function of volume rather than area. Ecological principles and concepts such as Bergmann's Rule, Gloger's Rule, carrying capacity, pollination, etc., were developed largely around macroorganisms in a two-dimensional paradigm. Some of these principles and concepts may have less relevance, are difficult to apply, and/or are not equally applicable

when the third dimension, the belowground, is added (Edwards and Stinner 1988). By adding this dimension, spatial and temporal scales are drastically reduced (e.g., bacterial turnover) or markedly extended (e.g., long-lived recalcitrant organic matter). Because of the difficulties inherent to the study of belowground systems, emphasis has frequently been placed on either process rates, i.e., the black box approach, or on the individual organisms responsible for the process, i.e., autecological approach. At a regional scale, little experimental attention has been placed on community structure and energetics and on interactions among soil populations. Neither of these approaches alone can adequately explain how ecological principles perform in a three-dimensional soil system.

Despite its expanse, very little information in the Southwest exists on belowground ecosystem functions, such as decomposition, carbon and nitrogen pools and fluxes, and mycorrhizal relationships. The operation of many soil processes helps determine above-ground structure and function (Allen 1991, Klopatek et al. 1992). To understand and manage entire ecosystems, it is necessary to comprehend how the belowground systems operate and how they are affected by disturbance. This information then needs to be integrated when assessing stability of ecosystems. The object of this chapter is twofold: one, to explain why soil systems are an integral part of ecosystem management; and two, to discuss how disturbances such as fire, grazing, and climate change may affect two key belowground components—nutrient cycling and mycorrhizae—in Southwestern arid and semiarid ecosystems.

CONCEPTUAL BACKGROUND AND TERMINOLOGY

Belowground

In soil-vegetation systems, soils are the resource base where nutrients and moisture are stored. Regu-

lation of nutrient availability to vegetation is, in part, a property resulting from actions of soil biota on substrate quality and quantity. Sustainability, in a general sense, depends upon the synchrony between vegetation demand, the microbial processes regulating the storage and flux of nutrients, and the return of nutrients and organic carbon through the death and decomposition of plants. Soil storage, in turn, depends not only on the immediate actions of biota but upon their past activities. Thus, the structure of the soil, its ability to hold water and nutrients, and indeed to sustain life, is the result of long years of activity by soil biota and interaction with the vegetation. Current management activities affecting belowground ecosystems within the Middle Rio Grande Basin include: grazing, prescribed burning, fuel wood harvesting, timber management, mining, agricultural development, and urbanization/recreational development and use. Table 1 lists factors involved in sustaining ecosystems and describes how belowground ecosystems are altered as a result of human disturbances.

Mycorrhizae

A mycorrhizae is a mutualistic (symbiotic) relationship between fungi and the plant roots of a host plant (Harley and Smith 1983). The fungi function to serve as nutrient and water absorbing organs for the

plant (Menge et al. 1978; Mosse 1973; Powell and Bagyaraj 1984; Safir 1987), whereas the plant provides photosynthate (carbon source) for the fungi (Mosse 1973). In fact, nearly all nutrient uptake (and in some cases total uptake) is due to this fungi. A second significant contribution the fungi play is protection against invading parasitic organisms (Davis and Menge 1981; Powell and Bagyaraj 1984; Schonbeck and Dehne 1977). There are two main divisions of mycorrhizae, ecto- and endomycorrhizae. Ectomycorrhizae are associated with coniferous forest trees such as pine, spruce, and fir. In contrast, endomycorrhizae, or more specifically VA mycorrhizae, are formed by the majority of all land plants, (e.g., ferns, grasses, cacti, shrubs, and trees). Although the study of mycorrhizae is fairly recent, the relationship between plant and fungi is not. In fact, one of the first land plants, *Rhynia* (Chaloner 1970), was found to be colonized by mycorrhizae (Kidston and Lang 1921, Nicolson 1975).

Nutrient Cycling

Nutrient cycling is defined as the movement of chemical elements in a cyclical fashion. Often it is referred to as biogeochemical cycling since biological organisms and their geological (atmosphere or lithosphere) environment play an active role in the cycle. Nutrient cycles are composed of four elements in belowground systems: (1) nutrient demand, (2) storage capacity, (3) rate of nutrient return to the soil, and (4) nutrient retention. Two of the most critical nutrients for plant development are carbon and nitrogen (tables 2 and 3). Nitrogen, being the backbone of nucleic acids (proteins), is an indispensable component of all living creatures. The elements of carbon and nitrogen are good examples of biogeochemical cycling as they have gaseous phases in the atmosphere, are stored components in the soil, and are cycled through both plants and microbes. Although nitrogen can enter the soil through a number of avenues (table 2), its cycling is completely dependent on microbes. Nitrogen cycling has a five step process: biological fixation, assimilation, mineralization, nitrification, and denitrification (figure 1).

Carbon Cycling

Carbon is continually fixed (CO_2) into organic form by way of photosynthetic organisms (both plant and microbe) (table 3). Once fixed and converted into

Table 1.—Belowground ecosystem productivity factors.

Factors that regulate belowground ecosystem productivity

- Temperature (climate)
- Moisture inputs (climate and hydrology)
- Soil nutrient supply, demand, and cycling (site quality)
- Plant reproductive strategies such as seed source and mortality
- Resource competition (water, nutrients, light, and space)
- Perturbations, both natural and human
- Soil (e.g., texture, depth, parent material)
- Site stability (community composition and successional stage)
- Topographic setting and landforms

Factors that may decrease ecosystem productivity

- Decrease in plant cover and diversity (e.g., by grazing, wood harvesting, and agricultural development.)
- Loss of soil (e.g., by vegetative losses, compaction, runoff, and erosion.)
- Loss of nutrients (e.g., by denitrification, nitrogen volatilization, leaching, and erosion.)
- Decrease in number and diversity of soil flora and fauna and mycorrhizae (e.g., due to vegetative changes, loss of symbiont, photosynthetic decline, and soil disturbances.)

Table 2.—Nitrogen sources (inputs) and sinks (losses).

N inputs	N losses
• precipitation • dry fallout • transported sediment • inflow of drainage water • nitrogen fixation • human & animal activities • litter fall	• denitrification • leaching • run-off and outflow • ammonia volatilization • harvesting • erosion

Table 3.—Carbon sources (inputs) and sinks (losses).

Carbon sources (inputs) and sinks (losses)	
C inputs	C losses
• CO₂ from the atmosphere • rock parent material • abscised debris from above-ground • decomposing plant material • decaying animal and microbial cells	• respiration • erosion • vegetation removal

organic form, carbon cycling and decomposition of organic material is dependent on microbial activity. Organic matter is central to the cycling of plant nutrients, influences water relations and erosion potential, and is a key factor in soil structure and stability (Tisdale and Oades 1982). In arid and semiarid systems, decomposition of organics is initiated by invertebrates that break down organic material into smaller fractions (Santos and Whitford 1981, Santos et al. 1981). Soil microbes and microinvertebrates further break down organic fractions. As organic residues decompose, they become part of the soil organic matter (SOM). SOM is composed of several fractions: (1) active SOM fraction consists of live microbes and microbial products, along with soil organic matter, with short turnover times (approximately 1–5 years), e.g., sugars and amino acids; (2) slow SOM is physically protected and/or in a chemical form with more biological resistance to decomposition, with intermediate turnover times (20–40 years), e.g., hemicelluloses; (3) passive or recalcitrant SOM may also be physically protected, with the longest turnover times (200–1500 years), e.g., lignin (Parton et al. 1987). Thus, through decomposition, microbes convert organic material into plant available nutrient forms, followed by re-releasing carbon into the atmosphere as CO₂ (i.e., respiration), hence, completing the cycle.

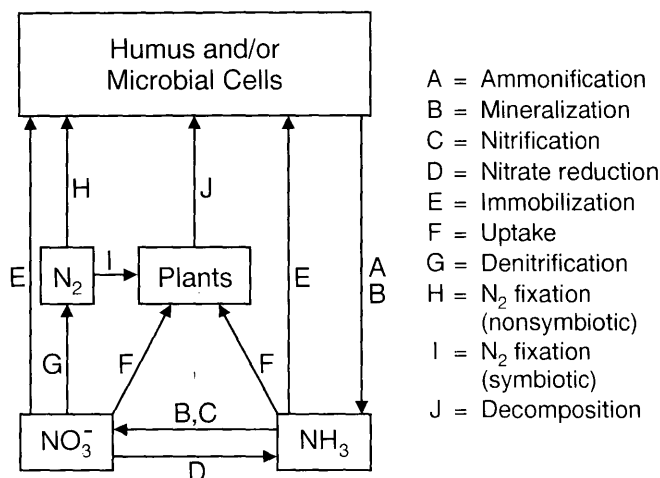


Figure 1.—Pools and fluxes of the nitrogen cycle. Adapted from *Introduction to Soil Microbiology*, second edition, by Martin Alexander (New York: John Wiley & Sons).

GLOBAL CHANGE

Ecosystem Effects

Current projections suggest a global warming between 1.5 and 4.5° C in the coming century (IPCC estimates, Mitchell et al., 1990 Schneider 1989). Schneider (1989), Neilson (1989), and others have shown, using general circulation models (GCM's), that the Southwest will not only experience a rise in temperature but a change in precipitation, confounding the already low water availability both above- and belowground. Neilson (personal communication) indicates that, as a result of this increase in temperature, areas will undergo a shift in precipitation from snow to rainfall events. In spite of high variability in predicted rainfall, soil moisture is anticipated to decrease in most of the Southwest (Manabe and Weatherford 1987, Washington and Meehl 1989). The effects of a temperature increase and soil moisture depletion may have profound consequences on the productivity, diversity, and extent of natural resources in this region resulting in major shifts in vegetation types. Schlesinger et al. (1990) suggest that climate warming may cause significant changes in global biogeochemical cycles that will then be further disrupted by positive feedbacks, resulting in a shift from semiarid to arid systems. Emanuel et al. (1985) also suggest that potential global climate warming may seriously affect the arid and semiarid southwestern United States, forecasting a 17 percent

increase in the desert land area (i.e., desertification). These predicted changes caused by climate warming will have effects on vegetation types and carbon storage and flux rates in southwestern ecosystems.

In arid or semiarid biomes, there appears to be a continuous change in species composition from the core to the edges, although plant life-form appears to be a more uniform characteristic over a larger area. These transitions between different biomes or ecosystems are a function of a wide range of processes that operate on many time and space scales. The environmental driving functions (e.g., temperature and moisture) causing these transitions are likely to exercise significant control on ecosystem level processes (e.g., primary productivity and nutrient cycling) (NATO 1993; Risser 1995; Turner 1989). Resource dynamics and resource limitations for commodities such as water and nutrients often significantly differ between biomes or across transition zones (e.g., deserts to grasslands and grasslands to pinyon juniper woodlands). For example, structural differences in leaves between grasses, shrubs, and trees affect nutrient cycling and decomposition rates. Presence of woody shrubs and trees affects properties such as ecosystem biomass, nutrient storage, and microclimate. These structural differences are often accompanied by distinct differences in carbon pools and partitioning of resources. Since species move about individually in the face of climate changes, studies of change need to be conducted at multiple spatial scales in order to anticipate the changes that also occur at multiple temporal scales. Thus, the relationship between vegetation and climate is symbiotic but not exclusive because soils, fauna, and human activities all impact vegetation (Klopatek et al. 1992, Riebsame et al. 1994).

Belowground Responses

Belowground processes are inextricably linked in time and space with biosphere responses to global climate change. Three direct effects of climatic change that may have important impacts on belowground systems are increases in atmospheric CO₂, increases in global temperature, and changes in precipitation patterns. At present, we are unable to predict the consequences of these changes to soil systems with any certainty as they have the potential for both amelioration or exacerbation of global climate change effects. Unfortunately, we have little direct experimental evidence available to predict these effects.

Responses of plants to climate change such as loss of plant cover, and changes in plant species diversity, density, or biomass, will regulate to some degree the belowground environment. Increasing CO₂ alone will primarily affect belowground systems through changes in photosynthate allocation. In a three-year CO₂-enrichment study of yellow poplar, Norby et al. (1992) showed increased carbon allocation belowground, although whole plant carbon storage did not change. This increase in carbon availability has implications for mycorrhizae and nitrogen fixers as well as other rhizosphere organisms (Norby 1987, O'Neill 1987). Confounding the potential for CO₂ enrichment effects on soil processes is the possibility of a concomitant rise in global temperature due to increases of greenhouse gases. As mentioned above, there is widespread agreement among scientists that during the next 35 years there will be a global temperature increase by about 1° C due to increases of greenhouse gases (NSF 1991). There is less agreement on the degree to which soil temperatures will rise and precipitation regimes will change as a result of increasing air temperature. Changes in soil temperatures will not only directly affect distribution and numbers of organisms, but also affect the rates at which these organisms process nutrients.

A predominant source of carbon for the soil compartment is plant litter and its subsequent decomposition. Decomposition is controlled by several factors including temperature, moisture, soil structure, and litter quality (Waring and Schlesinger 1985). Temperature and moisture regulate many ecosystem functions as they are the most critical driving forces in ecosystems (Swift et al. 1979). The resulting effect of temperature and moisture on decomposition will also vary according to the litter quality of that biome (Berg et al. 1990). Litter quality, typically referring to the carbonaceous component, and its relationship to the limiting nutrient(s) in an ecosystem, often defines the rate at which decomposition may proceed. Past studies have suggested that the ratios of carbon:nitrogen, lignin:nitrogen, and/or cellulose:nitrogen are the most significant indicators of the rate of decomposition (Moorhead and Reynolds 1991; Meentemeyer 1978; Schlesinger and Hasey 1981; Aber and Melillo 1982). High nutrient concentration in relation to stored energy (low carbon:nutrient ratio) will promote a higher rate of decomposition (Berg et al. 1982). Small changes in temperature or moisture may have a negligible effect on the decomposition rates of litter of poor quality, whereas a slight

change in either factor could greatly alter the decomposition rate of litter of good quality (Meentemeyer 1984, Berg et al. 1993). Since microbes and soil animals control processes such as decomposition, changes in litter quality that affect decomposers will be reflected in soil microfauna and eventually other compartments of the food web.

Research on the effects of global change on carbon cycling vary. Models derived from eastern deciduous forests show that decomposition rates may be depressed with CO₂ enrichment but may be offset if increased soil temperatures stimulate microbial activity and water is not limiting (Anderson 1991; Melillo et al. 1982; Whipps 1990). The process model presented by Paster and Post (1995) demonstrated that decomposition rates increased with higher temperatures and limited soil water, but the model predicted a decrease in productivity as a result of decreasing litter quality through increased lignin:nitrogen ratios. The effect of global change on belowground processes in the Southwest are uncertain as predictions for aboveground vegetation responses significantly differ (e.g., Parton et al. 1995, Schlesinger et al. 1990). If regional spatial shifts in vegetation GCM's forecasting occur (Solomon and Shugart 1993), they will have an effect on carbon dynamics across the landscape (Berg et al. 1990; Anderson 1991; Klopatek et al. 1992). Research by Klopatek C. et al. (1995a, 1995c) and Klopatek J. et al. (in press) has focused on how potential climate change may affect carbon pools and fluxes, documenting the relative pool sizes and aggradation rates of carbon as they change across the ecotonal boundaries from one system to another in the Southwest. They have shown that decomposition rates of different litter types of the Southwest significantly differ due to difference in climate (figure 2). Their experiment shows that the rate of decomposition was not significantly different between xeric sites (Great Basin shrublands and ecotones) with those of more mesic sites (ponderosa pine and ecotones). They have also shown that pinyon-juniper communities do not differ in their rate of decomposition from either the lower (DS) or upper elevational (PP) sites. This information substantiates their earlier contentions that PJ, with its different physiognomic and edaphic physiographic and climate characteristics, is truly an ecotonal area between mesic (PP) and xeric (DS) ecosystems (Klopatek 1987; Klopatek et al. 1988; Klopatek et al. 1990; Klopatek and Klopatek 1995). Such research has the potential to demonstrate a large

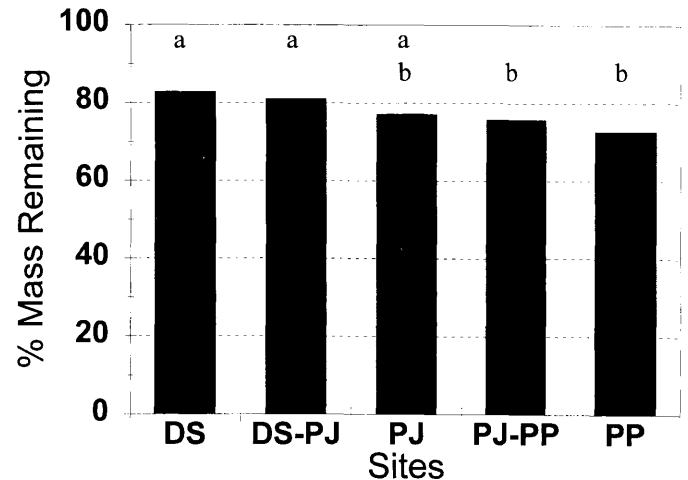


Figure 2.—The effects of climatic factors (i.e., temperature and moisture) on the rate of decomposition in blue grama (BOGR), one-seeded juniper (JUMO) and pinyon pine (PIED). Litter was placed along a gradient from a desert scrub site (DS), a transition zone (DS-PJ), a pinyon-juniper woodland (P-J), a second transition zone (PJ-PP) and a ponderosa pine forest (PP) (adapted from Klopatek et al. 1995c).

range of environmental changes that may come about as a result of climate change.

FIRE AND GRAZING EFFECTS

Ecosystem Effects

It has been reported that over 40 percent of the arid lands in North America have undergone severe to very severe desertification within the last 100 years (Dregne 1977, Schlesinger et al. 1990). Desertification has been directly attributed to heavy grazing (Costello 1972, Sheridan 1981). Grazing by domestic livestock has long been associated with decreases in ecosystem productivity (Chew 1982). The Rio Grande Basin has been grazed for centuries and has experienced long-term declines in plant and soil productivity (Conley et al. 1992; Daddy et al. 1988; Orodho et al. 1990; Webster and Wright 1987; Wilcox and Wood 1988). Both wild and prescribed fires are reoccurring phenomena in the Basin (Swetnam and Betancourt 1990). Prescribed burning has been a long-standing management activity in southwestern systems (personal communication, USDA Forest Service, Region 3) because it is thought to increase grass production. It is unclear what the long-term effects of burning are on overall ecosystem productivity in this

region, unlike intensively studied grassland areas such as the Kanza Prairie. Limited information on the post-fire successional patterns of the major vegetation types in the Southwest is available (e.g., Moir and Dietrich 1988, Swetnam and Betancourt 1990). However, the time for belowground systems to recover following fire and grazing and the subsequent long-term effects of these disturbances on primary productivity in the Rio Grande Basin is not well understood. An additional complication in the understanding of fire effects is the consequence of global warming, as increased fire frequencies are predicted during periods of dry years with a concomitant increasing risk of large forest fires (Sandenburgh et al. 1987, Turner and Romme 1990).

Recent studies have shown that repeated prescribed burning may cause significant changes in surface runoff and sediment production (Emmerich and Cox 1994; Weltz and Wood 1986; Weltz et al. 1989). Soil erosion, as a result of disturbance, is thought to be one of the major causes of nutrient loss in arid and semiarid ecosystems (Schlesinger et al. 1990). Chronic disturbances such as grazing and fire also produce significant changes in the cycling of nutrients, e.g., nitrogen, carbon, and phosphorus. Studies indicate that fire alters the biogeochemical cycling patterns in southwestern forested ecosystems. Fire acts as a rapid mineralizing agent and releases ammonium-N that is later converted into nitrate-N under conditions favorable for nitrification (Klopatek 1987; Klopatek et al. 1991; Kovacic et al. 1986). Inorganic P also is released by burning, but it too is quickly chemically immobilized (DeBano and Klopatek 1987) and may no longer be readily available for plants. Production of $\text{NO}_3\text{-N}$ presents a large potential loss of nitrogen from the ecosystem because it is easily leached from soils following precipitation events or denitrification. Organic carbon (litter and humus) following fire also decreases, usually a direct result of combustion. This potential loss of carbon has a great impact on nitrogen cycling as bacteria responsible for nitrification increase following burning (Klopatek et al. 1991). These bacteria do not require organic carbon, hence they convert readily available ammonium into nitrate. The above interactions strongly suggest that loss and retention of nutrients during and following fire are important processes affecting the long-term productivity of arid and semiarid ecosystems and must be better understood before these ecosystems can be managed on a sustainable basis in the Southwest.

Belowground Responses

Although the Rio Grande has undergone a variety of perturbations that continue today, no studies specifically address the effects of fire and grazing on the belowground microbial community in the Basin. Research is being conducted in the transition zone between Chihuahuan Desert and Great Plains grasslands. This area is composed primarily of C_3 and C_4 grasses, small shrubs, and scattered juniper trees. Most of the species (other than weedy invaders) are colonized by mycorrhizae, specifically, vesicular-arbuscular (VA) mycorrhizae (Klopatek, unpublished). It has been well documented that many plants have a strong dependency with mycorrhizal fungi. Without mycorrhizae many plants show a decreased growth rate or fail to grow past the germination stage (Harley and Smith 1983; Mosse 1973; Powell and Bagyaraj 1984). Studies have shown that this relationship is fragile and can be easily disturbed (Bethlenfalvy and Dakessian 1984; Daft and Nicholson 1974; Janos 1980; Klopatek 1991; Klopatek and Klopatek 1995; Reeves et al. 1979; Warner et al. 1987; Williams and Allen 1984; Zac and Parkinson 1982). These studies show that as the severity of disturbance increases, e.g., from livestock grazing (Bethlenfalvy and Dakessian 1984; Klopatek and Klopatek 1987; Reece and Bonham 1978) to surface mining (Allen and Allen 1980; Gould and Liberta 1981; Klopatek and Klopatek 1984, 1995; Zac and Parkinson 1982), there is a corresponding decrease in the frequency of VA mycorrhizae propagules and/or colonization.

Fire has been shown to impact ectomycorrhizae in other forest ecosystems (Mikola et al. 1964, Schoeneberger and Perry 1982), but until recently, little was known about the response of VA mycorrhizal symbionts to fire. Klopatek et al. (1988) showed that after a simulated fire, VA mycorrhizal colonization was reduced when burning temperatures exceeded 90°C , and that soil water availability played an important role in VA mycorrhizal survival. Klopatek found that dry soils were more of a detriment than wet soils because of higher resultant temperatures. Subsequently, Klopatek (1991) and Klopatek et al. (1994) demonstrated that mycorrhizae decreased even more significantly in field-burn studies (figure 3). In that study, although greater pre-burn mycorrhizal percentages were found in the plants grown in field soils than in the soils from the laboratory microcosms study, burning was significantly

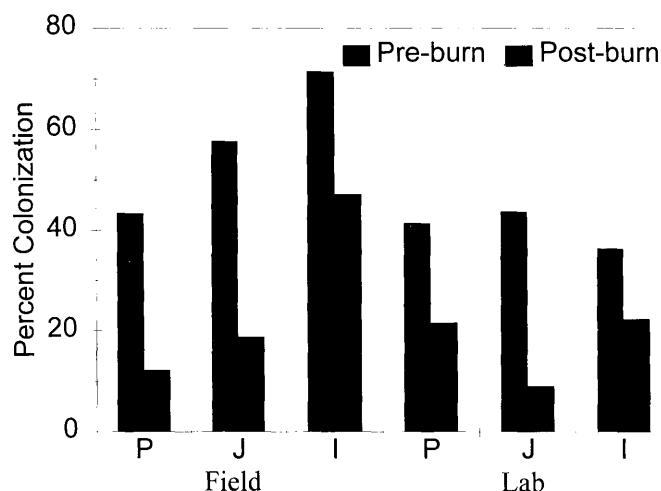


Figure 3.—Comparisons of VA mycorrhizal colonization on host plants grown in unburned and burned soils from under pinyon (P), juniper (J), and interspaces (I) between field and laboratory studies (adapted from Klopatek et al. 1994).

correlated with temperature. But, the effects of burning in the field were even more pronounced. In the field, it was also demonstrated that the length of time that the area burned played a role in the reduction of mycorrhizae. Canopy covered patches, having greater burning temperature and longer burning duration, were more effected by burning than interspaces (figure 3). This was due to the greater fuel loads under canopies. Five years following the fire, interspaces had recovered from the burn, but canopy covered patches had not (Klopatek, unpublished).

Results of other studies on mycorrhizal response in semiarid ecosystems vary. Gibson and Hetrick (1988) found significant reductions of three VA mycorrhizal species following a fire in the tall grass prairie of Kansas. In a similar experiment, Bentivenga and Hetrick (1991) stated that burning temporarily increased mycorrhizal activity in a tall grass prairie ecosystem. Dhillon et al. (1988) found that colonization levels of VA mycorrhizal fungi in little bluestem roots were significantly reduced on burned sites when compared to unburned sites but increased significantly after one growing season. Their results suggest that the response of VA mycorrhizal fungi to fire may be attributed to changes in the host plant rather than to the direct effect of fire. Fire temperatures did not reach a level high enough to kill all the plants, thereby leaving a large residual VA mycorrhizal pool in the soil and in plant roots. In fact, they showed that fire actually stimulated plant growth.

In contrast, Vilarino and Arines (1991) examined a forested ecosystem in Spain one year following a wildfire and found lower soil propagule densities and lower VA mycorrhizal colonization in post-fire herbaceous vegetation than in neighboring unburned areas. Although they had no information on the VA mycorrhizal distribution or activity prior to the fires, Vilarino and Arines (1991) suggest that VA mycorrhizae are negatively affected by fire and that mycorrhizal recovery in forested ecosystems is a slow process. In addition, they theorized that topographical and pedological properties may have played an important role in the losses and reestablishment of mycorrhizae on their study areas.

The time required for mycorrhizal populations (with emphasis on VA) to recover after fire in arid and semiarid systems is not well understood. Janos (1984), MacMahon (1987), and Allen (1991) have all suggested that mycorrhizal fungi are essential in the recovery of an ecosystem, facilitating plant establishment by regulating nutrient flow from the soil to the plant. Although researchers have documented plant succession and nutrient dynamics following disturbance, little work has been done to integrate these patterns with mycorrhizal succession. Determining how mycorrhizal and nutrient dynamics affect landscape patterns is important to understanding how ecosystems operate within the Middle Rio Grande Basin and crucial when assessing long-term ecosystem productivity and sustainability. Studies on belowground ecosystem ecology can provide highly useful information that has been up til now a missing dimension of the knowledge needed to manage the Middle Rio Grande Basin.

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